Genetics of Growth and Development in Cattle

By

Raphael Abiodun Afolayan
B.Sc (Hons.) Animal Science (ABU), M.Sc Breeding & Genetics (ABU)

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Dedication

This thesis is dedicated to my wife, Mrs Victoria Olubunmi Afolayan and my children; Master Stephen Boluwatife Afolayan, Master Israel Ayobami Afolayan and Miss Sharon Oyindamola Afolayan for their great support with love, patience, understanding and prayers during the period of the study.

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List of abbreviations

df = Degrees of freedom

h^2 = Heritability

r = Correlation coefficient

Very high = r_G (0.8 – 1.0), h^2 (> 0.6)

High = r_G (0.6 – 0.8), h^2 (0.4 – 0.6)

Moderate = r_G (0.4 – 0.6), h^2 (0.25 – 0.4)

Low = r_G (0.2 – 0.4), h^2 (0.1 – 0.25)

Very low = r_G (0 – 0.2), h^2 (< 0.1)

R^2 = Coefficient of determination

SAS = Statistical Analysis System

ANOVA = Analysis of variance

JJ = Jersey

LL = Limousin

LJ = F_1 cross between Limousin and Jersey

XJ = Back-cross between F_1 (LJ) and Jersey

XL = Back-cross between F_1 (LJ) and Limousin

JH = F_1 cross between Jersey and Hereford

WH = F_1 cross between Wagyu and Hereford

AH = F_1 cross between Angus and Hereford

SH = F_1 cross between South Devon and Hereford

LH = F_1 cross between Limousin and Hereford

BH = F_1 cross between Belgian Blue and Hereford

ns = not significant (P > 0.05)

* = P < 0.05, ** = P < 0.01, *** = P < 0.001

SD = Standard deviation

CV = Coefficient of variation (%)

SE = Standard error

YOB = year of birth

Bwt, Bht, Blh, Bgh = Birth- weight, height, length, girth

Wwt, Wht, Wlh, Wgh, Wmus, Wfd = Weaning (250 days)- weight, height, length, girth, muscle, P8 fat depth

400d- wt, ht, lh, gh, mus, fd = 400 days weight, height, length, girth, muscle, P8 fat depth

600d- wt, ht, lh, gh, mus, fd = 600 days weight, height, length, girth, muscle, P8 fat depth

Adg1 = Pre-weaning average daily gain

Adg2 = Post-weaning dry season gain

Adg3 = Post-weaning wet season gain

PC1 = First principal component

PC2 = Second principal component

BTA = Bos taurus chromosome

QTL = Quantitative trait loci

5BT = QTL for PC1 based on four birth-traits (BT) and located on BTA 5

6GT = QTL for PC1 based on six postnatal growth-traits (GT) and located on BTA 6

13Mus = QTL for PC1 based on three postnatal muscle-traits and located on BTA 13

14- BT, GT, HT, GH = QTL for PC1 on birth, postnatal- growth, height & girth-traits and located on BTA 14

16GT = QTL for PC1 on postnatal growth-traits and located on BTA 16

21FD = QTL for PC1 based on three postnatal P8 fat depth-traits and located on BTA 21

23GT = QTL for PC1 on postnatal growth-traits and located on BTA 23

24Mus2 = QTL for PC2 based on three postnatal muscle-traits and located on BTA 24

2aMus = First QTL on postnatal muscle-traits PC1 located on BTA 2

2bMus = Second QTL on postnatal muscle-traits PC1 located on BTA 2

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Declaration

This thesis contains no information accepted for the award of any other degree or diploma in any University. To the best of my knowledge, the thesis contains no material previously published or written by another person, except where due reference is made in the text. The thesis complies with the stipulations set out for the degree of Doctor of Philosophy by the University of Adelaide and I consent to it being deposited in University library for photocopy and loan.

03/07/03

Raphael Abiodun Afolayan

Department of Animal Science

The University of Adelaide;

Roseworthy, S.A. 5371, Australia

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Abstract

Growth and development is a good description of animal for size and shape as opposed to the conventional measurements of weight and changes in weight over time for the determination of growth across ages. The inclusion of body dimensions (eg. height), muscularity (defined as ratio of stifle- over hip-width), fat depth measurements with weight in multi-variate analysis would be appropriate for body composition evaluation in the Australian beef industry. It is expected that these component traits would predict beef carcasses for yield and possibly for quality.

Genetic variation in growth and development was examined in 12 different cattle breeds generated from two major projects [Southern Crossbreeding Project (SXB) and Davies Gene Mapping Project (DGM)] to enhance genetic improvement tools for carcass value through production traits. The SXB comprises 1215 progeny of 97 sires from seven breeds (Jersey, Wagyu, Hereford, Angus, South Devon, Limousin and Belgian Blue) mated to 766 mature Hereford cows with calves born across four years (1994-1997). The 591 DGM progeny were from 7 sires (2 Jersey, 2 Limousin and 3 F1crosses) mated to 280 cows (Jersey and Limousin) to produce purebred Jersey, purebred Limousin, Jersey x Limousin crosses, Jersey backcross and Limousin backcross with calves born across five years (1994-1998). Significant breed differences were obtained across ages for growth and development traits. Differences in cohorts (year of birth & sex of calf) were high across ages while the significance due to day or month of birth decreased as age advanced.

As a preliminary study, live animal measurements of weight, height, length, girth, P8 fat depth, stifle- and hip-width of 241 steers (second calf drop) from 10 breed combinations in both projects were used to predict seven carcass traits. A complete bone-out was carried out on all 1995-drop steers to allow for the stepwise regression of carcass traits on live measurement traits. The results of the first study demonstrated with reasonable precision that there could be value gained in defining carcass composition using the objective live animal measurements herein as an alternative to most commonly used subjective measurements.

Southern crossbreeding progeny were used to determine the heritability and genetic correlations between the measure of growth (weight and body dimensions) and muscular development (defined as ratio of stifle to hip width) plus P8 fat depth. Across ages (birth to 600-day), height was highly heritable (0.34-0.57). However, weight, length and girth were

low to moderately heritable (0.12-0.40) at the same ages. From weaning to 600 days, muscularity measurement was low to high (0.20-0.44) while measure of fatness was moderate to high (0.31-0.41). At the average age of 400 days, moderate and positive genetic correlations (r_G) existed between weight and height (0.47) but strong and positive r_G were between weight and other body dimensions of length (0.59) and girth (0.62). While the r_G between weight and muscularity was low, weight and P8 fat depth had zero relationship at this age.

An experiment was also conducted using 591 progeny from DGM to separate the additive from non-additive genetic effects on growth and development traits not possible in earlier studies because of the single dam used in the SXB. Direct effects were the most significant for most of the traits across ages, an indication of the importance of individual gene composition on growth regardless of age. There were significant maternal effects on some early postnatal growth traits. At weaning, heterosis was large and positive for fatness and moderate for weight and muscularity. There was also indication of the significance of epistasis on muscularity at older age.

The location and size of QTL effects on growth and developmental traits were tested on 370 backcross progeny of three F_1 sires from DGM. Chromosome-wide significance QTL for individual traits was observed on 17 of the 29 autosomes. However, the number of autosomes with significant QTL was reduced to eight using the first principal components of six genetically related trait groups that represent over 50% of the total phenotypic variance per group. Significant QTL for prenatal growth (size) had no effect on late growth. Interestingly, QTL for postnatal muscularity (BTA 2) and fatness (BTA 21) were mapped to different regions of the genome. This is an indication that the genetic improvement for beef cattle body composition should be possible in very early life before measurements.

The thesis concludes that strong evidence of separate associations between markers and QTL on pre-natal and postnatal growth and development exist. Thus, the problem of genetic antagonism between calf survival and growth (development) could be solved using new techniques in genetics in very early life. Furthermore, the size of estimates for breed and genetic effects in-conjunction with the genetic parameter estimates herein suggests that selection indices for desired carcass composition through multi-trait prediction of live-measurements is feasible.

Chapter 1

Introduction and Literature review

1.1 Introduction

Meat quality and yield are a function of growth and relative development of components of growth described by shape over time. Traditionally, only weight and change in weight over time, which do not adequately describe the shape and fatness of the animal, is the sole determinant of product yield from many animal species including beef cattle. However, inclusion of body dimensional traits (eg. height, length, girth, stifle and hip width) along with a fat depth measurement as component of growth and development (confounded in weight) might be more appropriate in describing the overall animal shape. The initial method by McKiernan (1990) to describe butt shape in cattle prompted the use of stifle-width by hip-width ratio to describe muscular development (Pitchford et al., 2000). It is expected that some of these component traits would describe the animal's general appearance according to the individual breed's standard and functionality for meat quantity, and that they may also be good in characterising the animal's productive ability in meat quality traits.

Within and between breed variations in growth and development exist for different beef cattle breeds. These variations provide opportunity for genetic improvement through selection and crossbreeding. Previous studies have indicated a relationship between growth traits of the parents and their progeny performance (Johnson et al., 1992; Mackinnon et al., 1991) making the use of individual estimated breeding value plausible for stock selection. A good understanding of genetic parameters of growth traits and their interactions are very important in estimating accurate breeding values, optimising breeding schemes and predicting genetic response to selection.

Regardless of the breeding objectives, the body or carcass composition of cattle at any weight reached in a short or a long period of time is dictated by its genetic potential (Long, 1980) and diet (quantity and quality). This animal potential is mainly associated with individual (direct) genetic and possibly maternal effects. However, the significance of

correlated impacts of additive and non-additive genetic effects in crossbreeding programs cannot be over emphasised. Clark et al. (1992) using data from research stations and commercial herds developed models that demonstrate significant improvements in profitability and sustainability of beef enterprises through combined use of crossbreeding and within-breed selection. In this regard, estimation of genetic potential in growth and development in early life (pre-weaning) of beef cattle can assist in improved selection of parents for future generations and can enhance rapid genetic gain. Moreover, early selection decisions for replacement of breeding stock based on prediction of merit is of substantial economic value to the beef cattle industry.

Many complications have retarded genetic improvement, particularly on carcass quality traits, using only traditional quantitative genetic method, since genetic evaluation and selection have been purely based on phenotypic and pedigree information. Until recently, little information has been available on individual quantitative trait loci (QTL) controlling important economic traits. However, the current developments in the use of genetic markers have further helped to localise genes with very large (genetic) effects on growth and development. For example, QTL or genes have been located for muscular hypertrophy in cattle (Charlier et al., 1995) and sheep (Cockett et al., 1998), growth and carcass characteristics in pigs (Andersson et al., 1994) and growth and fertility in mice (Maqbool et al., 1998). The use of marker-assisted selection (MAS) in selection for quantitative traits has helped to increase the rate of genetic improvement on traits for various species by 1 to 10% (van der Beek and van Arendonk, 1994) and could even be greater in the future as more genes are being identified. Thus, it is assumed that combining the use of marker technology with relevant phenotypic and pedigree information in predicting the genetic merit of individuals within a population will enhance genetic evaluation.

This review will focus on estimates of genetic effects and parameters for growth associated traits using quantitative approaches to identify key expression of changes in the context of biological variation. It will also consider aspects of the significance of marker technology in livestock improvement in general and on growth traits in particular. In addition, quantitative trait loci affecting milk production in relation to growth will be examined.

1.2 Literature review

1.2.1 Growth and muscle development in mammals

1.2.1a Definition of growth

Growth is commonly defined as production of new cells. However, because growth is measured as an increase in mass (Owen et al., 1993), growth includes not only cell multiplication (hyperplasia) but also cell enlargement (hypertrophy) and incorporation of specific components from environment (e.g. fat deposition). Although by definition in meat production, muscle mass is of primary interest, growth also includes deposition of fat.

1.2.1b Muscle growth and development

During embryonic development, all tissues grow by hyperplasia, but as mammals mature, specialized cells (e.g., nerves, skeletal muscle cells) lose their ability to replicate and grow only by hypertrophy or incorporation of satellite cells. Development therefore, does not only involve an increase in size and number of cells, but also may involve changes in the shape of cells, tissues, organs and the whole animal. Mature size is generally considered as the point when muscle mass reaches its maximum (Owen et al., 1993).

Most mammals are born with nearly their full complement of skeletal muscle fibres with the number of muscle fibres determined at birth (Essen-Gustavsson, 1993). Muscle hyperplasia occurs primarily prenatally (Allen et al., 1979), and muscle fibre numbers

increase only slightly postnatally (Bergen and Merkel, 1991). Growth of fibres is, therefore, defined by an increase in length and cross-sectional area (Essen-Gustavsson, 1993). Goldspink (1991) attested to the fact that postnatal growth of muscle mass occurs through hypertrophy and through satellite cell replication and incorporation.

Meat mainly contains skeletal muscle composed of fibres with various characteristics. Invariably, skeletal muscles consist of distinct or different fibre types identified or differentiated on the basis of their reaction of enzyme activity or contractile and metabolic properties (Muller et al., 2002). Slow-contracting (red) fibres (Type I fibres) are oxidative with low ATPase activity. Rapidly contracting (white) fibres are non-oxidative with a high ATPase activity (Type IIB fibres), while the third fibre type (Type IIA fibres) is both oxidative and fast-contracting (Ruusunen, 1994). Numerous factors that regulate the number of muscle fibres and nuclei have been elucidated (Goldspink, 1991). Most important is the fact that severe maternal under-nutrition during early-mid and possibly late pregnancy negatively affects the rate and development of postnatal muscle fibres and nuclei (Everitt, 1968).

1.2.2 Genetics of growth as a basis for carcass attributes of cattle

The potential growth of an animal, its pattern of development and, to a reasonable extent, its ultimate carcass composition in terms of the proportions of muscle, bone and fat are genetically predetermined (Oddy et al., 2001). However, interactions with environmental factors, particularly nutrition, during development influence the pattern of growth and mature size (the weight at which lean body mass ceases to grow). Thus, the overall rate and pattern of growth of a beef animal are the main determinants of the proportions of bone, muscle and fat in the carcass (Byers, 1982), and these in turn affect eating quality of the meat from such animals (Oddy et al., 2001). Oddy et al. (2001) asserted that the rate of growth in the period immediately pre-slaughter, which has been predetermined by the animal's genetic

composition much early in life (pre-natal), affects the glycogen content of muscle. The glycogen content of muscle (Shorthose and Harris, 1991), inturn, is an important determinant of pH fall post mortem and the ultimate pH (and thus colour and tenderness) of muscle.

1.2.3 Estimation of carcass traits from live-animal measurement traits

In the past, many live animal conformation measurements (e.g. muscle score and butt shape profile) have been studied for the prediction of carcass composition (Kempster et al., 1981; 1982; Tatum et al., 1998). The use of assessments of muscularity (eg. conformation score or butt shape profile) in grading/classification systems for meat-producing animals is based on the premise that visually discernible differences in muscle thickness among animals with similar skeletal dimensions (i.e., same frame size) are associated with differences in muscle mass, and therefore, are indicative of economically important differences in live animal and carcass composition (Tatum et al., 1998). However, since these measurements are mainly subjective, Kempster et al. (1981) in a study involving lambs representing a number of different breeds, found them to be poor indicators of carcass composition but only good for meat yield. The problem has been the associated confounding of the relationship of muscle and yield with that of fat and yield.

In determining the relationship between body dimensions and carcass traits, Gilbert et al. (1993), obtained strong correlations between head length and backfat (negative), between head width and marbling (negative), and between cannon bone circumference and warm carcass weight (negative). However, the same author observed low to moderate correlations between popular body dimensions (i.e. height at hips or withers, frame score, body length) and carcass measurements. The genetic and phenotypic correlations between carcass traits and body dimensions at weaning were similar but generally lower than the corresponding correlations using end of test (yearling age) measurements (Gilbert et al., 1993). In general, there are few studies carried out to relate body dimensions with carcass traits most of which

were based on a limited number of breeds. The advantage of estimation of carcass composition using multi-breed synthetic population has been reported (Meyer et al., 1993). There is a need, therefore, to determine this level of relationship in a larger data set involving a multi-breed synthetic population.

Ultrasound technology has been widely used on live-animal measurements in order to predict carcass quantity and quality traits in sheep (Herring et al., 1994) and in cattle (Wallace et al., 1977). While Herring et al. (1994) obtained an R^2 of 24-48% for prediction of various retail cuts from visual score and ultrasound measurements, Wallace et al. (1977) observed R^2 of 60% and 51% for percentage primal and retail yield using ultrasound rib fat measurements between 5^{th} and 6^{th} ribs. There have also been R^2 values of 46% and 62% for saleable meat yield of commercial stock based on live-weight, P8 fat depth and subjective muscle score (Perry et al., 1993a; 1993b). Apart from being a non-cost effective method, scanning technique may not enjoy wider application by all producers because of the expertise required for usage.

1.2.4 Direct and maternal effects on growth traits

Growth traits, especially early growth traits, in animals are determined not only by their own genetic potential (inherited gene from sire and dam) but also by genes inherited by their sire and dam (Grand- paternal and/or maternal gene combinations) and the maternal environment. Intrauterine environment, milk production and mothering ability of the dam plays a very important role in survival and general performance of the progeny. Meyer (1992) demonstrated that the efficiency of selection for daily weight gain in calves from birth to two months of age could be improved by incorporating maternal effects in the variance component estimation. Moreover, the importance of maternal effects have also been discovered on post-weaning growth traits of some breeds of beef cattle (Koch et al., 1985; Alenda et al., 1980; Meyer, 1992).

The direct genetic effect is the genetic merit of an animal (expressed as the performance for a particular trait) based on its gene composition. Consequently, the maternal effect in complement with the direct effect is assumed to enhance the expression of growth traits in early life of animals but not necessary in advanced ages. Most reported studies have indicated an antagonistic relationship between direct and maternal genetic effects in early life of animals. However, Robinson (1996a) suggested that the negative correlation between direct and maternal effects was more likely to be a consequence of additional variation between sires (due to different genetic origin) or sire by year variation (due to non-zero over inflated additive and maternal covariances between sibs) rather than evidence of a true negative relationship. Consequently, when including a sire by year interaction in a full animal model, Robinson (1996b), Lee and Pollak (1997), and Meyer (1997), obtained a decrease in the absolute value of negative direct-maternal correlations. Meyer (1997) also stated that lower negative correlations were obtained in experimental data than in field data and this observation was supported by recent studies of Plasse et al. (2002). The high magnitude of the negative correlations between the two genetic effects in many experiments could mostly be caused by the confounding between sires across years and/or sire by year confounding.

Plasse et al. (2002) calculated a negative correlation of –0.37 between direct and maternal effects on birthweight of a pedigree Brahman herd under selection for three decades. This value obtained by Plasse et al. (2002) was the same as the weighted mean of six estimates from the literature for *Bos indicus* (Mercadante et al., 1995). However, Meyer (1992) obtained a weaker negative correlation (-0.25) for the mean of 17 values from *Bos taurus* and *Bos taurus* x *Bos indicus* herds. Also, in the review of Koots et al. (1994b), the mean of –0.27 was given for the correlation between direct and maternal effects for birthweight.

At weaning, an estimated correlation between direct and maternal effects in Brahman herd was -0.13 (Plasse et al., 2002). This value was below the mean correlation of –0.31 for the Bos indicus population based on Mercadante and Lobo (1997) studies, when using a complete univariate model and close to –0.16 reported by Meyer (1992) when summarizing literature results from *Bos taurus* and crossbred. In the review of literature, Koots et al. (1994a) also obtained a weighted mean of –0.30 for direct-maternal correlation of weaning weight. The analysis of Gobra cattle (Bos indicus) in Senegal (Diop and van Vleck, 1998) yielded a higher value of –0.61 (s.e. 0.33) for correlation between direct and maternal effects on weaning weight with the best fitting model.

Several studies have also indicated non-zero estimates of genetic correlations between direct and maternal genetic effects for growth traits at advanced ages such as yearling weight for most tropical and temperate beef cattle. For example, estimates of –0.39 and 0.01 for Zebu crosses, -0.48 for Herefords and 0.49 for Angus have been reported in Australia for yearling weight (Meyer, 1992; Mackinnon et al., 1991) and –0.50 and –0.28, respectively for yearling and 18-month weights of Gobra cattle in Senegal (Diop, 1997). Lee et al. (2000) also reported negative genetic correlation (-0.81) between direct and maternal genetic effects for yearling weight of Korean Native cattle.

Differences in production environments have been shown to affect genetic effects of post-weaning growth in beef cattle (Brown et al., 1993; Arthur et al., 1994c). This is primarily due to the effect of seasonal differences in feed availability within years. Lee and Pollack (1997) and Robinson (1996b) reported inflation of the negative direct-maternal genetic correlation included growth beyond weaning when the effects of sire by year interaction were excluded in the estimation model. Dodenhoff et al. (1998) also suggested that including sire by herd-year interaction effects in models for genetic evaluation might result in considerable re-ranking for estimated breeding values for maternal weaning weight.

In conclusion, most of the studies have indicated an antagonistic relationship between the two genetic effects, most especially at the post-weaning level, and the effectiveness of the utilization of both genetic effects to maximise meat production appears to be hindered, although still possible.

1.2.5 Genetic parameters for growth traits

Heritability estimates give the average proportion of performance superiority in parents that can be transferred to their progeny. In the past, various models have been used in the estimation of genetic parameters in animals. Most estimates of maternal heritabilities and direct maternal genetic correlations have been obtained either by equating variance component estimates from sire-maternal grandsire (Trus and Wilton, 1988) or sire-dam model analysis (Brown et al., 1990). Estimate has also been obtained by using an animal model with maternal effects on both pre- and post- weaning traits (Mackinnon et al., 1991). This was because considerable bias in variance components and genetic parameters has been obtained from models not including maternal genetic and permanent environmental effects in the data of *Bos taurus* (Meyer, 1992) and *Bos indicus* (Mercadante and Lobo, 1997), leading to inflated heritability values when compared to models including dam effects.

Many studies have found the estimates of direct heritabilities to be higher than those of maternal heritabilities in growth traits such as body weight at different ages, birthweight and postweaning average daily gain in beef cattle (Liu et al., 1994; Arthur et al., 1994a; Pang et al., 1994). This is an indication that these growth traits are influenced more by the genotype of the progeny rather than the genotype of the dam (primarily milking ability). Arthur et al. (1994a) reported moderate to high (0.23-0.68) direct heritability estimates for all growth traits studied except for weaning weight, which was low (0.06). However, the same author recorded a higher estimate for maternal heritability at weaning compared to the direct

heritability in both purebred Hereford (0.41 vs 0.06) and multi-breed synthetic herd (0.27 vs 0.14).

Koots et al. (1994a) review of the literature obtained direct and maternal heritability estimates of 0.31 and 0.14 for birthweight calculated as a weighted mean from 172 and 34 values, respectively. Plasse et al. (2002) in a univariate analysis also gave an estimate of 0.33 for direct heritability on birthweight similar to the means calculated from the literature for *Bos indicus* (Mercadante et al., 1995) and *Bos taurus* or *Bos taurus* x *Bos indicus* crossbreds (Meyer, 1992) which were 0.33 and 0.36, respectively. However, birthweight maternal heritability was 0.08 or 24% of that of direct heritability for Brahman cattle (Plasse et al., 2002), 0.12 or 36% of the mean direct genetic value for Zebu cattle (Mercadante et al., 1995) and mean of 0.17 or 47% of the direct value for some crossbreds (Meyer, 1992). Total heritability (Plasse et al., 2002) was 0.28, close to the value of 0.29 given in Meyer (1992)'s summary from literature for birthweight.

In general, the variance of weaning traits could be less homogenous among analyses than birth traits. From a univariate analysis, Plasse et al. (2002) obtained values of 0.07, 0.14 and 0.12 for direct, maternal and total heritabilities for weaning weight in a Brahman herd. Eler et al. (1995) also found higher maternal heritability than direct heritability in Brazilian Nelore cattle at weaning. In the contrary, direct heritability (0.13) estimate was higher than maternal heritability (0.07) in Korean Native cattle for weaning weight (Choi et al., 2000). A similar trend was observed in Mercadante and Lobo (1997)'s calculated means of 0.26, 0.16 and 0.22 for direct, maternal and total heritability from the literature of *Bos indicus* and Meyer (1992) obtained values of 0.25, 0.20 and 0.30 respectively for the same traits in a literature summary for *Bos taurus* and crossbreds.

The weighted means for direct and maternal heritability in the review by Koots et al. (1994a) were 0.24 and 0.13 for weaning weight. In Senegalese Gobra cattle, direct, maternal and total heritabilities were 0.20, 0.21 and 0.12 (Diop and van Vleck, 1998) for weaning weight indicating no differences between direct and maternal heritability at this age. Liu et al. (1994) also found no obvious differences between the direct and maternal heritabilities for both overall average daily gain and relative growth rate which is an indication that it may be worthwhile to utilize the maternal genetic variation for estimation of the post-weaning growth performance.

For yearling weight in Bos indicus cattle, Mercadante and Lobo (1997) gave a summary of 0.21, 0.15 and 0.18 for direct, maternal and total heritability while for a Nelore herd the estimates were 0.33, 0.10 and 0.38 for the same traits using the best fitting bi-variate model. Also for a data set from 57 Nelore herds in Brazil, Eler et al. (1995) reported 0.17, 0.12 and 0.18 for the above-mentioned parameters while Lee et al. (2000) found similar values and trend or Korean native cattle. Koots et al. (1994a) obtained a weighted mean direct heritability of 0.33 from literature for yearling weight.

Observations by Arthur et al. (1994a) further indicate that the estimates of direct and total heritabilities were higher in the multi-breed SY1 (crossbred) than the purebred Hereford cattle, thus giving an insight to the additive breed effects and heterotic gains that are associated with crossbreeding. This finding confirmed the study of Meyer (1992) with crossbreds from *Bos taurus* x *Bos indicus* having higher estimates of both direct and maternal heritabilities compared to mainly pure *Bos taurus* breed. Despite the extensive genetic parameter estimates done within and between breeds of cattle, such estimates have been limited to weight traits as a measure of growth. Little or no literature has cited the level of inheritance associated with growth related body dimensional (eg. height) traits and their relationship with weight traits.

1.2.6 Heterosis effect on growth traits

Complete expression of heterosis is measured by the difference between the average performance of reciprocal F_1 crosses and the average of the parental breeds joined to produce the reciprocal crosses. Heterosis is caused by non-additive effects of genes such as dominance and epistasis and can be seen through individual animal and maternal effects on the traits.

Diverse breeds in growth characteristics are required for heterosis and complementarity through crossbreeding. The importance of genetic effects due to heterosis on growth related traits have been found to vary with the age of animal. In a composite US breeding population of 9 parental beef cattle breeds, Gregory et al. (1991) reported heterosis retained heterozygosity in combined F3 and F4 generations for birthweight, ADG from weaning to 368 d, and for 368-d weight in males and female progeny. Newman et al. (1993) found significant individual and maternal heterosis for birth-weight in Charolais x Tarentaise crosses and Davis et al. (1998b) also gave a similar report on mean birthweight from Hereford, Tarentaise and F_1 reciprocal cross between these straightbreds. Breed direct and breed maternal heterotic effects for several cattle breed comparisons for birthweight reported by Wyatt and Franke (1986) ranged from –1.7 kg to 3.5kg (direct) and –3.3 kg to 1.8 kg (maternal). However, Dillard et al. (1980) and Cunningham and Magee (1988) found non-additive genetic effects to be unimportant source of variation in birth-weight.

The report of Kress et al. (1996) indicated that there were both significant individual and maternal heterosis for animals at 40 and 120-day of age. Dillard et al. (1980) and Cunningham and Magee (1988) also observed positive and significant effects due to individual and maternal heterosis on weight before and at weaning. Pre-breeding weight, post-breeding weight, weaning weight, and average daily gain were influenced by individual and maternal heterosis (Davis et al., 1998b) with higher maternal estimates in early calf life,

dropping as calf matured. The same observation was reported on similar traits in cattle from Hereford, Angus, and Simmental breeding (Kress et al., 1992). It could therefore be deduced that in order to fully exploit the heterotic effect, the genetic potential of crossbred animals should be matched with an improved maternal genetic and maternal environment. Newman et al. (1993), however, did not find significant amounts of individual or maternal heterosis for weaning weight or average daily gain in their study involving Charolais x Tarentaise crosses.

Very little has been reported on heterosis effects on fat depth and even less on muscularity or meat yield. Expressed as a percentage of straight-bred means, Gregory et al. (1994) observed retained heterosis levels in three composites lines for leaness and fat trim. Pitchford et al. (1993) also reported positive heterosis for condition score on Brahman-Hereford crosses. Mean calf condition score at weaning was also influenced by individual heterosis, but not by maternal heterosis in Hereford, Tarentaise cross (Davis et al., 1998b). Davis et al. (1998b) also reported positive and significant individual and maternal heterosis on calf hip height at weaning. In a review by Marshall (1994) individual and maternal heterosis estimates were relatively large (average 10.1%) and positive for fat thickness compared to other carcass traits.

1.2.7 Genetic parameters for body measurement traits as a measure of growth

In the past, selection practices in the beef cattle industry have placed a large emphasis only on weight measurement in productivity determination. However, body dimensions or linear measurements could supplement body weight as a measure of productivity or be used as predictors of some less-visible characteristic (Gilbert et al., 1993). Some selection pressure has been applied to body dimensions, especially measures of height in order to be able to efficiently describe the shape and conformation characteristics in certain segments of the industry. Nevertheless, reports of genetic parameter estimates for these traits are sparse.

As consumers become more concerned with diet and health issues and as the beef industry focuses more on value-based marketing, then the emphasis on body composition traits (Marshall, 1994) both in live animals and carcasses are expected to become increasingly important in the breeding objectives. In essence, specifying meat products in a predictable and cost effective manner could be achieved by testing the magnitude of genetic effects on the total live body measurements. Also, genetic and phenotypic relationships between body dimensions and even as related to carcass measurements are not available in the literature.

Among the few studies conducted on body dimensions include those reported by Shimada et al. (1994) on Japanese Black cattle (Wagyu) and Seo et al. (1998) on Korean native cattle based on extremely small samples. Shimada et al. (1994) observed that the estimates of both direct and maternal heritabilities for hip height, body length and chest depth were generally low compared to other body measurements under consideration. Moreover, it was noticed that body weight, body length and thurl width maternal heritability were larger than hip height and girth (Shimada et al., 1994). However, the magnitude of the direct heritabilities for the body dimensions were medium to high in Hereford and Angus purebreds (Gilbert et al., 1993). The findings of Seo et al. (1998) also reported low heritability values (0.09-0.22) for body measurements such as weight, withers height, body length, hip width, thurl width, rump length and chest girth. All estimates of genetic gains by regression of the breeding values for body measurements showed significant ($P<0.05$) positive progress with both body weight and chest girth having values of 349g and 1.0cm per year (Seo et al., 1998).

Although, heritabilities estimates for linear dimensions seem to low, partly due to the limited data set used, the correlated response of many of these traits with live-animal weight, muscle and fatness in defining animal shape and hence body composition, could be plausible for beef quantity and, possibly, beef quality.

1.2.8 Phenotypic and genetic correlations for growth and carcass traits

Correlation studies provide information on the degree of relationship between traits important in selection experiments. The knowledge of the magnitude and direction of relationships between traits is required to design effective breeding programs because selection for one trait may yield undesirable responses in the other traits.

Bullock et al. (1993) reported genetic correlations between mature weight and birth-weight, weaning weight, yearling gain and yearling weight of 0.63, 0.80, 0.76 and 0.89 respectively in polled Hereford cattle. Yearling hip height was also highly correlated genetically (0.73) with mature weight (Bullock et al., 1993) and this value was similar to that reported by Wilson and Northcutt (1992) between mature hip height and mature weight.

Marshall (1994) observed positive genetic (0.48-0.94) and phenotypic (0.59-0.74) correlations between pre- and post-weaning growth rate with carcass weight, longissimus muscle area, and retail product weight based on age or time-on-feed-constant analyses. The observation for fat thickness was positive for pre-weaning growth (averaged 0.37), but quite variable for post-weaning growth (ranged from -0.02 to 0.62, averaging 0.13). From weight-constant analyses, Arnold et al. (1991) reported that fat thickness was negatively genetically associated with weaning weight (r_G = -0.28), but positively associated with post-weaning gain (r_G =0.17).

There is also an indication of a favourable relationship between pre-weaning growth and marbling score with an average genetic correlation of 0.39 reported between these two traits (Marshall, 1994). This is an indication that selection for one of the traits can lead to an improvement in the other. However, the same author found that the average genetic correlation between post-weaning gain and marbling was low (0.05). Arnold et al. (1991), on

the other hand, reported that marbling was uncorrelated with weaning weight (r_G = -0.01) and positively correlated with post-weaning gain (r_G = 0.54) on a weight-constant basis.

In determining the relationship between body dimensions and carcass traits, Gilbert et al. (1993), obtained similar values at weaning and at the end of test (yearling age), which were generally low for phenotypic and genetic correlations except those for hot carcass weight. Koots et al. (1994b) summarised published estimates of genetic and phenotypic correlations between a number of traits and concluded that general genetic antagonisms exist between some carcass fatness traits and carcass yield. However, the same authors attested that many of the genetic relationships between traits of economic value were still poorly understood.

Very few estimates of phenotypic and genetic relationships between body compositions (mostly linear dimensions traits) that relate to carcass quality are available and many of those that have been published have large standard errors, meaning they may not be reliable for use in breeding programs. The large errors associated with most of these estimates were partly due to analysis based on limited data points and partly due to few breeds utilized. The advantage of estimation using multi-breed synthetic population has been reported (Meyer et al., 1993). There is a need, therefore, to determine this level of relationship in a larger data set involving a multi-breed synthetic population.

1.2.9 Genetic markers and its usefulness in livestock improvement

Genetic variability for economically important traits is assumed to be due to the segregation of alleles at the quantitative trait loci (QTL). QTL are regions of chromosomes at which alleles of one or more genes of unknown primary function affect a quantitative trait of interest. QTL can be either polygenes (Chevenrud et al., 1996) or major genes (Kinghorn and Kerr, 1995). In essence, QTL provide insight into (questions about) the genetic control of

complex traits. Thus, QTL analyses can be used to address specific questions concerning genetic architecture, such as the number of loci potentially affecting the trait, the distribution of gene effects, and the underlying patterns of gene action, including additivity, dominance, sex-specificity, epistasis and pleiotropy (Vaughn et al., 1999).

The effectiveness of genetic evaluation schemes and breeding programs in utilising marker technology involves detection and development of QTL and genetic markers that are closely linked in a population. However, until about a decade ago when detailed linkage maps based on DNA markers started emerging, there were only vague ideas about the number, location, and action of loci controlling quantitative variation in traits of economic importance. At the moment, panels of mapped markers are available from the genetic and physical maps of human (Weissenbach et al., 1992; Cuticchia et al., 1993), cattle (Fries et al., 1993; Bishop et al., 1994), sheep (Maddox et al., 2001), swine (Anderson et al., 1993) and mice (Dietrich et al., 1992; Copeland et al., 1993). These markers can be used to systematically search the genome and localise QTL (genetic loci) that are segregating in a population.

QTL mapping is a major step towards identifying and positional cloning of causative genes affecting quantitative traits. It is also important for effective introgression and marker-assisted breeding. Thus, the search for QTL, now a major activity in almost all of our commercially important species, is built upon the premise that marker assisted selection (MAS) could increase the rate of genetic improvement in those species by 1 to 10% (van der Beek and van Arendonk, 1994). The success of MAS application, however, depends on its efficiency and cost effectiveness as well as a number of other factors. Among these other factors are the ability to identify the genes or closely linked markers to genes underlying the QTL, the ability to test whether allelic variations at these loci are segregating in the population, and an understanding of how these genes interact with the environment or with

other genes affecting economic traits. Interestingly, the nature of the QTL does not need to be known in order to map the QTL or to use their effects for MAS.

1.2.10 Importance of marker technology in genetic improvement of livestock

Genetic improvement of domesticated animals uses a variety of selection strategies. Selection programs are typically species, breed and even product specific. These programs that aimed at identifying best animals suited for specific situations and conditions, and could benefit immensely from genetic marker technologies such as marker-assisted selection, parentage identification and gene introgression.

1.2.10a Marker-Assisted Selection. Marker assisted selection (MAS) uses information about quantitative trait loci (QTL) in livestock selection programs to identify individuals with favourable combinations of QTL alleles in these regions. The markers utilised in MAS programs are closely linked to the QTL. However, recombination between the markers and QTL will occur as a function of the distance between them. Thus, if the linkage is not tight, then there may be recombination and the accuracy of selection will decrease. However, in a situation where the exact location of the sequence change controlling the trait is known, then direct gene markers can be used (genotype-assisted selection) (Davis and DeNise, 1998). In practice, linked (indirect) markers may be better utilised for selection within families segregating the marker and QTL alleles following the establishment of the phase relationship while direct gene markers could be applied across families after the allelic effect for a given genetic background has been predicted. Though direct markers is the ideal, both linked and direct markers could be used in selections programs that incorporate other pedigree and phenotypic information for the genetic evaluation of animals.

Identification of molecular markers that are linked to QTL is a prerequisite for MAS in animals. Several experimental procedures and statistical techniques have been used to

identify markers that are closely linked to QTL (Striker et al., 1995; Uimari et al., 1996; Gringola et al., 1996). Research during the last decade has resulted in the identification of a large number of polymorphic marker loci and a few candidate gene markers (Bishop et al., 1994; Archibald et al., 1995; Rothschild et al., 1996). It is expected that these closely linked markers will be combined with relevant phenotypic information to improve genetic evaluation and selection through MAS. However, to date, few such MAS programs have been attempted in livestock.

1.2.10b Parentage or breed identification. Another area of selection programs that can benefit from the use of marker technology is parentage identification. The use of DNA markers for confirmation of pedigree or sire assignment is commercially available in many livestock industries (for examples see Moore and Vankan, 1994). The use of such technology will allow wider application of advanced genetic evaluation procedures reliant on knowledge of pedigrees such as BLUP. In particular, multiple-sire mated herds in the beef industry can now better access national genetic evaluation systems using animal model technologies. In addition, more wide-scale use of DNA identification will lead to a reduction in pedigree errors (Davis and DeNise, 1998), and hence, an increase in accuracy of breeding value predictions.

Genetic erosion and extinction threaten an increasing number of livestock breeds as a major consequence of the global loss of genetic diversity. In order to prevent this type of loss and preserve unique traits associated with many animal breeds, sets of genetic markers that characterize distinct populations need to be developed. In essence, breed characterisation requires knowledge of genetic variation (eg. mitochondrial and nuclear DNA polymorphisms) that can be effectively measured within and between populations (Hetzel and Drinkwater, 1992; Rassmann et al., 1991; Suzuki et al., 1993; Tautz, 1992).

1.2.10c Genetic introgression or Transgenesis. Gene introgression is the incorporation of favourable alleles for a certain trait from one breed (donor) into another breed or line (recipient). This may be through backcrossing and selection for marker alleles linked to the favoured allele and against marker alleles throughout the rest of the genome typical for the unfavourable background. This is a form of MAS, but that does not necessarily account for total phenotypic performance because of effect due to genotype by environment interaction or gene mutation. In its most extreme form (unselected population), it can be allied with advanced reproductive technologies such as multiple ovulation and embryo transfer, embryonic stem cell cultures, and in vitro oocyte maturation and fertilization to enable rapid move of a favoured allele into a breed (Georges and Massey, 1991; Earl et al., 1995). This form of MAS in-conjuction with pedigree and performance data could be used to make rapid directed genetic changes (Davis et al., 1997).

Cloning of specific genes for the purpose of introgression is being considered as part of genetic enhancement strategies. Apart from the functional characterisation of genes responsible for traits of economic values, its also allows the duplication of such genes. The principle of introgression in this regard has been proposed for situation such as incorporation of the high-litter-size alleles from Meishan pig strains into high-performance breeds for commercial use (Rothschild et al., 1994) and the movement of disease-resistance alleles from tropically adapted strains into high performance but susceptible strains of beef cattle (Frisch, 1994; van der Waaij and van Arendonk, 2000).

1.2.11 Gene mapping of growth and carcass traits in beef cattle

In most populations, body growth (measured as weights and body dimensional traits eg. height) has been considered the quintessential quantitative phenotypic trait; that is, a trait that does not exhibit classic Mendelian inheritance attributable to a single genetic locus, although it is strongly heritable (Vaughn, et al., 1999). Thus, body growth traits are

quantitative in nature with a normal phenotypic distribution but are being controlled by many genes, each having a relatively small additive effect on phenotype (Falconer, 1953). However, quantitative (or polygenic) inheritance can be due not only to the action of alleles at several loci but could involve fewer genes with large effects and those genes or loci could also be influenced by environmental (nutrition).

Quite a number of studies have been done in the area of QTL identification for growth traits in beef cattle for marker-assisted selection. Some of such reported experiments were those on pure Hereford cattle (Moody et al., 1996) and F_1 progeny of Charolais x Brahman sires crossed with a composite dam herd (Davies et al., 1998a). Moody et al. (1996) genotyped for allele substitution in K-Cas (kappa-casein), B-Lac (beta-lactoglobulin), GH (growth hormone), PIT1 (pituitary transcription factor 1), GHR (growth hormone receptor), IGF-I (insulin-like growth factor I) and PRL (prolactin) loci in Line 1 (closed population selected for increased postweaning growth) Hereford population and observed significant ($P<0.01$) effects on birth weight and 180-day pre-weaning expected progeny differences (EPD) and maternal EPD only for the K-Cas allele substitution.

Davis et al. (1998a) detected five regions of the bovine genome that accounted for variation in birth-weight using progeny from three F_1 Charolais x Brahman sires crossed with a composite dam herd. In that trial, significant effects on birth-weight were detected on five chromosomes (BTA 5, 6, 14, 18 and 21) using a total of 167 markers that provided up to 81% genome coverage. Stone et al. (1999) also have compelling evidence for a QTL allele of Brahman origin affecting an increase in rib bone and a decrease in dressing percentage on chromosome 5 (BTA5). They also observed a QTL giving an increase in retail product yield and component traits on BTA2 and BTA13, an increase in Longissimus muscle area on BTA14 and an increase in birth-weight on BTA1.

Other mapping studies in beef cattle reported QTL for birth-weight (Davis et al., 1998a), pre- and post-weaning growth, and fat and rib eye area (Stone et al., 1999), and muscle hypertrophy (Grobet et al., 1998). A recent study by Casas et al. (2000) suggested that QTL were segregating in 10 regions (BTA 5, 6, 7, 13, 14, 17, 19, 22, 27, and 29) for carcass composition and growth in a Piedmontese paternal half-sib family and in a Belgian Blue family.

1.2.12 Gene mapping studies on other animal species

Quantitative trait loci for growth and carcass traits have been detected also in experimental and commercial populations of other stock including swine, sheep and goats, and mice. These results can be used for cattle through comparative mapping and positional cloning of valuable genes.

1.2.12a Swine. Since a comprehensive porcine map was constructed (Archibald et al., 1995; Rohrer et al., 1996), quantitative trait loci (QTL) mapping for economically important traits in swine has been a high priority. Andersson et al. (1994) studies involving a 3-generation pedigree from crossing European wild boars with Large White sows has provided evidence of QTL on pig chromosome 4 with large effects on growth, length of the small intestine, and fat deposition. In this study, wild boar alleles were reported to be associated with reduced growth, a shorter small intestine, and a higher fat content consistent with the differences between the founder populations (Andersson et al., 1994). Suggestive evidence of a QTL with relatively large effect for average daily gain was also detected by Wang et al. (1998) using a pooled analysis on the same chromosome.

On chromosome 13, there are indications of a QTL affecting back-fat near *PIT1* gene (Yu et al., 1999) and a birth-weight and early growth QTL on the same chromosome (Andersson et al., 1994). The gene action of the loci on chromosomes 13 and 4 was found to

be largely additive for the growth traits with an indication of dominance for the increase fat depth (Andersson et al., 1994).

A paternally expressed QTL for fat deposition was mapped to *IGF2* locus on pig chromosome 2 (Jeon et al., 1999; Nezer et al., 1999). The location of a QTL on chromosome 6 corresponded to that of a candidate gene for fatness, H-FABP (Gerbens et al., 1997). Also, QTL for fatness were found on chromosomes 1, 7, and X (Rohrer and Keele, 1998; Bidanel et al., 2001). In a population of progeny generated by an advanced backcross and sib-mating from the original founder of a Landrace boar and a Yorkshire sow, Wu et al. (2002) recently obtained significant QTL effects for back-fat thickness on pig chromosomes 1, 3 and 18.

1.2.12b Mice. Falconer et al. (1978) found that body size growth in rodents appears to occur through two general physiological mechanisms that act at different life stages (Atchley et al., 1997; Atchley and Zhu, 1997). The ability to separate the evolution of these two growth periods was illustrated by the results of an index selection experiment for high and low early growth, holding late growth constant, and for high and low late growth, holding early growth constant by Atchley et al. (1997). A recent report on the mice, has also indicated distinct differences on QTL affecting early and late growth and these QTL were mapped to separate chromosome locations (Vaughn et al., 1999). Although, much earlier work by Famula et al. (1988) on mice did not suggest a differential effect of a specific growth gene (*hg*) on growth of tissue or organ system but may not necessarily be inconsistent with others on separate QTL for early and/or late growth of these systems.

1.2.12c Sheep. One outstanding gene mapping study in sheep involved the work on callipyge gene. The locus, designated callipyge (CLPG), maps to the telomeric region of ovine chromosome 18 (Cockett et al., 1994). The gene action of CLPG was further elucidated by Cockett et al. (1996) based on limited number of offspring from five different mating

combinations, where the maternal and paternal alleles were inferred from five DNA markers on chromosome 18. Cockett et al. (1996) and Freking et al. (1998a) also proposed a genetic model of paternal polar over-dominance to explain the relationship between callipyge phenotypes and genotypes.

The gene action at the CLPG locus was reported by Freking et al. (1998b) not to affect any measure of growth but to be characterized by unique muscle hypertrophy and low carcass fatness in heterozygous animals that inherited the allele from their sire. This implies an unusual situation, in which carcass composition is changed dramatically without affecting growth patterns. A recent study has indicated four genes in the CLPG locus with preferential expression in skeletal muscle, two of which were expressed exclusively from the paternal allele and the other two from the maternal allele (Georges et al., 2002).

1.2.13 Gene mapping studies on dairy cattle

Most economically important traits in milk production as in growth traits are influenced by many genes as well as environmental factors. Selection for dual-purpose cattle (cattle that will be moderate in dairy and beef cattle characteristics) will involve systematic breeding programs that can effectively combine production, conformation and functional traits. As with the analysis of important traits in beef cattle breeds, evaluation procedures like BLUP (Henderson, 1984) are used to estimate breeding values of animals for dairy traits using quantitative approaches. However, in order to understand the relationship between the milk and meat production traits, the nature of the underlying genes (quantitative trait loci) affecting both sets of traits in cattle breeds has to be investigated using molecular approaches. Identifying QTL or markers close to QTL for these traits in a region within the genome with non-antagonistic correlated responses will go a long way for marker assisted selection of cattle breeds with potential for use as dual purpose breeds.

In most dairy cattle experiments, microsatellites have been used to perform genome scans mainly for QTL affecting milk production and component yields (Cowan et al., 1990; Hoeschele and Meinert, 1990; Bovenhuis et al., 1992; Georges et al., 1995). Many workers, using grand-daughter designs (Weller et al., 1990), have reported candidate genes involved in milk, fat and protein production (Arranz et al., 1998; Coppieters et al., 1998, Georges et al., 1995; Ron et al., 1998; Spelman et al., 1996; Freyer et al., 2002). Some markers associated with low heritable functional traits, like fertility and health traits, have also been reported widely (Ashwell et al., 1996; Ashwell et al., 1997; Zhang et al., 1998).

However, there are few studies that relate milk production with body weight and conformation in dairy cattle using molecular approaches (Table 1.1). One of the few studies conducted used a grand-daughter design in a Dutch Holstein Friesian population to locate QTL for conformation and functional traits (Schrooten et al., 2000). In this trial, QTL for stature, size, and dairy characters were located in the same region (0 to 11cM) on chromosome 6 with strong genetic correlation (0.80) between stature and dairy characteristics. The authors found also QTL for calving ease (at 166 cM) and birth weight (at 132 cM) in the same region of chromosome 5, suggesting that QTL for size-related traits might also affect calving ease and birth weight. Ashwell et al. (1998a) in seven large grandsire families of US Holsteins using granddaughter design also reported a significant QTL effect related to stature on chromosome 21.

Milk production QTL have been reported for chromosome 14 (Coppieters et al., 1998), some 15 to 20 cM close to reported QTL for stature (36 cM) on the same chromosome in the New Zealand dairy population (Spelman et al., 1999). The highly genetically correlated trait [0.96, Coppieters et al., 1998) of live weight also had a peak at the same chromosomal position as stature, even-though the test statistics was not significant at the suggestive threshold level (Spelman et al., 1999; Table 1.1).

Table 1.1. QTL for body size and growth mapped in dairy cattle

Chr.	Trait	Position (cM)	References
2	Chest width & body capacity	139	Schrooten et al., 2000
	Rump width	117	"
	Calving ease	139	"
	Milking speed	57	"
	Dairy form	Not reported	Ashwell et al., 1998a
	Dairy capacity	Not reported	"
5	Stature	122	Schrooten et al., 2000
	Chest width	156	"
	Body capacity	154	"
	Rump width	181	"
	Size	123	"
	Birth-weight	132	"
	Dairy character	27	"
	Calving ease	166	"
6	Stature & size	11	Schrooten et al., 2000
	Angularity	84	"
	Dairy character	0	"
	Calving ease	44	"
8	Stature & size	127	Schrooten et al., 2000
10	Angularity	12	Schrooten et al., 2000
11	Angularity	0	Schrooten et al., 2000
	Rump angle	Not reported	Spelman et al., 1999
12	Angularity	31	Schrooten et al., 2000
14	Stature	36	Spelman et al., 1999
	Live-weight & milk production	15 – 20	Coppieters et al., 1998
19	Rump angle	Not reported	Ashwell et al., 1998b
21	Stature	Not reported	Ashwell et al., 1998a
	Dairy capacity	Not reported	"
23	Body depth & form	Not reported	Ashwell et al., 1998a
	Dairy capacity & form	Not reported	"
	Milking speed	30	Schrooten et al., 2000
24	Angularity	16	Schrooten et al., 2000
25	Stature & capacity	Not reported	Spelman et al., 1999
	Dairy character	74	Schrooten et al., 2000
29	Body capacity	60	Schrooten et al., 2000
	Rump angle	53	"
	Rump width	20	"
	Birth-weight	29	"

Understanding the underlying gene/s in growth and milk production traits and their relationship could help in commercial breeding systems with terminal-cross matings to allow complementary use of breeds for maternal traits in dams vs growth and carcass traits in sires, thus reducing the problems associated with genetic antagonisms. Such antagonisms are of particular concern in situations in which breeding females and commercial market animals are produced from the same types of matings (Marshall, 1994). If the underlying gene/s involved in size-related (beef traits) and dairy characters are inherited together with strong genetic correlations, then seed-stock with potential in both types of traits could probably be produced through terminal matings in commercial breeding systems.

1.2.14 Candidate genes for growth and carcass traits

Polygenic traits (e.g. growth) are sometimes difficult to dissect genetically using genome mapping scans to find the chromosomal location of genes (mostly with major effects) with phenotypic effects. A more rewarding alternative strategy would be to identify candidate genes with high genetic variation within the population (e.g. Limousin x Jersey) for the trait of interest. Any verified candidate gene could then be introgressed into favoured population of domestic livestock to further enhance their economic performance. A number of candidate genes for growth related traits have been found in different species in earlier studies.

1.2.14a High growth (*hg*) locus. The high growth locus (*hg*), which was originally described as a recessive gene with nearly complete penetrance (Bradford and Famula, 1984), is known to be a major locus that increases weight gain and mature body size of mice by 30-50%. Physiologically, the high growth locus caused an increase in the efficiency of growth by influencing energy metabolism (Calvert et al., 1986) without altering overall body composition (Calvert et al., 1985).

The putative location of high growth locus (*hg*) between two loci (Igf 1 and Steel) on mouse chromosome 10 has been reported (Medrano et al., 1992; Horvat and Medrano, 1995). This region of the mouse chromosome 10 has also been reported to contain QTL (s) that increase growth in a population of Quackenbush-Swiss (QS) mice (Collins et al., 1993).

Many loci from the distal half of mouse chromosome 10 have also been found to belong to a block of homologous genes on human chromosome 12 q13-q24 (Copeland et al., 1993; O'Brien et al., 1993). Therefore, a human homolog of *hg* would be expected to reside in this region.

1.2.14b *GH-IGF* endocrine axis gene or Insulin-like growth factor-1 (*Igf 1*). A physiological study by Medrano et al. (1991) supported by subsequent genetic analyses by Medrano et al. (1992) established linkages between *hg* and insulin-like growth factor-1 (*Igf 1*). So, the *Igf 1* gene was considered a possible candidate for *hg* because of genetic linkage (Medrano et al., 1992) and because elevated levels of *Igf 1* plasma protein were detected in high growth mice (Medrano et al., 1991). However, subsequent findings of Horvat and Medrano (1995) demonstrated that *Igh* and *hg* are two separate loci and that *hg* is located distally from the *Igf 1* locus.

The growth hormone receptor gene maps at approximately 65 cM on BTA13 (Barendse et al., 1994) and the *IGF-I* gene maps at 73 cM on BTA5 (Kappes et al., 1997). These genes are part of the endocrine axis that controls visceral organ and skeletal development (Cohick and Clemmons, 1993). Moody et al. (1996) attribute 5% variability in 180-day pre-weaning gain increase of USDA line 1 Hereford cattle to the substitution of growth hormone A allele for B allele in the *IGF-I* gene. A 16% variability on birth weight EPD was also ascribed to genotype substitution of *IGF-I* alleles in the Line 1 population (Moody et al., 1996).

1.2.14c Decorin (*Dcn*) gene. Another closely linked candidate gene to *hg* on chromosome 10 is the murine decorin (*Dcn*) gene. This gene, a homolog of human decorin (*Dcn*) gene (an ubiquitous interstitial proteoglycan) is involved in cell proliferation and extracellular matrix assembly control (Ruoslahti and Yamaguchi, 1991) and was mapped within the *hg* LOD 2 support interval in males and falls 1.2 cM beyond the distal border of the *hg* LOD 2 support interval in females (Horvat and Medrano, 1995). Though there was suggestive evidence that *hg* is located proximally to *Dcn*, the combination of the *hg* interval map and the test-cross results provide genetic evidence that *hg* is not an allele of either *Igf 1* or *Dcn* (Horvat and Medrano, 1995). However, the knowledge that *Dcn* is closely linked with *hg* may be applied to some domestic stock. For example, the cDNAs of *Dcn* have already been sequence in cattle (Day et al., 1987) and chickens (Li et al., 1992).

1.2.14d Myostatin gene. The *Myostatin* gene has been identified (Smith et al., 1997) as a strong probable positional candidate gene for *mh* locus known to be responsible for muscle hypertrophy in mice (McPherron et al., 1997). Charlier et al. (1995) and Dunner et al. (1997) mapped the *mh* locus to cattle chromosome 2 (BTA2) between TGLA44 and centromere. The analysis based on more additional centromeric marker (BMC9007) and BY5 from a YAC library containing TGLA44 has further showed the maximal F-statistic for some growth and carcass traits to be between 3 and 7 cM (Kappes et al., 1997; Sonstegard et al., 1997). Casas et al. (1998) using retail product yield as a model in a simulation procedure predicted with more than 95% certainty that the *mh* locus is between BMC9007 and INRA40 or between 2 and 6 cM of the linkage map of BTA2.

Homozygous double-muscled animals have been generally reported to have a higher dressing percentage, a larger proportion of muscle, and lower proportion of fat and bone compared to normal animals (Menissier, 1982; Hanset and Michaux, 1985; Arthur, 1995). In fact, historical evidence has led to the conclusion that double muscling is a major gene in

beef cattle causing the same physiological events in all breeds expressing the condition (Menissier, 1982; Arthur, 1995). Casas et al. (1998) also concluded that the effect of the *mh* allele on carcass traits is independent of breed origin since those inheriting the *mh* allele either from the Belgian Blue or Piedmontese had a higher proportion of muscle mass and were leaner than those inheriting the alternative allele. Shackelford et al. (1995) stated that for most breeds of cattle, the majority of the variation in retail beef yield and USDA yield grade could be attributed to variation in fat content. In cattle, inheriting the *mh* allele, retail beef yield and USDA yield grade were influenced by both a decrease in fat and an increase in muscularity.

Double-muscled animals have been reported in the past to be associated with tougher meat (Menissier, 1982; Hanset and Michaux, 1985). However, a study by Arthur (1995) indicated that meat from double-muscled animals is tenderer than meat from animals with the alternative alleles. Casas et al. (1998) results also suggested that a single copy of the *mh* allele had no effect on tenderness as measured by longissimus shear force at 3 and 14-day post-mortem. An important reproductive trait under the influence of the double muscling gene is calving difficulty. This trait has been reported to be associated with double muscling when compared in dams with alternative alleles (Hanset el al., 1989; Hanset, 1991). However, when birth weight and calving ease were analysed as traits of the calf, individuals inheriting the *mh* allele were observed to be slightly heavier at birth with no association with calving ease if only one single copy of *mh* is inherited (Casas et al., 1998). Previous reports have also indicated that birth weight was not increased in individuals inheriting a single copy of the *mh* allele (Menissier, 1982; Hanset, 1991).

1.2.14e *PIT1* gene. The *PIT1* gene, which has been mapped to pig chromosome 13 (Archibald et al., 1995), is an essential transcriptional regulatory factor of growth hormone, prolactin and the thyrotropin β subunit (Radovick et al., 1992). Due to the biological

importance of *PIT1*, the possible association between this gene and several economic traits was studied in different pig resource families. *PIT1* polymorphisms were significantly associated with pig birth weight and back-fat measures in the Iowa State University (ISU) pig resource families (Yu et al., 1995). In the Edinburgh resource families, *PIT1* polymorphisms were significantly associated with birth weight and early growth (Yu et al., 1996).

1.2.14f Kappa-casein (*κ-Cas*). *κ-Cas* is a milk protein gene. Several studies have reported a trend for increase in milk yield associated with either the *κ-Cas* B allele (Lin et al., 1989; van Eenennaam and Medrano, 1991; Cowan et al., 1992) or *κ-Cas* A allele (Ng-Kwai-Hang et al., 1986; Gonyon et al., 1987; Bovenhuis et al., 1992; Bovenhuis and Weller, 1994). However, Moody et al. (1996) has shown large and significant effects of substitution of the B allele for an A allele of *κ-Cas* on progeny birth weight and 180-day pre-weaning gain EPD. A close link between the *κ-Cas* and Beta-casein (*β -Cas)* genes has also been established (Hines et al., 1981; Threadgill and Womack, 1990). Consequently, Bovenhuis et al. (1992) and Bovenhuis and Weller (1994) suggested that the observed effects of *κ-Cas* on milk yield in Dultch dairy cattle population actually resulted from linkage to the *β -Cas* gene.

1.2.15 Summary

In the past, genetic improvement of livestock has been accomplished purely by selecting animals that express either superior phenotypes or have quantitative genetic evaluations predictive of superior additive genetic merit for particular traits of interest. However, the new techniques in molecular genetics now allow the actual genotype of an animal to be determined for specific loci. This information may accelerate future genetic improvement of livestock through marker assisted selection programs, if significant associations can be found between specific genotypes and traits of economic importance such as growth. Moreover, virtually all the earlier findings were design, station, species and even breed specific. This review, therefore, investigated the mode of inheritance of growth traits

(measured as actual and gains in weight and skeletal development) using quantitative and molecular approaches in cattle. The relationship between growth and milk production QTL were also examined.

1.2.16 Project objectives

A significant number of gaps in knowledge have been identified in the literature reviewed above that has prompted the need for the present investigations. This study involves primarily the utilization of the Davies Gene Mapping (DGM) project herd comprising purebred Jersey, purebred Limousin and their crosses to obtain live-measurements associated with growth traits at different ages. These measurements were taken to answer one of the major hypotheses of DGM project: Are there genes with major effect on meat production traits? The DGM was design to complement the worldwide effort to map the cattle genome for several production and meat quality traits.

In order to expand the scope of the present study, which includes the prediction of carcass products from live measurements and the estimation of genetic parameters for growth and body developmental traits, data sets from Southern Crossbreeding Project (SXB) herd comprising many breed crosses were also used. The SXB was developed to examine the potential for genetic improvement of terminal sire breeds in South Australian beef production system to meet a range of meat market specification.

The overall aim of this present study is to utilize quantitative and molecular approaches to evaluate genetic improvement tools for growth and development in cattle through analysis of component traits namely:

1. Weight
2. Body dimensions (Height, length, girth, stifle and hip)
3. Muscle defined as Stifle/Hip x 100

4. Fat depth (subcutaneous)

The study will also identify the genetic linkage between principal component traits to enhance quantity and quality determination in cattle body composition. Thus, the specific aims of this study are:

1. To predict carcass products from live measurements
2. To estimate breed effects and genetic parameters for these traits
3. To estimate genetic effects for weight and body dimensional traits
4. To map quantitative trait loci (QTL) throughout the cattle genome for all these traits

While the expected outcomes from the study are as follows:

1. Equations for prediction of carcass composition from live animal measurements
2. Estimates of age specific genetic effects on weight and body dimensional traits.
3. Breed differences in growth and developmental traits.
4. Genetic parameters for all the traits related to growth and development.
5. Identification of QTLs linked with markers for all traits under consideration.

Chapter 2

Materials and Methods

2.1 Introduction

The information utilised for the thesis was from two major projects: the Davies Gene Mapping Project (DGM) and Southern Crossbreeding Project (SXB). Each project was used to investigate different aspects of the aims and objectives of the study. There were similarities between the two projects with regards to many live-animal measurements, but the two projects were also different from one another in terms of the size and experimental design. As a common goal, the two projects were both designed to examine potential for genetic improvement in both meat yield and quality (specifically marbling). Therefore this part of the thesis would avoid repetition of the common aspect by just referring to such appropriately.

2.2 Davies Gene Mapping Project (DGM)

The J.S. Davies Bequest to The University of Adelaide primarily funded this project. The two major aims of the project are: 1) to study the mode of inheritance of important meat quality traits, and 2) to map major genes controlling these traits.

2.2.1 Experimental design

This project comprises 591 calves born from 1994 through 1998 by two very different *Bos taurus* breeds (Jersey and Limousin). The choice of the two breeds (Jersey and Limousin) was basically to maximise between breed variations in traits of interest within progeny from their crosses for gene mapping purposes. The Jersey is a small frame dairy breed, whereas the Limousin is a moderate-large frame, well-muscled beef breed. The design was double-backcross. In the design, which involved two phases, year and breed were partially confounded (Table 2.1). In phase 1 (1994-95), two Jersey bulls were mated to Jersey cows to produce purebred Jersey (JJ) calves and two Limousin bulls were mated to Jersey and Limousin cows to produce purebred Limousin (LL) and F_1 (LJ) calves. Phase 2 consisted of backcross calves resulting from the mating of three F_1 bulls from the first phase of the experiment to purebred Jersey or Limousin cows to produce Jersey backcross (XJ) or

Limousin backcross (XL) calves born in 1996 – 1998. Because of the large breed differences in meat yield and marbling, the backcross progeny (¾ Jersey and ¾ Limousin) varied greatly, representing both purebred progeny and first cross progeny (Figure 2.1). In addition, there were some purebred Jersey calves generated in phase 2 (1996) from the original two Jersey bulls. Within phases, there were common sires and across the phases, there were many common dams (total 280).

Table 2.1. Number of calves per breed and year combination

Breed	1994[a]	1995	1996	1997	1998	Total calves	Sires[b]	Dams[b]
Jersey (JJ)	19	31	29	-	-	79	2	67
LJ x JJ (XJ)	-	-	38	94	73	205	3	134
LL x JJ (LJ)	28	33	-	-	-	61	2	52
LJ x LL (XL)	-	-	43	60	62	165	3	78
Limousin (LL)	26	55	-	-	-	81	2	63
Total	73	119	110	154	135	591	7	280

[a]**Hip and stifle width not recorded**
[b]**Sires and dams used across years and breed combinations**

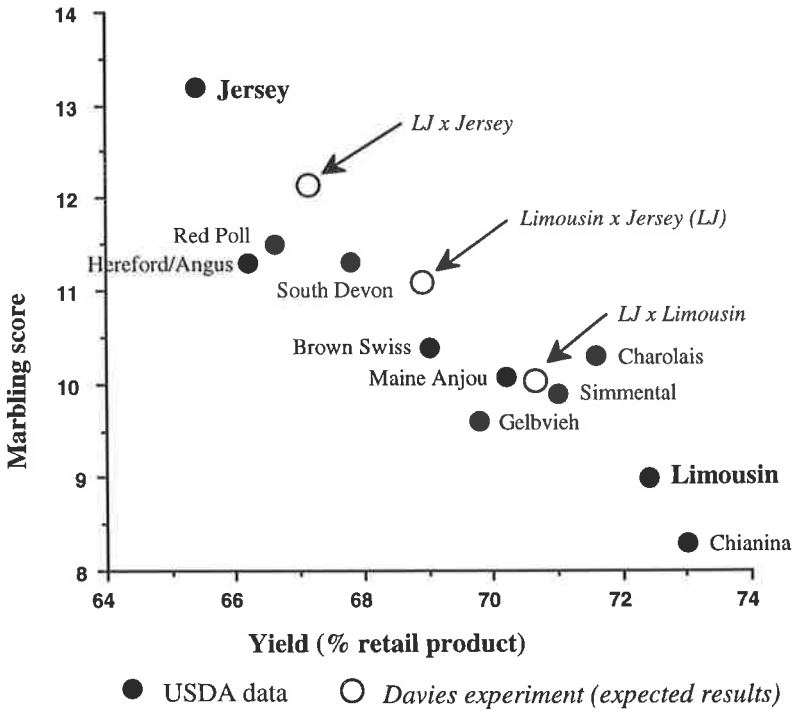


Figure 2.1. Marbling score vs meat yield

2.2.2 Animal environment and management

Calves were born at Martindale, a property located about 150 kilometres north of Adelaide, near Mintaro in the cereal zone of South Australia's mid-North. Calves were born in autumn (March – May, average 26th April), single suckled and weaned in summer (first week in February) at an average age of 250 days. After weaning, calves grazed pasture and/or hay supplemented for 430-500 days. The seasonal annual rainfall distribution pattern during the experiment (1994-1998) varied, with an annual average of 586mm, of which 34% fell in summer period (October-March) and 66% fell in winter period (April-September), a pattern typical of "Mediterranean" climates. Calves stayed with their dams on pasture and also have free access to oaten hay supplements provided to dams during the critical feed shortage period of the first year (January-June).

2.3 Southern Crossbreeding Project (SXB)

The South Australian Cattle Compensation Trust Fund, A.W. & P.R. Davis Pty Ltd and South Australian Research and Development Institute (SARDI) principally funded this project. The main aim of the project was to characterise between and within-breed genetic variation for production, carcass and meat quality traits.

2.3.1 Experimental design

The Southern Crossbreeding Project (SXB) comprised 1215 calves born over 4-year periods (1994-1997). In this project, 97 sires from seven breeds (Jersey, Wagyu, Angus, Hereford, South Devon, Limousin and Belgian Blue) were mated to mature Hereford cows (766) in a topcross design. These breeds were chosen to produce progeny that represent a large range of biological types similar to the Germ Plasm Evaluation Program at Clay Centre, Nebraska, USA (Cundiff et al., 1998). The design was a compromise between sampling many sires and accurate estimation of sire performance to allow for estimation of breed differences and sire breeding values for meat quality and quantity traits. The seven breeds represent the

major breeds targeted at meeting a range of market specifications for beef production in South Australia. In general, there were 12-15 progeny per sire, with an average of 13 calves per sire and 14 sires per breed. Sires were generally used in one year only with few exceptions, whereas dams were commonly used for more than one year.

2.3.2 Animal environment and management

Calves were born in autumn (average birth date 3rd April), about three weeks before the characteristic Mediterranean environment's "break of season" on two properties (Struan and Wandilo) in the south-east of South Australia under three management groups. Struan is located on flat plains and Wandilo is more of a sandy terrain. All calves were weaned in summer (December-early January) at an average age of 250 days. After weaning, the animal grazed on pasture for a period ranging from 400-600 days. Calves were in 1-3 post-weaning management groups, all grown out at Struan Research Centre, Naracoorte, until 12-18 months of age and then transported to a commercial feedlot. In the feedlot, they were fed a minimum of 60% grain (various but primarily barley) with approximately 12MJ/kgDM energy and 13% protein for 70-90 days (heifers) or 150-180 days (steers). The exception to this was the 1997-drop steers that were finished in a good season on lush, perennial, spring pasture and were able to reach marketable weights without requiring grain finishing.

2.4 Animal measurements (DGM and SXB)

Calves were tagged at birth with bull calves castrated within three days of birth. At birth, all calves were weighed and measured for height (measured as the distance from hip to the ground), length (measured as the distance between the first spinal cord bone on the shoulder and pin-bone) and girth (measured as the body circumference immediately posterior to the front leg).

Calves were again weighed (WT) and measured at weaning while full and at two other ages. These ages were approximately 400 days and 600 days after birth, i.e. during winter after the dry season and summer after the wet season, respectively. Height (HT) was measured as the difference between the distance from the top of the crush down to the top of the hips and the distance to the ground. The length (LH) and girth (GH) were measured similarly to that at birth. Other measurements at weaning and other ages were fat depth (FD) scanned at the P8 site on the rump using Ezi-scan® sonic device (AMAC Pty. Ltd.) plus hip width (bone) and stifle width (muscle) measured using calipers. Stifle width as a proportion (%) of hip width was used as an indication of the muscularity (MUS). This is similar to that used previously by McKiernan (1990) who developed visual techniques for assessing meat yield.

In the SXB animals, there were no muscularity measurements for the 1994-drop at all ages, for 1995-drop at weaning and also for 1997- drop at 600 day of age. At weaning, P8 fat depth was not measured for 1995 drop and also for both 1994 and 1995 drops at 600-day. Calves born in 1995 and 1997 had no 600-day measurements of height, length and girth. For the DGM animals, there were no 600 days measurement of height, length and girth for heifers born in 1994. In general for SXP animals, weaning or post-weaning traits were measured at close but different ages between years and particularly at 600-day of age there were very limited number of animals measured for all traits.

Growth rate (per day) was calculated between ages for each of the traits measured [(birth and weaning, i.e. pre-weaning gain), weaning and 400 days (dry season gain=January to June) and 400 and 600 days (wet season gain=July to December). Thus, seasons were confounded with age. The general pre- and post-weaning growth pattern of calves in different seasons is presented (Figure 2.2).

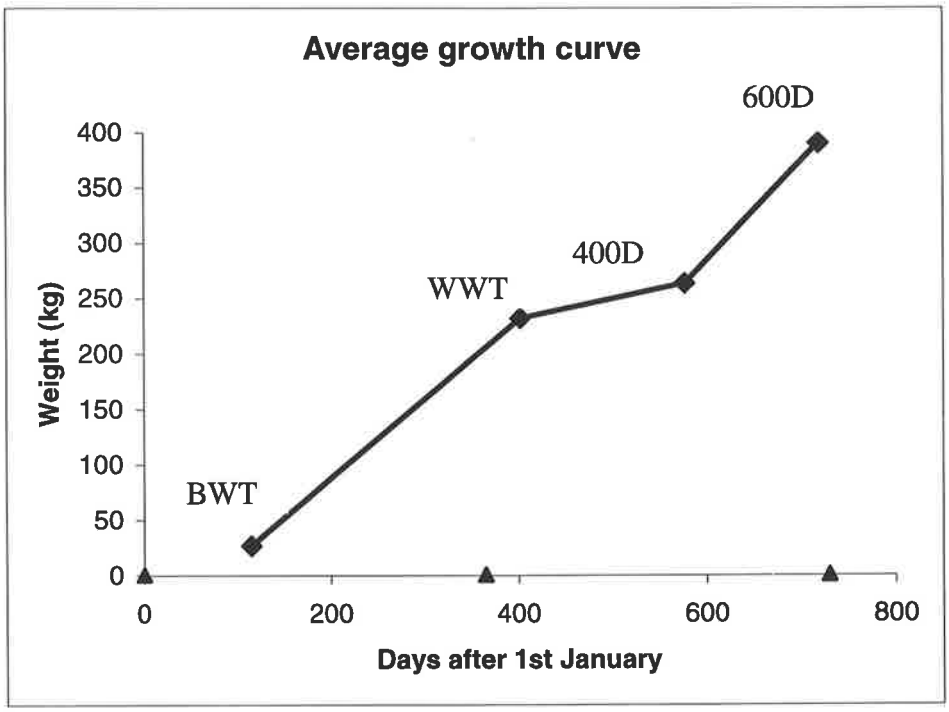


Figure 2.2. Pre- and post-weaning growth pattern for calves in different seasons
BWT= Birth-weight, WWT= Weaning-weight
400D= 400-day weight, 600D= 600-day weight

Chapter 3

Prediction of carcass traits from live animal measurements

3.1 Introduction

The accuracy of functions used to predict carcass composition from live animal measurements is of immense potential contribution to livestock production enterprises. The value of beef cattle lies in their ability to efficiently produce a carcass composed of optimal proportions of muscle, bone, and fat at market weight (Tatum et al. 1986b) or market specifications. The ability of the producer and buyers of livestock to relate objective live animal characteristics to carcass characteristics is essential for optimum production and value based trading systems. This ability will also enable processors to more accurately determine returns from meat processing and it may increase the rate of genetic gains in meat quantity traits in breeding herds.

In the past, many subjective live animal assessments (e.g. conformation score and butt shape profile) have been found to be poor indicators of carcass composition (Kempster et al. 1982). The problem has been the associated confounding of the relationship of muscle and yield with that of fat and yield. Other live measurements studies include the use of ultrasound technology (Hearing et al. 1994) that may not be cost-effective and/or may be of less application. In view of these challenges, this study examines the effectiveness of predicting carcass yield from objective live animal measurements.

3.2 Materials and Methods

3.2.1 Animal. The animals used in the study were 241 steers born in March/April 1995 that were a subset of the two projects outlined in Chapter 2. One hundred and eighty two of the steers were the second calf-drop of the Southern Crossbreeding Project, from a total of 26 sires mated to Hereford cows. There were also 59 steers born to four sires from the second drop in the first phase of the Davies Gene Mapping Project (Chapter 2). Animal management and feeding from birth to 600 days of age (including feedlot management prior to slaughter) have also been described in Chapter 2. Prior to slaughtering, empty weight (24h off feed) of

all the steers were taken at the lairage. The description and type of body measurements taken, apart from live-weight, were outlined previously (Chapter 2).

3.2.2 Slaughter and bone-out procedure. Calves were slaughtered when the majority of steer carcasses would be >300kg (average 25 months) at Metro Meat International, Murray Bridge, South Australia between 28 April and 30 May 1997. In general, the slaughtering started with the heaviest steers and progressing to the lightest. All the carcasses were electrically stimulated immediately after slaughter using a low voltage rectal-nostril stimulator. Ear tag numbers were matched with corresponding abattoir kill numbers and laminated labels were attached to the carcasses with metal skewers to aid identification in the boning room. Excess fat on the topside and brisket of each carcass was not removed in order to maximise the information gained from the carcass.

The carcasses were boned out on the same premises, one to three days after slaughter. Prior to boning out, the left sides of each carcass were quartered between the 10^{th} and 11^{th} rib and they were assessed by an Ausmeat accredited assessor for hot standard carcass weight based on a standard trim (AUSMEAT® 1995), fat depth over the rump at the P8 position, fat colour at the site of quartering (generally 10-11^{th} rib), and various other traits on the slaughter floor (Table 3.1). Fat on the topside and brisket was not removed in order to increase the accuracy of information gained from the carcass measurements. The processing was carried out by a group of one boner, one slicer and one packer supplied by the abattoir. Individual animal weights for all the primal cuts before and after slicing were recorded. The trimmings from the primal cuts (including subcutaneous fat, inter-muscular or seam fat and manufacturing meat trims) were weighed including also each of the bones. The primal cuts were trimmed to 6mm of fat.

Table 3.1. Additional phenotypic measurements

Carcass traits	First measurement
Hot carcass length, weight, P8 fat depth, bruising	Fresh
Dentition Butt shape, pelvic area Marbling, eye muscle area Fat cover, fat depth (site of quartering) Fat and meat colour Meat texture	Chiller
Meat fat content, tenderness Fatty acid composition: meat, fat B-carotene concentration: meat, fat	Chiller Samples

3.2.3 Statistical analysis. The traits analysed included carcass, total meat, fat and bone weights and percentages (Table 3.2). Equations were formulated on a whole-carcass basis. The REG procedure in SAS (1992) was used to determine the relative importance of live-animal variables in a model designed to estimate the seven carcass traits. The stepwise method was used and the inclusion and exclusion significance were set at $P<0.01$. The variables included by the stepwise regression method were then used to develop an equation for each of the traits. The amount of variation due to breed differences before and after inclusion of model variables were then determined using the GLM procedure (SAS, 1992).

3.3 Results

On the average, the saleable meat yield as a percentage of cold carcass weight was 68.2% with fat trim and bone values being 13.4% and 18.5%, respectively. The meat, fat trim and bone weight as a percentage of the empty weight were 40.5, 7.9 and 11.0% respectively (calculated from values in Table 3.2). The average dressing percentage was 59.4%, so that the ratio of meat: fat: bone was 5:1:1.4.

Table 3.2. Summary of live-measurements and carcass traits

Item	Mean	CV (%)	Minimum Actual value	Maximum Actual value	Minimum Predicted value	Maximum Predicted value
Wt (kg)	555.3	13	391.0	736.0		
Ht (cm)	134.5	4	119.0	156.0		
Lh (cm)	146.8	4	102.0	159.0		
Gh (cm)	202.4	5	169.0	221.0		
Hip (cm)	48.5	6	38.0	63.0		
Stifle (cm)	44.9	10	33.0	55.0		
Fd (mm)	11.9	32	1.0	22.0		
Carcass (kg)	329.8	14	203.2	436.0	208.0	417.0
Meat (kg)	224.8	16	133.2	325.2	132.9	290.3
(%)	68.0	5	59.9	77.1	63.6	76.4
Bone (kg)	61.0	12	41.8	78.0	43.3	75.4
(%)	18.6	17	14.8	26.1	13.5	20.4
Fat (kg)	44.1	26	14.8	77.9	15.0	74.2
(%)	13.4	12	5.7	21.7	10.4	24.8

Live-weight was the most accurate predictor of carcass quantity components: meat (R^2=0.70) and bone (R^2=0.62) weight (Table 3.4). Of the live measurements apart from live-weight, stifle (R^2=0.13) was next most accurate in estimating meat weight and the correlation between these two traits was 0.80 (Table 3.3). Variables like height, length, girth, stifle, hip and measure of muscularity (defined as stifle/hip x 100, Chapter 2), which are directly related to both size and shape, displayed moderately to high positive correlations with quantity carcass components (0.24 – 0.94). For the percentage carcass components, the highest correlation (0.64) was found between muscularity and meat percent (Table 3.3). A negative correlation (-0.26) was obtained between meat percent and P8 fat depth and a positive correlation (0.53) existed between the latter and percent carcass fat (Table 3.3). All of these correlations obtained were significant (P<0.001). Correlations between meat percent and height, length or girth measurement were not significant (Table 3.3).

Table 3.3. Raw correlations of body measurements with kilogram and percent carcass traits

Trait	Carcass	Meat		Bone		Fat	
	kg	kg	%	kg	%	kg	%
Wt (kg)	0.94***	0.87***	0.21***	0.79***	-0.45***	0.56***	0.05
Ht (cm)	0.75***	0.75***	0.39***	0.80***	-0.22***	0.15*	-0.30***
Lh (cm)	0.51***	0.46***	0.09	0.56***	-0.03	0.21***	-0.08
Gh (cm)	0.85***	0.75***	0.08	0.78***	-0.32***	0.59***	0.12
Mus. (%)	0.48***	0.58***	0.64***	0.27***	-0.39***	-0.16**	-0.47***
Fd (mm)	0.36***	0.24***	-0.26***	0.19***	-0.35***	0.68***	0.53***
Stifle (cm)	0.76***	0.80***	0.55***	0.59***	-0.42***	0.10	-0.36***
Hip (cm)	0.49***	0.39***	-0.16*	0.54***	-0.07	0.47***	0.23***

*P<0.05, **P<0.01, ***P<0.001

A minimum of three and a maximum of six live measurement variables were significant (P<0.01) for the prediction of the carcass traits in the stepwise procedure (Table 3.4). Carcass weight was predicted at the 1% level of significance by using three live measurement variables. These variables (live-weight, stifle width and height) accounted for 93% of variation in the prediction equation (Table 3.4). Live-weight (R^2=0.88) was the best contributor variable but the addition of the other two variables (stifle width and height) increased the R^2 value and hence decreased the residual standard deviation. The plots of actual against predicted values (Figure 3.1) indicated an even distribution across the mean line.

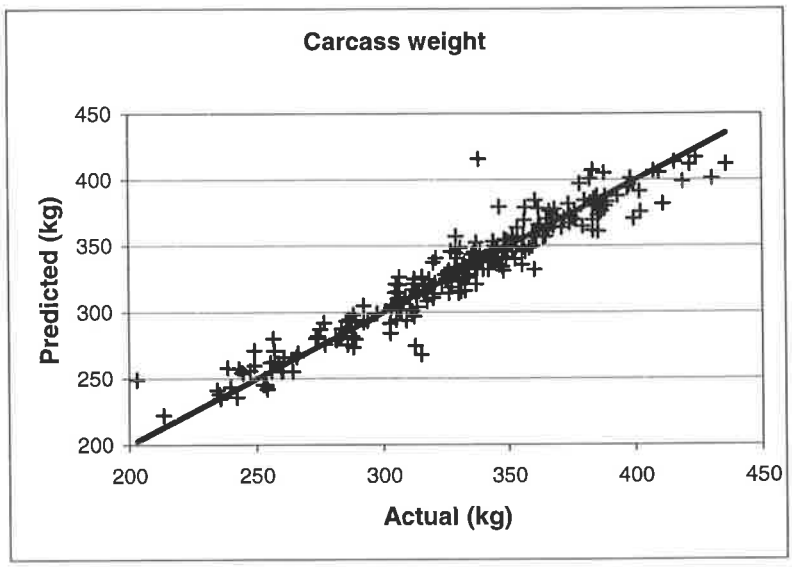


Figure 3.1. Plot of actual against predicted carcass weight

A large (87%) variation in meat weight was accounted for by the same variables in carcass weight with two additional variables (hip width and P8 fat depth). However, the inclusion of hip width alone without P8 fat depth does not significantly decrease the value (R^2=86%) for the meat weight model.

The model with live traits accounted for 74% of variation in bone weight and 65% of variation in fat weight (Table 3.4). The major variable fitted to each trait differed. Live-weight explained 62% of the variation and was the best in order of predictive significance for bone weight whereas P8 fat depth (45%) was the best for fat weight. However, adding other important variables to each of the model accounted for an additional 19 and 23% of variation in predicting bone and fat weights, respectively. Live measurements accounted for 56, 56 and 39% prediction for differences in meat, fat and bone percent of the carcass yield. The single measurement that accounted for the highest prediction was live-weight (18%) for bone, stifle (31%) for meat and P8 fat depth (27%) for fat percent. Weight was insignificant for the prediction of meat percent (Table 3.4).

Table 3.4. Regression equations using live-measurements to predict carcass traits

Dep. Var.	Const.	Wt kg	Ht cm	Lh cm	Gh cm	Hip cm	Stifle cm	Fd mm	R^2 %	Res. SD
Carc. Kg	-183.23	.48 (88)	1.01 (1)				2.45 (5)		93	11.8
Meat kg	-178.81	.31 (70)	1.23 (2)			-1.38 (1)	3.15 (13)	-.85 (1)	87	13.2
***kg**	-194.22	.28 (70)	1.42 (2)			-1.49 (1)	3.20 (13)		86	13.4
%	53.24		.12 (3)			-.37 (6)	.44 (31)	-.30 (17)	56	2.3
***%**	61.89		.20 (6)		-.14 (4)	-.33 (11)	.51 (30)		52	2.3
Bone kg	- 82.24	.03 (62)	.25 (4)	.17 (2)	.28 (3)	.32 (1)		-.35 (3)	74	3.7
***kg**	-83.37	.03 (62)	.32 (4)	.21 (2)	.21 (3)	.29 (1)			72	3.9
%	8.31	-.02 (18)		.05 (5)	.06 (3)	.12 (4)	-.09 (3)	-.13 (4)	39	1.2
***%**	13.28	-.01 (20)		.07 (5)		.12 (4)	-.07 (2)		31	1.3
Fat kg	33.24	.10 (8)	-.41 (2)			.66 (7)	-.89 (2)	1.39 (45)	65	6.9
***kg**	-1.70	.10 (4)	-.70 (6)		.49 (28)	.68 (2)	-1.09 (13)		52	8.0
%	30.99	.02 (2)	-.17 (2)			.20 (3)	-.37 (23)	.39 (27)	56	2.1
***%**	11.66		-.21 (7)		.18 (16)	.25 (3)	-.40 (15)		42	2.4

() Percentage contribution of each measurement to each prediction equation
***Prediction values excluding P8 fat depth**

Prediction equations were also calculated for all the seven traits when excluding P8 fat depth (Table 3.4). Basically, carcass (R^2=0.93) and meat weight (R^2=0.86) were predicted with the same level of accuracy but the R^2 values were lower for fat and bone traits. In general, the range of values for the predicted carcass traits indicated a slight over- and under-estimation for the smaller and larger animal respectively (Figure 3.2).

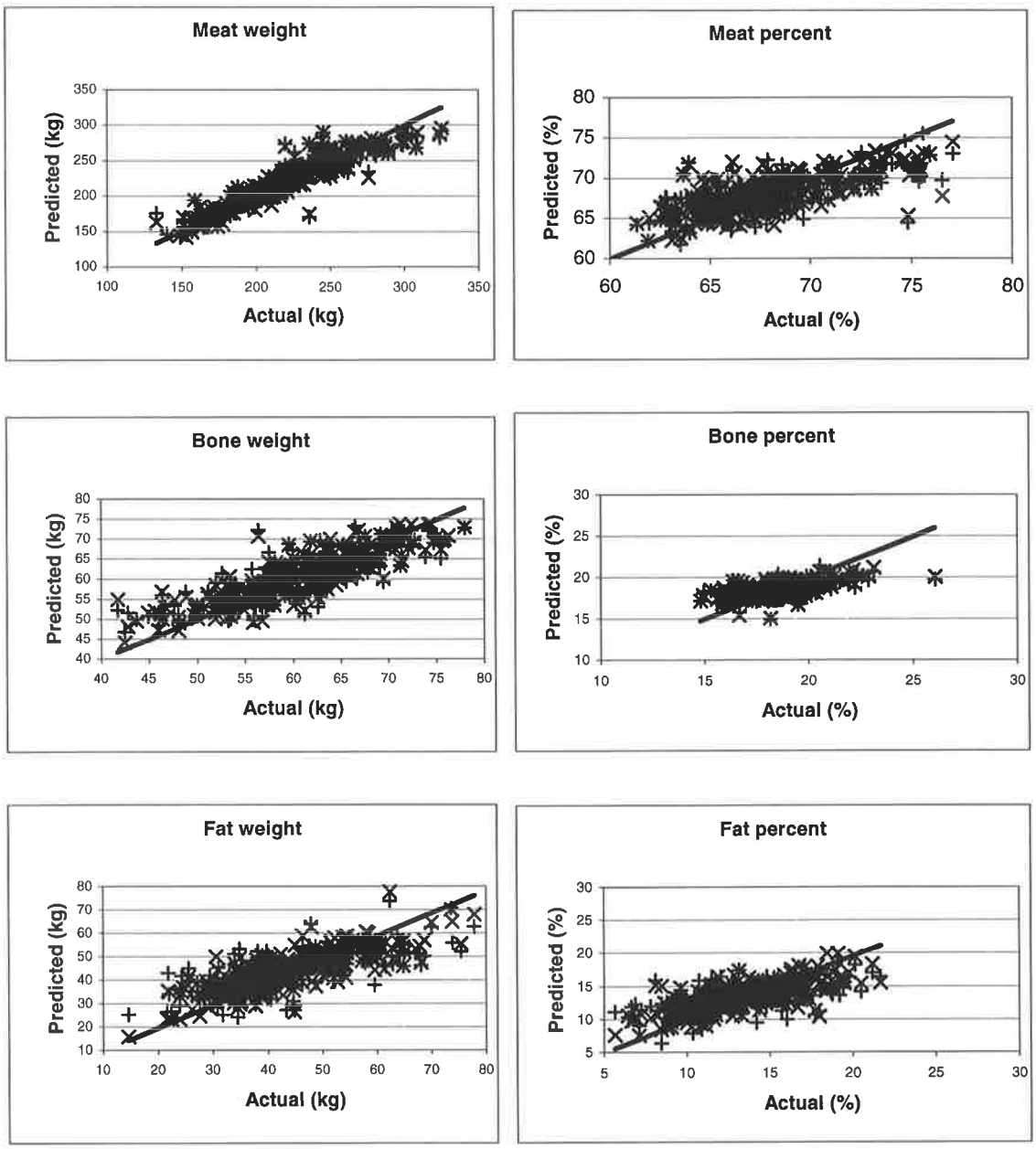


Figure 3.2. Plot of actual against predicted carcass kilogram and percentage traits [with (x) and without (+) P8 fat depth in model]

Breed differences were highly significant (P<0.01) for all seven traits. However, when breed was fitted after the live measurement traits (Table 3.4), it was no longer significant for carcass weight, but was for the component traits (Table 3.5).

Table 3.5. Modelling breed differences in carcass traits

Trait	BBreed R^2 %	Model R^2 %	ABreed R^2 %	Test of significance
Carcass kg	46	93	2	Ns
Meat kg	59	87	7	***
***kg**	59	86	9	***
%	68	56	23	***
***%**	68	52	27	***
Bone kg	52	74	14	***
***kg**	52	72	16	***
%	38	39	29	***
***%**	38	31	31	***
Fat kg	30	65	11	***
***kg**	30	52	20	***
%	54	72	18	***
***%**	54	66	28	***

Bbreed= Breed alone in the model, Abreed= Breed after model
P> 0.05= ns, P< 0.001= *

3.4 Discussion

Use of practical methods of estimation of carcass components would assist development of breeding objectives and meat marketing. Estimation of carcass components (meat, fat and bone) by dissection in commercial boning rooms is difficult, expensive and becoming almost impossible as regulations related to export licenses become tightened. The results presented here show that carcass weight and meat weight can be predicted accurately from measurements taken on live animals, thus avoiding the high cost and difficulties of dissection.

The R^2 values of 93% (Table 3.3) for predicting carcass weight and 86% for meat weight using weight, height, stifle and hip measurement indicated a reasonable prediction based on these traits with or without P8 fat depth. There were indications herein that the body dimensional traits, as measured in this study, are directly related to size and weight. The good relationship between stifle (greater than other live measurements apart from live-weight) and meat weight explained the higher ranking compared to other studies in percentage contribution to the prediction equation. For the meat percent, the R^2 value of a 56% in this study was in the range of 60% and 51% obtained by Wallace *et al.* (1977) for predicting percentage primal and retail yield, respectively, using ultrasound rib fat measurement between 5^{th} and 6^{th} ribs but higher compared to that reported by Herring *et al.* (1994) for the prediction of various retail cuts from visual score and ultrasound live animal measurements (24 – 48%). Perry *et al.* (1993a;b) indicated R^2 values of 46% and 62% for saleable meat yield of commercial stock based on live-weight, P8 fat depth and muscle score. Live animal measurements by real time ultrasound scanning alone was reported to account for 56% of observed variation in retail beef yield (Wolcott et al., 2001). This study has demonstrated an alternative estimation of percent carcass meat based on some objective live-body measurements plus P8 fat depth with a similar level of accuracy.

The negative correlation between muscularity as defined here and fat depth suggests that the measure used did not over estimate fatter animal when assessing shape due to muscle and intermuscular fat. This measure of muscle therefore compared well with the visual muscle score by Perry et al. (1993a;b), which could be subjective and difficult to standardise. Tatum et al. (1986a) also found that a visually assessed score for muscle thickness independent of fatness and in relation to skeletal size, for live animals, did not appear to be influenced by variation in subcutaneous fatness.

As expected and found by Perry *et al.* (1993a), an animal with higher P8 fat depth had lower meat percentage. This is also reflected by the negative correlation (-0.26) between these two traits. Consequently, the compromise for the producers will then be to use antagonizing relationship of P8 fat depth and McKiernans' (1990) muscularity measurement to predict saleable meat yield in selecting live animals for targeted markets. Moreover, this result has supported an earlier study (Perry *et al.* 1993b) that some carcass traits may be predicted without P8 fat depth (which may require trained, skilled assessor) measurements while the precision of prediction for others significantly decreased without this information. For the carcass quantity of meat and bone, P8 fat depth added very little accuracy to their estimation but was very important for fat traits. There were no systematic departures from expectation when the plots of actual against predicted values (Figure 3.1) were examined for the carcass traits. Thus, even at extremely low and high values, the predictions were reasonable.

In conclusion, carcass weight may be reasonably predicted based on live animal measurement regardless of the breed type. However, prediction of carcass composition would still be aided by adjustment for breed effects. That said, effective and reliable prediction of carcass yields from the low-cost objective rather than high-cost objective (e.g. ultrasound) and/or subjective (muscle score) live animal measurements would reduce production costs and enjoy wider application by producers.

Chapter 4

Breed effect and Genetic parameters on growth and development

4.1 Introduction

Carcass value assessment through growth and body composition of life animal could rapidly increase the rate of genetic gains of meat quality traits in breeding herds. For a long time, cattle breeders have evaluated growth performance characteristics in diverse breed resources using weight and gain in weight at different ages (Jenkins et al., 1991; Meyer et al., 1993; Plasse et al., 2002). However, recent feedlot trials with crossbred cattle (D.L. Rutley unpublished) have shown that in addition to weight, height, fat depth and visual muscle scores (score developed by McKiernan, 1990) are good descriptors of feedlot performance for most economically important traits (average daily gain, carcass weight, fat depth and saleable beef yield). Gilbert et al. (1993) asserted that using body dimensions or linear measurements could also serve either to supplement body weight as a measure of productivity or as predictors of less visible characteristics. In dairy cattle, Hoffman (1997) included wither height with body weight to develop growth guidelines when evaluating skeletal growth in replacement heifers.

Accurate prediction of carcass quality based on body composition measurements would enhance early selection of animals by beef producers as well as seed-stock breeders. Moreover, the sire breed evaluation schemes under this type of system could add substantial benefit or economic value to beef cattle production enterprises. However, for early prediction to be effective, reliable estimates of genetic parameters are needed for associated traits measured at both young and older ages and their relationships determined. In addition, knowledge of the nature of the relationship between estimated breeding values for one trait measured early (e.g., weaning) and another trait measured at a later age (e.g., yearling) would facilitate the decision making process. As stated earlier, evaluation of growth based on weight and weight gains abound in the scientific literature. However, there are limited references describing genetic factors affecting objective live developmental traits that define body composition. The aims of this study were to: 1. Relate specific body measurement traits

with animal growth and development. 2. Estimate the genetic parameters for growth and muscular development. 3. Look at the effects of breed and age differences on the growth and development of progeny from seven sire breeds crossed with Hereford dams in different seasons.

4.2 Materials and Methods

The animals used for this study were the total 1215 calves born over four-year periods (1994-1997) in the Southern Crossbreeding Project (SXB). A full description of the design and management of these animals (including the live-animal measurements used) have been reported (Chapter 2).

Data were analysed using ASREML (Gilmour et al., 2000). All traits were analysed with a univariate animal model containing fixed effects of cohort (8 categories of year and sex: 1994-drop heifers to 1997-drop steers), management group (total of 30 levels describing pre- and post-weaning groups, 4-6 per cohort), birth month (March or April), and sire breed (7 levels). Birth month was used to test age effects rather than a linear covariate of birth-day to avoid bias (high leverage) resulting from small numbers of very early or very late calves. Factors with more levels were tested but birth month was the most appropriate.

Two-way interactions were generally not significant and were not included. The significance of sire breed was effectively tested against sire as outlined by Gilmour et al. (2000, pg. 137). Bi-variate animal models with the same fixed effects were used for estimation of phenotypic, genetic and environmental correlations. Significance was defined as $P<0.05$. Additionally, cluster analysis using Proc cluster (SAS, 1992) of 22 x 22 matrix genetic correlations was carried out on the main traits to determine the number of group of traits independently controlled by the same genetic loci.

4.3 Results

Characteristics of the data structure are summarised in Table 4.1. There was considerable variation in weights, body dimensions and composition due to age and seasonality differences, which was confounded within age. Also, as the coefficient of variation (CV) demonstrated, variability in the traits at weaning and post-weaning differed between ages with fat traits having the highest variation, followed by weight, muscle and skeletal dimensional (height, length and girth) traits. For example, fat depth at weaning was 5.1 mm with a corresponding 51% CV compared to weight (276.1kg and 15%), muscle (87% and 8%) and even skeletal dimension, which were considerably less variable (e.g. Height as a value of 1126cm and 4%). The apparent large variability in fat depth was probably a function of the threshold nature of the trait with the mean (5.1) being close to the threshold (1mm).

Table 4.1. Summary statistics of traits at different ages

Traits	Mean	CV (%)	Minimum	Maximum
Birth:				
Wt (kg)	37.5	17	18.0	61.0
Ht (mm)	748.6	6	530.0	890.0
Lh (mm)	611.3	9	410.0	780.0
Gh (mm)	730.5	7	540.0	950.0
Weaning:				
Age (days)	273.9	9	200.0	331.0
Wt (kg)	276.1	15	148.0	423.0
Ht (mm)	1125.5	4	985.0	1260.0
Lh (mm)	1202.5	5	1000.0	1410.0
Gh (mm)	1537.3	5	1220.0	1810.0
Mus. (%)	87.0	8	67.5	108.6
Fd (mm)	5.1	51	0.0	19.0
400-day:				
Age (days)	445.1	14	370.0	575.0
Wt (kg)	349.3	12	219.0	496.0
Ht (mm)	1222.4	7	1050.0	1500.0
Lh (mm)	1304.9	4	1120.0	1500.0
Gh (mm)	1677.4	5	1370.0	1920.0
Mus. (%)	85.1	8	64.3	107.7
Fd (mm)	5.2	59	0.0	25.0
600-day:				
Age (days)	619.0	7	544.0	691.0
Wt (kg)	498.0	16	304.0	740.0
Ht (mm)	1384.8	5	1200.0	1580.0
Lh (mm)	1422.2	5	1240.0	1650.0
Gh (mm)	1909.6	4	1630.0	2110.0
Mus. (%)	87.9	10	68.2	113.9
Fd (mm)	9.5	57	0.0	32.0

4.3.1 Non-genetic effects

There were large cohort differences in birth traits between different years. In general, male (steer) calves were 8% heavier, 3% taller and 2% bigger in size (length and girth) than the female (heifer) calves (Table 4.2). Management group effects were generally of low magnitude or non- significant. However, birth month also had an impact on birth traits with those calves born in March being significantly smaller in weight (5%), height (2%), length (2%) and girth (2%) compared to those born in April.

Cohort differences (Table 4.2) were large for most of the weaning and post-weaning traits due to variation in pasture availability induced by rainfall pattern in different year and season (e.g. 1995-drop calves at weaning were 11% heavier, 2% taller, 4% longer and 1% bigger in girth than the 1994-drop calves). There were also large cohort effects on muscularity and P8 fat depth at weaning with 1997-drop calves on average more muscular (7%) and fatter (40%) than 1996-drop calves. The differences between birth months at weaning were more pronounced for weight (4%), height (1%), length (1%), girth (1%) and fat depth (8%) with insignificant differences for muscularity. However, in contrast to what was observed at birth, March born calves were bigger (weight and skeletal dimensions) and fatter (P8 fat depth) compared to calves born in April. This was because March born calves were older than April born calves when measurements were taken.

Table 4.2. Least square means on cohorts and birth months for pre- and post-weaning traits

Traits	Cohorts								Birth Month	
	Heifers				Steers				March	April
	1994	1995	1996	1997	1994	1995	1996	1997		
Birth:										
Wt (kg)	30.7±0.9	36.2±1.1	37.6±0.8	38.8±0.7	34.9±0.8	39.7±0.7	38.2±0.7	40.7±0.8	36.0±0.4	38.2±0.4
Ht (mm)	706.6±7.6	731.5±9.6	754.2±6.8	749.8±6.0	747.7±6.4	763.2±5.9	766.4±5.7	759.9±6.7	740.7±3.0	754.1±3.1
Lh (mm)	598.5±8.0	559.8±10.1	612.4±7.1	652.7±6.0	615.1±6.6	579.9±6.1	625.4±5.8	650.6±6.8	606.5±3.1	617.0±3.1
Gh (mm)	693.9±7.8	710.7±9.9	729.1±7.1	741.6±6.0	723.2±6.6	735.7±6.0	736.5±5.7	748.7±6.7	719.5±3.0	735.4±3.1
Weaning:										
Wt (kg)	257.2±4.6	286.2±5.8	248.2±4.1	285.3±3.5	267.9±3.8	296.3±3.5	263.9±3.4	300.6±3.9	280.8±1.8	270.6±1.8
Ht (mm)	1094.4±6.4	1109.8±8.1	1097.7±7.8	1124.7±5.1	1125.4±5.6	1157.8±5.0	1110.5±5.3	1154.8±5.5	1126.0±2.4	1117.8±2.4
Lh (mm)	1174.2±8.8	1219.0±11.2	1177.7±7.9	1227.7±6.9	1173.6±7.5	1232.9±6.9	1189.5±6.6	1251.0±7.5	1211.9±3.5	1199.5±3.6
Gh (mm)	1517.6±10.2	1539.0±13.1	1471.0±9.2	1596.9±7.8	1526.3±8.6	1543.3±7.8	1498.9±7.4	1619.3±8.6	1550.6±4.0	1527.5±4.0
Mus (%)	86.6±0.5	86.6±0.5	84.4±0.7	90.3±0.6	86.6±0.5	86.6±0.5	86.6±0.5	93.3±0.7	87.9±0.4	87.4±0.4
Fd (mm)	4.5±0.4	6.5±0.5	5.0±0.3	7.4±0.3	3.8±0.3	4.4±0.3	4.0±0.3	6.0±0.3	5.4±0.1	5.0±0.2
400-day:										
Wt (kg)	350.3±5.2	336.1±6.5	351.3±4.7	376.3±4.2	364.6±4.4	370.4±4.1	300.9±2.8	338.3±4.5	352.9±2.1	344.1±2.1
Ht (mm)	1189.6±6.6	1157.5±8.1	1189.6±6.6	1176.6±5.4	1219.8±5.6	1207.9±5.2	1361.0±5.0	1189.6±6.6	1213.7±3.2	1209.1±3.2
Lh (mm)	1303.8±8.2	1256.0±10.5	1294.1±7.5	1334.9±6.4	1344.7±6.9	1308.9±6.4	1293.4±6.1	1303.8±8.2	1311.8±3.4	1298.0±3.4
Gh (mm)	1689.0±9.8	1583.7±12.3	1724.5±8.8	1736.0±7.7	1699.9±8.2	1653.6±7.5	1646.1±7.3	1689.0±9.8	1686.9±4.1	1668.5±4.1
Mus (%)	87.0±0.7	83.9±1.2	85.6±0.8	87.9±0.7	87.0±0.7	87.0±0.7	81.9±0.7	87.0±0.7	85.7±0.4	86.1±0.4
Fd (mm)	5.9±0.4	3.5±0.5	7.1±0.3	8.3±0.3	4.1±0.3	4.7±0.3	5.9±0.4	2.2±0.3	5.3±0.2	5.1±0.2
600-day:										
Wt (kg)	442.7±6.9	442.7±6.9	442.7±6.9	442.7±6.9	510.2±5.8	462.2±5.4	580.7±5.1	442.7±6.9	471.0±4.7	470.7±4.7
Ht (mm)	1319.7±5.1	1319.7±5.1	1319.7±5.1	1319.7±5.1	1319.7±5.1	1319.7±5.1	1439.5±4.5	1319.7±5.1	1332.3±5.2	1337.1±4.6
Lh (mm)	1429.7±8.4	1429.7±8.4	1429.7±8.4	1429.7±8.4	1429.7±8.4	1429.7±8.4	1407.3±7.1	1429.7±8.4	1420.0±8.7	1433.9±7.5
Gh (mm)	1931.7±9.1	1931.7±9.1	1931.7±9.1	1931.7±9.1	1931.7±9.1	1931.7±9.1	1863.2±7.8	1931.7±9.1	1918.9±9.5	1927.4±8.2
Mus (cm)	86.1±0.8	86.1±0.8	86.1±0.8	86.1±0.8	86.1±0.7	86.1±0.7	90.7±0.7	86.1±0.8	86.8±0.7	86.6±0.8
Fd (cm)	11.3±0.6	11.3±0.6	11.3±0.6	11.3±0.6	10.1±0.5	3.5±0.5	13.2±0.4	10.0±0.5	10.3±0.4	10.2±0.3

The patterns observed at weaning were similar for the 400-day traits except for the reduction in magnitude of the differences (Table 4.2). However, at 600 days of age, cohort effects were mainly significant between sexes for weight and fat depth with steer calves on average being heavier (499kg) but leaner (9mm) compared to the smaller (443kg) but fatter heifer (11mm) calves (Table 4.2). Also, feedlot finished steers on average were less muscular (87%) compared to the pasture finished 1997-drop steers (93%). The birth month differences were mostly insignificant for all traits at 600 days of age (Table 4.2).

4.3.2 Breed effect and genetic parameters

a). Breed effect

At birth, sire breed effects were important (Table 4.3) for all traits. Breed ranking as a percentage of purebred Hereford (the only purebred) indicated three larger breeds (South Devon, Limousin, and Belgian Blue) averaged 3% heavier and 1% taller than Hereford breed (Figure 4.1). Angus (by 8% and 2%), Wagyu (by 13% and 2%) and Jersey (by 18% and 4%) were lighter and shorter than the purebred Hereford. However, the larger breeds were on average slightly lower in length but still slightly higher in girth compared to the purebred Hereford. Among the lighter breeds, Angus ranked higher for length and girth at birth after the purebred Hereford, followed by the Wagyu and Jersey breeds, respectively (Figure 4.1).

Table 4.3. Least square means on sire breed for pre- and post-weaning traits

Traits	Sire breed						
	Jersey	Wagyu	Angus	Hereford	South Devon	Limousin	Belgian blue
Birth:							
Wt (kg)	31.8±0.6	34.1±0.5	35.8±0.6	39.3±0.6	39.7±0.5	39.2±0.5	39.7±0.5
Ht (mm)	724.8±5.0	734.8±4.5	737.6±5.2	751.0±5.7	766.2±4.8	765.0±4.7	752.6±4.7
Lh (mm)	585.9±4.4	595.1±4.1	609.3±4.5	625.0±5.0	630.0±4.4	615.5±4.3	621.8±4.3
Gh (mm)	696.2±4.6	707.9±4.2	718.9±4.7	740.4±5.2	744.3±4.5	735.8±4.3	748.5±4.4
Weaning:							
Wt (kg)	252.5±2.8	253.9±2.5	283.0±2.8	282.1±3.1	288.6±2.7	281.4±2.6	288.5±2.6
Ht (mm)	1105.5±4.4	1106.0±3.9	1120.6±4.6	1116.1±5.0	1134.6±4.2	1141.4±4.0	1129.1±4.1
Lh (mm)	1198.2±5.6	1183.6±5.1	1210.9±5.8	1214.3±6.4	1217.2±5.4	1204.4±5.2	1211.2±5.3
Gh (mm)	1506.2±5.7	1510.9±5.3	1555.9±5.8	1543.4±6.4	1549.3±5.7	1545.1±5.5	1562.5±5.5
Mus (%)	83.4±0.7	86.8±0.6	88.2±0.8	86.4±0.9	88.9±0.7	90.2±0.7	89.7±0.7
Fd (mm)	5.4±0.2	6.0±0.2	6.5±0.3	5.7±0.3	4.5±0.2	4.6±0.2	3.5±0.2
400-day:							
Wt (kg)	320.5±3.6	319.0±3.2	361.5±3.7	353.0±4.0	364.3±3.4	356.0±3.3	365.4±3.3
Ht (mm)	1194.1±5.4	1191.6±5.0	1209.2±5.5	1204.3±6.1	1227.1±5.3	1236.2±5.0	1217.4±5.0
Lh (mm)	1293.0±5.3	1284.8±5.0	1310.7±5.4	1312.3±6.0	1320.1±5.3	1304.1±5.0	1309.7±5.0
Gh (mm)	1639.4±6.5	1643.1±6.2	1708.8±6.8	1679.4±7.5	1691.7±6.5	1680.6±6.2	1700.9±6.2
Mus (%)	78.8±0.8	83.7±0.7	86.2±0.8	84.8±0.9	85.7±0.8	90.2±0.7	91.9±0.8
Fd (mm)	5.5±0.3	5.7±0.3	7.0±0.3	5.8±0.3	4.8±0.3	4.3±0.3	3.2±0.3
600-day:							
Wt (kg)	435.1±6.4	420.5±6.3	486.1±6.8	469.0±7.4	503.2±6.8	485.9±6.5	496.4±6.5
Ht (mm)	1323.5±7.7	1314.8±7.3	1325.6±8.4	1328.1±8.7	1353.1±7.7	1359.5±8.0	1338.0±7.6
Lh (mm)	1406.5±11.8	1391.8±11.2	1433.1±12.1	1431.1±12.9	1448.4±11.7	1448.7±12.1	1428.9±11.5
Gh (mm)	1891.2±13.2	1869.3±12.6	1952.8±14.0	1914.9±14.7	1938.9±13.2	1936.6±13.7	1958.1±13.1
Mus (%)	76.3±1.2	83.1±1.2	87.0±1.1	83.1±1.4	87.8±1.3	94.9±1.2	94.8±1.2
Fd (mm)	10.1±0.5	10.9±0.5	13.1±0.5	11.3±0.6	9.1±0.5	9.6±0.5	7.8±0.5

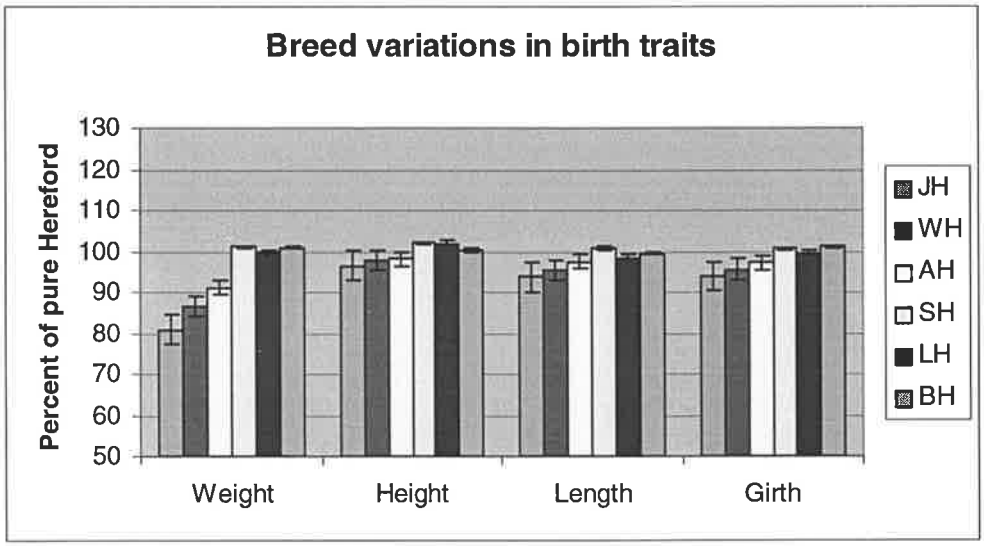


Figure 4.1. Breed variations in birth traits as a percentage of purebred Hereford.

At weaning, the sire breed means for weight and height grouped four breeds has heavy breeds (apart from purebred Hereford) rather than three breeds observed at birth (Table 4.3). Angus with the three larger breeds (South Devon, Limousin, and Belgian Blue) averaged 2% heavier and 1% taller, but almost similar in length, compared to purebred Hereford with the exception of Limousin (1% shorter than purebred Hereford) (Figure 4.2). The four heavy breeds on average were 1% bigger in girth than Hereford at weaning. In addition, the larger breeds (Angus, South Devon, Limousin and Belgian Blue) were 4% more muscular on average than the Hereford. However, the Wagyu (by 9% and 2%) and Jersey (by 10% and 1%) were lighter (weight) and smaller (height, length, and girth) than the purebred Hereford. Muscularity measurements ranked Wagyu similar to Hereford at weaning but Jersey was 5% lower than Hereford at the same age. Among the 7 sire breeds, Angus had by far the highest P8 fat depth at weaning (12% more than Hereford and Wagyu), with Jersey being 5% lower than Hereford, then South Devon and Limousin (19% lower) and Belgian Blue (39% lower).

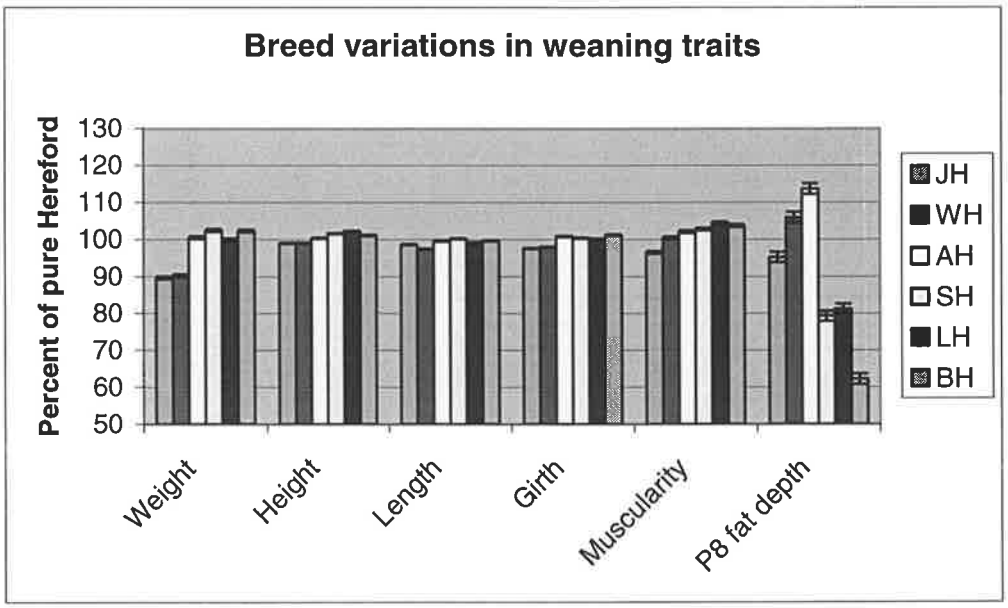


Figure 4.2. Breed variations in weaning traits as a percentage of purebred Hereford.

The significant breed differences at weaning in weight, body dimensions (height, length and girth), muscularity and P8 fat depth were still observed at 400 and 600 days postpartum (Table 4.3). At 400 days of age, the four heavy breeds Angus, South Devon, Limousin and Belgian Blue ranked above Hereford for weight, height, and girth but still not on length. Purebred Hereford was longer than Limousin (1312mm vs 1304mm), close with Angus and Belgian Blue (1312mm vs 1310cm) but shorter (1312mm vs 1320mm) than South Devon at 400 days of age (Figure 4.3).

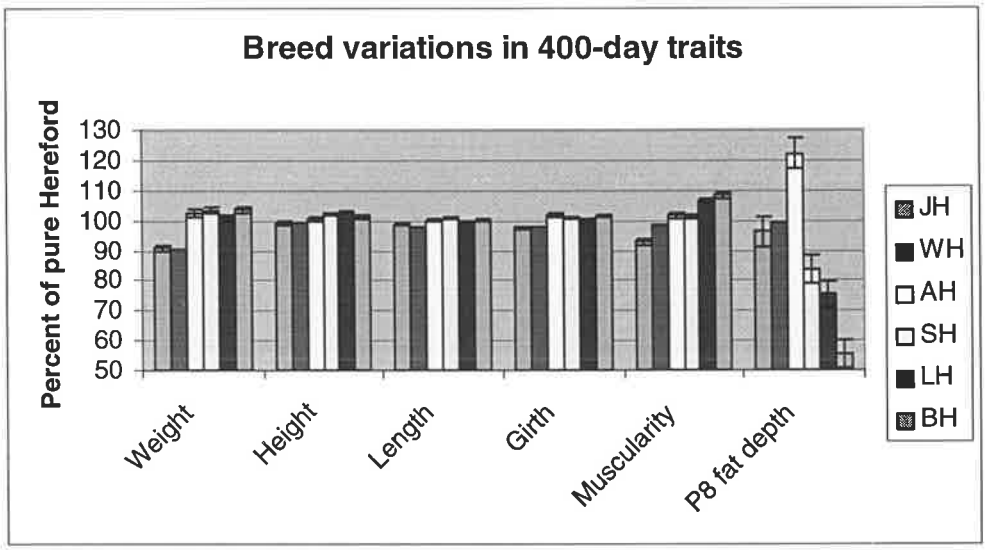


Figure 4.3. Breed variations in 400-day traits as a percentage of purebred Hereford.

Muscularity of the Wagyu (lighter breed) at 400 days was close to the Hereford (Figure 4.3). However, both breeds (Wagyu and Hereford) on average were 7% more muscular than Jersey but 2% less muscular than Angus and South Devon and 6% less muscular than the two heaviest breeds (Limousin and Belgian Blue). The ranking for P8 fat depth at 400 days of age was similar to that at weaning except that the difference between the groups were more pronounced at the early age.

At 600 days, the trends were similar for the breed ranking at 400 days of age for all traits. The exception was height where Jersey (smaller breed) was close to Angus and Hereford (1324cm vs 1325cm vs 1328cm) (Table 4.3; Figure 4.4).

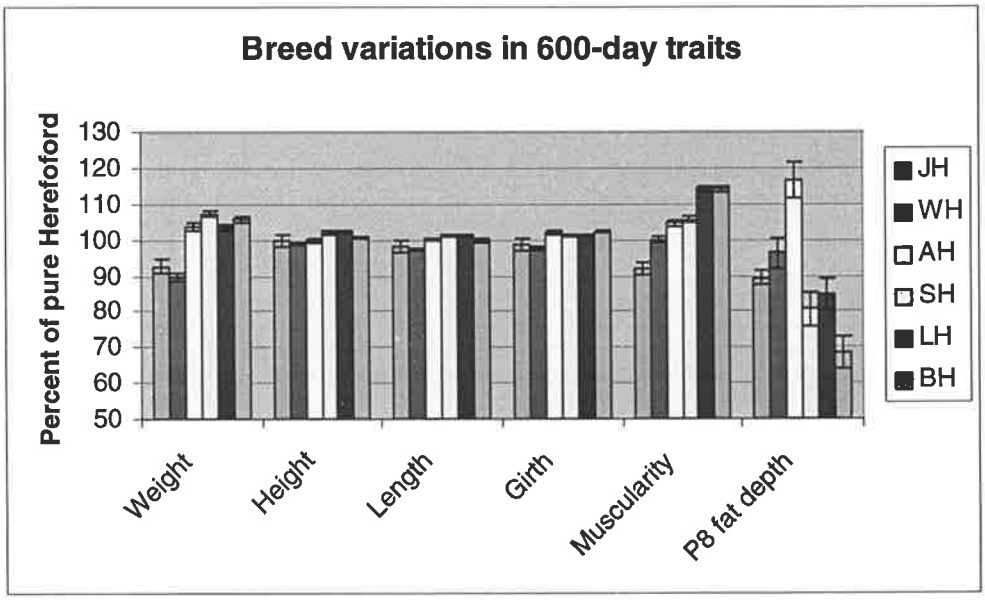


Figure 4.4. Breed variations in 600-day traits as a percentage of purebred Hereford.

b). Heritability estimates and correlations

Heritability was calculated after adjustment for environmental (cohort, management group, birth month) fixed effects and sire breed (Table 4.4) at all ages. At birth, the heritability of height was high (34%), weight was moderate (22%), while that of length (14%) and girth (19%) were low (Figure 4.5).

Table 4.4. Heritabilities [a] and genetic and phenotypic correlations among weight and body dimensions taken at pre- and post-weaning ages [b] and a measure of muscularity and fatness (shape)[c]

Traits	Wt (kg)	Ht (cm)	Lh (cm)	Gh (cm)	Mus (%)	Fd (mm)
Birth:						
Wt	**0.22±0.09**	0.53±0.01	0.34±0.02	0.50±0.01		
Ht	0.80±0.09	**0.34±0.08**	0.15±0.01	0.26±0.01		
Lh	0.81±0.12	0.42±0.09	**0.14±0.07**	0.16±0.01		
Gh	0.93±0.08	0.57±0.09	0.49±0.07	**0.19±0.07**		
Weaning						
Wt	**0.12±0.06**	0.50±0.02	0.42±0.01	0.56±0.01	0.14±0.03	0.35±0.02
Ht	0.64±0.09	**0.37±0.08**	0.25±0.01	0.21±0.01	0.03±0.20	0.11±0.02
Lh	0.65±0.08	0.44±0.07	**0.23±0.08**	0.18±0.01	0.07±0.02	0.15±0.02
Gh	0.78±0.06	0.23±0.06	0.30±0.06	**0.14±0.09**	0.11±0.02	0.26±0.01
Mus.	-0.05±0.26	0.20±0.20	0.24±0.18	0.20±0.16	**0.20±0.11**	0.17±0.04
Fd	0.09±0.16	-0.03±0.11	0.07±0.09	0.32±0.08	0.53±0.28	**0.31±0.08**
400-day:						
Wt	**0.40±0.09**	0.40±0.02	0.31±0.02	0.51±0.02	0.10±0.03	0.21±0.02
Ht	0.47±0.09	**0.53±0.10**	0.23±0.02	0.20±0.01	-0.03±0.03	0.03±0.02
Lh	0.59±0.09	0.49±0.09	**0.23±0.08**	0.14±0.01	0.03±0.02	0.10±0.02
Gh	0.62±0.08	0.26±0.07	0.38±0.07	**0.39±0.10**	0.04±0.02	0.18±0.02
Mus.	0.38±0.13	0.27±0.12	0.25±0.11	0.11±0.09	**0.44±0.11**	0.02±0.04
Fd	-0.00±0.00	-0.24±0.10	0.05±0.10	0.09±0.08	0.21±0.18	**0.41±0.09**
600-day:						
Wt	**0.33±0.12**	0.32±0.03	0.15±0.02	0.25±0.02	0.05±0.03	0.24±0.02
Ht	0.49±0.15	**0.57±0.22**	0.15±0.02	0.13±0.02	0.02±0.06	0.02±0.04
Lh	0.21±0.11	0.10±0.11	**0.27±0.19**	0.08±0.02	0.02±0.04	0.05±0.02
Gh	0.21±0.10	0.02±0.10	0.11±0.09	**0.37±0.20**	-0.02±0.03	0.24±0.02
Mus.	-0.08±0.26	0.54±0.41	-0.29±0.30	-0.38±0.27	**0.22±0.17**	-0.06±0.06
Fd	0.31±0.15	0.29±0.19	0.09±0.14	0.25±0.13	-0.18±0.41	**0.34±0.10**

[a]Heritabilities±standard errors on the diagonal, genotypic correlations±standard errors below the diagonal, and phenotypic correlations±standard errors above the diagonal.
[b] Weight, Height, Length and Girth at all ages.
[c] Muscle and Fat depth at weaning and post-weaning ages.

At weaning and subsequent ages, height was still the most highly heritable trait with ranges from 37 to 57% (Table 4.4). Heritability estimates for weight, length and girth traits were low to moderate (12 to 40%) from weaning to 600 days of age. Muscularity measurements were low to high (20 to 44%), while the measure of fatness (P8 fat depth) was moderate (31 to 41%) in inheritance between weaning and post-weaning ages of up to 600-day (Figure 4.5).

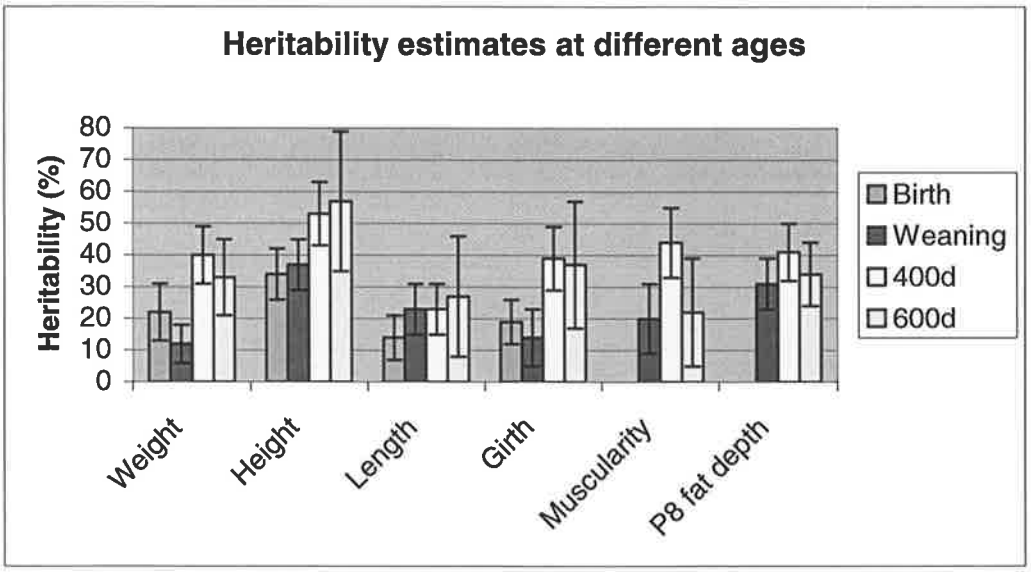


Figure 4.5. Heritability estimates for body composition traits at different ages

The genetic correlations were generally greater in absolute value consistently at every stage of growth for weight and body dimensional traits, although subject to larger standard errors at 600 days than those of the phenotypic correlations. However, there was not always a consistent pattern for measure of muscularity and fatness in relation to weight and body dimensional traits between ages. While weight seems to be genetically unrelated to muscle at weaning and 600-day of age, it had a correlation of 0.38 at 400-day of age. Also, there was a genetic correlation of 0.31 (although with high standard error) between weight and P8 fat depth but only at 600-day of age. Weight had higher phenotypic correlations with body dimensional traits, followed by P8 fat depth and muscle at every stages of growth (Tables 4.4).

Estimates of genetic correlations between birth traits (Table 4.4) were moderate to very high (0.42 to 0.93) with very low standard errors (average 0.1). However, the phenotypic correlations between birth traits were low to moderate. At weaning and ages beyond weaning, while the genetic correlation between weight and height was just moderate (on average 0.55), it was high between weight and length (on average 0.65) and between weight and girth (on average 0.70). Also, the genetic correlations between body dimensional (height, length and girth) traits and muscularity were generally low (on average 0.21) but

positive at weaning and 400 days of age (Table 4.4). However, at the same age, while the genetic correlation between height and P8 fat depth was low and negative, that between length or girth or muscularity and P8 fat depth were positive but low.

The phenotypic correlations were low but positive between weight and muscle (0.05-0.14) and very low or near zero between dimensional traits and muscle at weaning or post-weaning ages (Tables 4.4). However, there were moderate phenotypic correlations between weight and P8 fat depth (0.21-0.36) but zero to low correlations between dimensional traits and P8 fat depth at weaning and post-weaning ages.

Appendix 1 presents the result of correlations between same traits measured at different ages. Birth weight had moderate genetic (0.44-0.63) and low phenotypic correlations (0.32-0.39) with weight at older ages. However, higher genetic (0.67-0.95) and phenotypic (0.42-0.73) correlations were obtained on weight at older ages. Estimates of genetic correlations between body dimensions measured at birth and at subsequent ages were low (<0.3) and the corresponding phenotypic values were close to zero. Postweaning, height and weight were highly genetically correlated across ages (0.67-1.02), muscle and fat moderate (0.44-0.75) and length and girth lowly correlated (0.20-0.62). Evironmental correlations were generally much lower than genetic correlations (Appendix 1).

Genetic correlations between weight gains at specific ages (pre- and post- weaning) and main traits were tested (Appendix 2 - 4). Correlations between weight gains and gains in body dimensional traits were generally not estimable at all ages. Few of those estimated values were outside the parameter space (< -1.0 or 1.0), especially the correlations with gains in muscularity or fat depth. As expected, weight gains had very high correlations with the weight traits at any age compared to height, length and girth. The genetic correlation between

weight gains and muscle or fat depth were generally low and negative with high standard errors (Appendix 2 - 4).

The cluster analysis of genetic correlations between and within weight, body dimensions, muscularity and fatness traits resulted in 6 genetically related trait groups. The groups were:

1. All the birth traits (Bwt, Bht, Blh, Bgh)
2. Weaning and post-weaning weight and length (Wwt, 400-d wt, 600-d wt, Wlh, 400-d lh, 600d lh)
3. Weaning and post-weaning height (Wht, 400-d ht, 600-d ht)
4. Weaning and post-weaning girth (Wgh, 400-d gh, 600-d gh)
5. Weaning and post-weaning muscle (Wmus, 400-d mus, 600-d mus)
6. Weaning and post-weaning P8 fat depth (WP8, 400-d P8, 600-d P8)

The birth traits group alone accounted for 83% of the total variation of traits under consideration. However, inclusion of the weight, body dimensions, muscularity and P8 fat depth traits at weaning described more than 90% of the body composition.

4.4 Discussion

4.4.1 Non-genetic effects

The calves in this study were born and managed in two different properties in South Australia, meaning that calves were subjected to different pre-weaning management systems. However, the effect of calf groups on birth traits and partly on pre-weaning traits would appear to be insignificant except for unique herd management peculiarities within properties. Therefore, the interpretation of the findings for birth and weaning traits could reflect a more accurate breed differences in weight, body dimensional and compositional traits. In each of the four years of the project, post-weaning management differed for heifers and steers. This

brings difficulty in making good sex comparison at 400 and 600 days. Incidentally, there were fewer records mostly for body dimensional traits also at these ages.

The pre-weaning cohort differences in weight and body dimensional traits in this study were mainly a reflection of pre- and post-natal progeny nutrition due to pasture availability to the dams. Quality and quantity of pasture availability are a consequence of the pattern and distribution of rain each year and this could impact on pre-weaning (Chapter 5) and even post-weaning (Arthur et al., 1994b; Hearnshaw et al., 1994; Chapter 5) growth and development of cattle. In sheep, prenatal and/or early postnatal growth retardation induced by under-nutrition during early life has been demonstrated to be a potential source of long-term consequences for growth, body composition and body size (Greenwood et al., 1998; Greenwood et al., 2000). It is pertinent to note that different sires were generally used each year so that year and sire were confounded. However, this is unlikely to be responsible for the observed variations between years in growth traits. This is because the probability of the average breeding value of the 26 sires from seven breeds being significantly different across years is low.

This study also indicated differences between males and females in weight, height, length and girth at birth and at pre-weaning growth phases. Similar findings have been reported between pure and cattle crosses (Gilbert, et al., 1993; Chapter 5) and this advantage of males over females in weight (7%) and body dimensional traits (eg. Height, 3%) can be maintained to weaning if the cows have the maternal ability to foster bigger calves (Newman et al., 1993). Studies involving Jersey and Limousin crosses (Chapter 5) also supported the observed higher weaning and post-weaning weight and leaner muscle in bull calves compared to lower weight and higher fatness in heifer calves. However, the non-significant differences between steers and heifers in muscularity measurement especially in much older age (400-

600 days) may be a reflection of differences in management systems of both sexes at the time of measurement and limited data at these ages.

4.4.2 Breed effect and genetic parameters

There were strong indications of large breed differences in both body weight and body compositional traits across ages. As age progressed, breed variations increased for weight, muscle and fat traits but decreased for bone traits (body dimensions). For all traits, sire breed means herein may contain both additive (direct) and non-additive genetic effects (eg. heterosis) and could not be estimated separately from the data sets due to common dam. In this study, many of the larger breeds may not necessarily be longer in length or some may not be significantly higher in muscularity than moderately size beef cattle at ages beyond birth. This is an indication that some big breeds may be smaller in stature (e.g. Hereford and Limousin) but with longer and deeper bodies. Thus, breed with moderate size when evaluated on multi-trait could be comparable in muscular development with some larger size breed usually evaluated only on weight or frame score. The study of Vargas et al. (2000) on Brahman cattle suggested that selection for heavy weight animals of moderate height could be realised by including both hip height and weight in a multiple-trait selection scheme. Since the same level of muscularity between breeds could be indicative of similar yield obtainable at slaughter, emphasis on multi-trait evaluation of growth traits would be beneficial in beef cattle breeding program.

Fatness traits like subcutaneous fat depth are positively correlated with internal fat (Chapter 3) and genetically associated with intra-muscular fat content (Koots et al., 1994b), which are determinants of carcass and meat quality. In a recent study, Pitchford et al. (2002) using the same data set also indicated moderate and positive genetic correlation between carcass P8 and intramuscular fat (0.36) and between carcass P8 and melting point (0.20). However, within breed antagonistic relationship between meat yield (lean yield) and

marbling (Koots et al., 1994b; Shackelford et al., 1994; Gregory et al, 1994) across breed poses serious concern in meat quality improvement for specific market requirements. Moreover, some within breed genetic correlations deviate from expectations as you move from small- to larger-size breeds, or from highly marbled to lowly marbled breeds, or from well muscled to pooly muscled breeds. In this study, the moderately sized breeds (eg. Angus or Hereford) had a comparable level of muscularity with larger breeds (e.g. South Devon) and were equal or higher in fat depth than highly marbled small size breed (e.g. Wagyu or Jersey). This indicates that selection in specific breeds or breed crosses can meet optimum carcass quality requirements for various market specifications with little or no compromise in meat yield. Newman et al. (2002) observed a re-ranking of sire's performance for EBV on weight-related traits from different breeds mated to Brahman cows with little change on carcass traits.

In most of the past studies, heritability and genetic correlations estimates for growth at birth and ages beyond birth have been based on weight (Meyer, 1992; Koot et al., 1994a; 1994b; Mercandante et al., 1995; Dodenhoff et al, 1998; Plasse et al., 2002). Few other studies, mostly at post-weaning level only, included additional body measurements like hip height and body length (Gilbert et al., 1993; Vargas et al., 2000). However, there are no published heritability estimates for other body dimensional traits such as girth and muscularity at different ages for any cattle breeds.

In this study, the direct heritability estimates obtained for birth-weight (22%) and weaning weight (12%) were lower than both the unweighted (35% and 27%) and weighted (31% and 24%) mean estimates reviewed from over 170 papers by Koots et al. (1994a). However, the direct yearling weight heritability estimate obtained for unweighted and weighted (35% and 33%) means by the same author on an age-constant basis was close to 40% and 33% estimates of 400- and 600-day weight herein. The differences may be a

reflection of large breed variation attributable to real differences in the breeds in the study herein and possibly due to sample size variation in the pooled studies (Koots et al., 1994a).

The estimates of heritabilies for weaning traits (most especially weaning weight) that were lower than other postnatal ages trait (400-day and 600-day) may reflect large impact of pre-weaning management on these traits. However, the heritability estimates in this study for 400-day weight could represent a more accurate value compared to that of Koots for yearling weight because of the close to significant lower standard error (9% vs 11%). In a study that involved Angus, Hereford, Shorthorn, Brahman, Belmont Red and Santa Gertrudis sires mated to Brahman dams, Newman et al. (2002) also obtained an heritability estimates of 45-49% with a lower standard error (6%) for 400-day weight.

The heritability estimates for weaning height (37%) were lower but 400-day height estimates (53%) were similar to those reported (Koots et al., 1994a) for weaning (43%) and yearling (54%) height, respectively. Also, higher estimates were obtained for weaning height in the studies of Vargas et al. (2000) on a single breed (Brahman) measured at an older age (18 months) and Gilbert et al. (1993) on Hereford and Angus breeds at the same age. However, apart from the work by Gilbert et al. that provided heritability estimates for weaning- and post-weaning length, as an additional body dimensional trait, the results herein on body length and girth from birth to 600-day of age represent the first estimate on inheritance of these traits. Moderate to high post-weaning estimates (23-27% for length and 37-39% for girth) obtained for both traits suggest that selection based on inclusion of these additional body dimensional traits with weight could enhance age-specific evaluation for animal size.

The range of heritability estimates for scanned weaning and post-weaning P8 fat depth (31-41%) were close to those reported by Koots et al. (1994a) as weight constant back-

fat (44%). Though the estimates herein was not weight adjusted but no significant difference would be expected if adjusted because of the low genetic correlations between weight and fat depth. This report is the first estimate of heritability for weaning and post-weaning muscularity (20-44%) since no comparable values could be found in literature. The moderate heritability estimates for post-weaning muscularity is an indication that reasonable genetic progress in meat yield by selection could be realised using live-muscle measurements as described herein for beef cattle breeds. Gutierrez and Goyache (2002) opined that breed standard conformation described by animals skeletal and muscular development could be effectively used to evaluate the animal's productive capacity. Moreover, the negative (e.g. height) and positive (e.g. girth) genetic association between some body dimensional traits and fat traits (P8 fat depth) in this study could also be used for either sire breed or direct animal evaluation for specific market requirements.

Strong and positive genetic correlations of birth traits imply that selection for or against one trait would result in concomitant genetic change in the other traits. Consequently, the clustering of weight with body dimensional traits at birth could be a reflection of pre-natal and early post-natal growth being controlled by the same or similar genes. Jacob and Kwitek (2002) recently illustrated the use of additional phenotypes in rat in order to dissect a QTL into subregions that are associated with specific functions.

The post-weaning relationships between weight and fat or muscle are more determined by environment (feed availability). However, the cluster analysis of the genetic correlations between traits in this study indicated that specific loci switch to post-weaning growth and development, which could be determined as early as weaning. This was because at weaning and post-weaning growth phases, weight was only clustered with length while girth traits and height traits were separately grouped. Because of a high and positive genetic correlation (0.73) between weaning weight and height in Brahman cattle as obtained herein,

Vargas et al. (2000) concluded that the same genes affect the two traits. However, Gilbert et al. (1993) concluded based on their findings that increased height might not necessarily be associated with increased growth potential or slaughter weight at a constant body composition. The cluster analysis result herein supported the findings of Gilbert et al. (1993).

The higher genetic correlation between weight and length (0.59) or girth (0.62) compared to the correlation between weight and height (0.47) at 400-day of age (higher estimates for correlations were found at weaning) suggests that length and girth traits is genetically more related to weight than height traits. Also, there was a stronger genetic relationship between weaning weight and length or girth at 400-day compared to weaning weight and height at 400-day. Moreover, the cluster analysis result grouped the weaning and post-weaning growth of the length traits with weight traits but height traits were grouped separately. Thus, (in some practical management situations) measurement on length or girth may be better indicator of weight rather than height as suggested by Vargas et al. (2000) for Brahman cattle.

The high genetic relationship between traits across ages indicated that genetically superior progeny for breeding objective traits should be expected to be the same at advance maturity. However, the trend of increased genetic and decreased environmental correlations in traits of weight and height across ages may be indicative of the impact of the switch between prenatal (maternal) and postnatal (maternal) environment (nutrition) on the progeny. Also, the high genetic correlations between posweaning measures of height or weight suggest that each trait across ages is control by the same genes. Surprisingly across postweaning ages, correlation (r_G) was very low for length or girth. The contrary observation in these other body dimensions (length and girth) may be partly because of high risk of measurement errors (mostly on fat animal) in them or because of slower physiological maturation rate in length or girth compared to height.

The observed moderate to high r_G for many of the body compositional traits between weaning and 400d postnatal could indicate the best period of measurements for most of the traits (Appendix 1). It is expected that the across age postweaning relationship between measures of muscle and fatness could be similar, but the low phenotypic correlations in muscle could suggest higher influence of genotpe rather than environment (nutrition) at this age. It may also be speculated based on cluster analysis result that weaning and post-weaning muscularity measures could be under the influence of the same loci, which were distinct and separate from the loci for fatness (P8 fat depth). This indicates that genes regulating muscle or fat traits in early growth (weaning) had a similar influence on post-weaning growth for these traits (i.e., genes that increase weaning muscle or decrease weaning fat are likely to increase post-weaning muscle or decrease post-weaning fat). This outcome may further provide an opportunity for genetic selection on fat traits in beef cattle breeds for desired meat fat content.

The positive but lower genetic correlation between post-weaning weight and body dimensional traits compared to weaning traits coupled with a higher environmental correlation (not presented) may be an indication of the existence of compensatory growth. Thus, calves with poor early growth, either due to poor pre-weaning maternal effects (maternal ability of Hereford breed) or poor direct early post-weaning environmental effect (feed availability), tended to grow more post-weaning than calves that grew better initially. As expected, postweaning dry season (adgwt2) weight gain had no phenotypic relationship (-0.08±0.04) with postweaning wet season gain (adgwt3). However, there was positive genetic correlation (0.54±0.34) and negative environmental correlation (-0.29±0.11) between the two gain traits (result not presented). This is an indication that regardless of the season, genetically superior animals always perform better than their inferior counterpart. Moreover, a loss in performance during scarcity of feed (dry season) is proportionately compensated for

in the proceeding wet season when feed becomes abundant. Not withstanding, the interpretation of these correlations, especially at older ages (eg. 600-day) should be made with caution because of the high standard errors.

It could be possible that seasonal differences affected measurement of some traits like muscularity. This coupled with fewer data at the older ages (600-day) for the traits, the lack of consistency in the P8 fat depth measurements and the confounding of age with management may be reflected in post-weaning genetic parameter estimates of these traits which had high standard errors. Nevertheless, this study clearly pinpointed the need to further understand the biology of gene action on body composition at birth and subsequent ages of beef cattle breeds. Hierarchical clustering of genetically correlated traits herein assisted to some extent in recognising the kinship of individual traits.

Many of the earlier studies have indicated the importance of non-additive genetic effects on growth most of which are mainly determined by weight and weight changes in different cattle breeds (Rodriguez-Almeida et al., 1997; Davis et al., 1998b; Dodenhoff et al., 1998). Vargas et al. (2000) emphasised the importance of considering maternal effects for growth traits in general and for hip height in particular when developing selection strategies for Brahman cattle. However, because of the single dam breed utilized, the separation of direct breed from non-additive (e.g. maternal effect and heterosis) genetic effects is a limitation to this study. Thus, additional experimentation is needed in order to determine the non-additive gene action on growth and body development. This will be explored in the next chapter.

Chapter 5

Additive and non-additive genetic effects on growth and development

5.1 Introduction

Some important growth traits (eg. body weight) in beef cattle improvement programs are known to be under the influence of both direct and maternal effects (Dickerson 1969; Pitchford *et al.* 1993). Most reports, however, limited the assessment of these effects to weight and changes in weights in the early life of calves. Recent evaluation of weight traits by some workers has indicated an under-estimation of these genetic effects without the inclusion of grand maternal genetic effects (Davis *et al.*, 1998b; Dondenhoff *et al.*, 1998). Pitchford et al. (1993) reported an effect due to heterosis on weight and height of crossbred cattle from diverse parental breeds (Brahman and Hereford). The genetic improvement realized from heterosis, direct and maternal effects might be further enhanced by factors associated with gene recombination expressed in the pre- or post- weaning performance of calves. Though, ample evidence exists that genetic effects may not be the same in different production and/or nutrition environment (Long *et al.*, 1979a;b; Barlow, 1981; Bolton *et al.*, 1987a;b; Brown *et al.*, 1993), there have been few studies specifically designed to investigate the interaction of genetic effects with environmental changes.

Breed diversity in growth performance characteristics is a useful genetic resource for improving the efficiency of beef production. The advantages of composite breeds as an alternative to continuous crossbreeding have been previously reported (Dickerson, 1973; Gregory and Cundiff, 1980). Breed differences, rather than intra-population selection, can generally be exploited to optimise performance levels more quickly in crosses or in composite populations (Cundiff *et al.*, 1998). Therefore, the objective of this study was to evaluate four genetic effects (direct, maternal, heterosis and epistasis) on growth and development of crossbred progeny from two diverse breeds (Jersey and Limousin) in different seasons and stages of growth.

5.2 Materials and methods

The animals used for this study consisted of a total of 591 calves born over five-year period (1994-1998) in the Davies Gene Mapping Project (DGM). A full description of the design and the management of these animals are in Chapter 2.

Thirty-nine traits were analysed with a model containing fixed effects of year of birth (1994-98), day of birth (5 classes with each comprising 20% of calves born in succession), sex of calf (heifer or steer) and breed of calf (JJ, XJ, LJ, XL, LL). Day of birth was classfied into five groupings rather than two (as in Chapter 4) to restrict age effects bias resulting from significant differences in calving dates between Jersey and Limousin. The groupings help to restrict between calves variation in calving dates.

The model also included random effects of sire (2 Jersey, 2 Limousin and 3 F_1) and dam (189 Jersey and 91 Limousin). Since there were no values for weaning muscularity (WMUS) in 1994 and 400-day muscle in 1996, the model for WMUS included the fixed effects of phase and year nested within phase and that for 400 day muscle included only phase and year nested within phase (to aid linkage across years). Also, dry season muscle gain included fixed effect of phase, year nested within phase and of breed nested within phase. The year of birth by sex interaction was included in the analysis since it was significant for some traits at weaning. All other two-way interactions tested were not significant. The analysis was conducted using the mixed procedure (SAS, 1992).

Genetic effects were estimated similarly to those originally proposed by Dickerson (1969) but were modified because of the specific breed combinations used. Effects were estimated in a similar manner to Pitchford *et al.* (1993). Four genetic effects were estimated from linear combinations of least-square solutions from the five breed combinations (as shown below).

Jersey direct = JJ – LL – XJ + XL = - Limousin direct

Jersey maternal = (LL – JJ)/2 + XJ – XL = - Limousin maternal

Heterosis = LJ – LL – XJ + XL

Epistasis = 2(XJ) – LJ – JJ

All effects were estimated as deviations from the purebred mean. Since there were only five breed combinations, epistasis was completely confounded with paternal heterosis. The effects were calculated as linear contrasts between least square means with T-tests for significant deviation from zero. Significance was defined as $P<0.05$.

5.3 Results

5.3.1 Non-genetic effects

a. Birth traits: The largest calves (weight, height, length and girth) were those born in 1995 whereas the smallest were those born 1998. At birth, the first 20% of calves born had 10% lower weight, 6% smaller girth, and 4% shorter height and length compared to the remaining 80%. Male (bull) calves at birth were 3% heavier and 1% bigger in size (height, length and girth) than the female (heifers) calves (Table 5.1).

Table 5.1. Analysis of variance and tests of significance for pre-weaning and weaning traits

Trait	Effect							
	YOB [a]	DOB [a]	Sex [a]	Breed [a]	YOB x Sex [a]	Sire [b]	Dam [b]	Resid. [b]
Birth:								
Wt (kg)	10.1***	8.0***	46.4***	172.2***	0.5	0.4	2.8	12.0
Ht (cm)	29.4***	9.1***	8.6**	48.2***	2.3	0.5	2.8	12.1
Lh (cm)	5.7***	9.9***	5.6*	35.0***	0.3	0.6	2.2	8.1
Gh (cm)	11.7***	13.5***	11.5***	152.0***	0.1	0.0	3.5	9.8
Weaning:								
Wt (kg)	92.7***	17.2***	61.6***	39.0***	3.1*	43.5	206.7	514.2
Ht (cm)	20.7***	12.6***	57.0***	57.0***	2.9*	1.7	1.2	13.7
Lh (cm)	10.2***	6.1***	1.3	3.3**	1.6	2.5	6.3	26.8
Gh (cm)	44.1***	15.2***	36.0***	26.6***	1.6	0.9	8.7	31.5
Fd (mm)	116.0***	1.6	13.1***	13.6***	0.9	0.0	0.1	1.3
Mus (%)	4.6***	1.2	15.4***	195.7***	1.6	0.3	0.2	29.0
400 days:								
Wt (kg)	59.9***	16.6***	96.6***	51.6***	3.3**	38.2	173.4	552.0
Ht (cm)	22.9***	4.0**	101.8***	44.8***	5.2***	2.2	2.5	15.9
Lh (cm)	14.7***	4.1**	21.7***	2.8*	0.2	1.1	3.6	44.6
Gh (cm)	40.7***	10.6***	82.3***	28.1***	1.9	0.8	5.7	31.0
Fd (mm)	211.1***	2.5*	10.0**	8.6***	0.4	0	0	0.7
Mus (%)	42.0***	0.8	8.3**	210.9***	6.6***	0.5	3.2	24.3
600 days:								
Wt (kg)	30.4***	6.4***	637.7***	62.2***	176.2***	119.9	265.6	949.3
Ht (cm)	11.8***	4.5**	471.4***	54.5***	29.1	3.1	3.5	14.1
Lh (cm)	5.8***	1.2	96.4***	12.6***	33.4***	1.2	6.4	27.1
Gh (cm)	5.8***	5.4***	428.9***	29.4***	144.0***	2.4	5.2	38.7
Fd (mm)	35.7***	2.4*	9.3**	7.2***	53.0***	0.2	0.8	3.6
Mus (%)	67.9***	0.6	84.5***	44.2***	22.6***	0	0.4	63.5
ADG1:								
Wt (g/d)	101.6***	1.0	50.6***	26.1***	2.6*	510.6	2091.5	5390.7
Ht (mm/d)	38.9***	6.4***	18.7***	2.6*	1.2	13.9	7.3	206.1
Lh (mm/d)	27.1***	13.7***	0.5	2.2	1.5	15.2	25.7	364.8
Gh (mm/d)	70.2***	11.5***	13.3***	8.1***	0.8	5.3	77.1	1359.6
Fd (µm/d)	110.3***	1.1	13.8***	12.8***	1.0	0.2	13.5	153.0
ADG2:								
Wt (g/d)	114.2***	1.9	10.1**	4.1**	8.3***	0	824.7	10225.9
Ht (mm/d)	94.0***	2.8*	19.4***	2.5*	6.7***	1.4	21.9	613.7
Lh (mm/d)	23.6***	0.3	12.2***	0.5	0.2	57.2	100.1	2937.7
Gh (mm/d)	247.8***	2.1	24.1***	0.3	1.8	26.8	153.3	1273.9
Fd (um/d)	174.0***	2.8*	1.1	8.4***	0.2	0.9	1.7	59.0
Mus. (%/dx10^{-3})	0.7	1.5	7.4**	4.3**	10.1***	0	81.9	2588.2
ADG3:								
Wt (g/d)	175.3***	1.4	1958.5***	27.6***	1221.0***	1120.6	1809.4	24181.8
Ht (mm/d)	44.5***	0.2	339.0***	4.0**	110.5	10.3	2.5	633.8
Lh (mm/d)	20.8***	1.8	93.2***	6.6***	101.0***	14.9	66.2	1807.6
Gh (mm/d)	88.8***	1.8	889.2***	7.3***	766.0***	13.5	0	1456.3
Fd (um/d)	81.3***	1.6	105.4***	8.8***	152.2***	4.9	26.2	170.3
Mus. (%/dx10^{-3})	95.3***	1.0	62.3***	40.9	58.8***	16.9	0	6059.8

[a] Fixed effects type III mean squares, [b] Random effect variances
***P<0.05, ****P<0.01, *****P<0.001, YOB, Year of birth, DOB, Date of birth**
ADG (1, 2 & 3) = Pre- and post-weaning dry & wet season average daily gains

b. Weaning traits: At weaning, effects of year of birth significantly ($P<0.01$) influenced all the traits and average daily gain (ADG) in all traits (Table 5.1). Calves born in 1995 were fatter and on the average performed better with regards to weight, length and girth than calves from other years. In other years, the majority of calves had no detectable subcutaneous fat. The most highly muscled calves were those born in 1996 (85±0.6%), while the least were the 1998-drop (82±0.6%). The effect of the sex of calf was not significant for length, but was highly significant ($P<0.01$) for every other trait at weaning. Steers were 9% heavier, 2% taller and 2% bigger in girth; more muscled and with less fat than the heifers.

There were also significant year by sex interactions for weight and height. The steers born in 1995 were 12% heavier and 4% taller than heifers born in the same year. However, in the other years on the average, steers were only 7% (weight) and 2% (height) bigger than heifers. For the pre-weaning average daily gains, the year by sex interaction was only significant ($P<0.05$) for weight with steers born in 1995 growing 12% faster than the heifers of the same year. The rate of growth of the former as compared to the latter was lower on the average (6%) for other years. Day of birth reflected age and was significant at weaning for weight, height, length and girth but not for fat depth or muscle score. For weight, the first 60% of calves born were similar (238kg), followed by the next 20% (229kg) and the last 20% (215kg). However, for height, length and girth, the first 80% were similar (111cm, 115cm, 146cm) and larger than the last 20% (108cm, 112cm, 141cm) respectively. Effects due to day of birth were significant for ADG in height, length and girth but not for weight and fat depth (Table 5.1).

c. 400- and 600-day performance: The weight and height at 400-day postpartum were influenced by all the fixed effects (Table 5.1). However, the year of birth by sex interaction was only significant for 400-day weight, height and muscle score and not for length, girth and fat depth. While steers born in 1994 were heavier than heifers in weight (14%) and muscle

score (6%), it was the 1995 born steers, on the average, that were 5% taller than heifers born in the same year. The age (Day of birth) effect was still significant for all the 400-day traits with the exception of the muscle score. The pattern was similar to the weaning weight, height, length and girth. However, for fat depth, the first of 80% of calves born were the same (2.0mm), while the last 20% were leaner (1.3mm).

At 600-day postpartum, effects due to the year of birth by sex interaction were significant ($P<0.01$) for all traits (Table 5.1), reflecting different management for the sexes around this age. The steers born in 1995 were bigger than heifers of the same year in weight (7%), height (12%), length (11%) and girth (21%), respectively. Steers were also fatter (167%) and more muscular (20%) than heifers. It was, however, observed that the steers were only fatter than heifers in the first phase of the experiment (1994-1995), but the reverse was the case in the second phase (1996-1998). This was because phase 1 steers were measured for growth and body dimensions at an older age than heifers but male and female calves were always measured at the same time in the second phase (1996-98) of the experiment. Regardless of the year, the heifers were consistently less muscular than the steers. Also, the significant effect due to day of birth was the same as observed for 400-day postpartum traits with the exception of length. This is an indication that at 600 days, age differences at birth (DOB) still reflected on growth performance.

d. Dry and wet season post-weaning gains: All fixed effects significantly influenced the weight gain in both seasons except the day of birth (Table 5.1). However, the result for gain in height, length, girth, fat depth and muscle score were not consistent in both seasons. For the dry season post weaning gain, there was a significant ($P< 0.01$) year by sex interaction in weight, girth and muscle. While the steers born 1994 were 5% heavier than heifers of the same year, the 1995 born steers were bigger than heifers in girth and muscle. However, the observed significant ($P<0.01$) year by sex interaction in wet season post-weaning gain for all

the traits were consistent except for gain in length. Steers born in 1995 grew faster than the heifers in weight (23%), height (7%), girth (18%), fat depth (64%) and muscle (3%). With regard to length for this season, the best gain was obtained in 1996 and the heifers were generally longer than steers in all the years.

5.3.2 Breed and genetic effects

a. Birth traits: At birth, breed rankings for all traits (P<0.001) depended primarily on the proportion of Limousin genes: LL>XL>LJ>XJ>JJ (Figure 5.1). Thus, there was a gradual increase in breed mean as proportion of Limousin genes increased for all birth traits from purebred Jersey to purebred Limousin (Table 5.2). The direct genetic effect of the Jersey decreased birth weight, height, length and girth (Table 5.3). Jersey maternal effects were not significant for all the birth traits except for girth (-9mm), which was negative. Heterosis and epistatic effects were not significant for any of the birth traits.

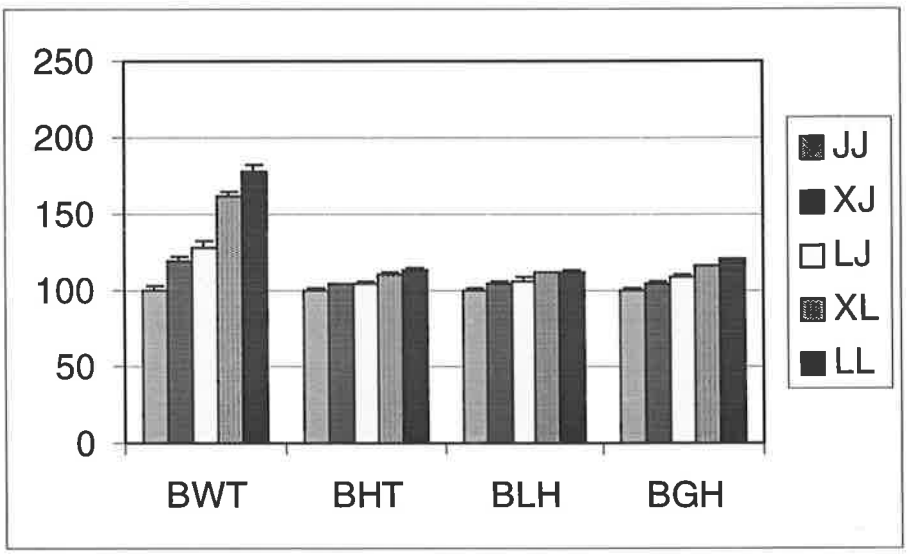


Figure 5.1. Breed means as a proportion (%) of purebred Jersey genes for birth traits.
Bars- indicates standard errors.
BWT= Birth-weight, BHT= Birth-height, BLH= Birth-length, BGH= Birth-girth.
JJ= Jersey, XJ= Jersey backcross, LJ= F_1 (JJ x LL), XL= Limousin backcross, LL=Limousin.

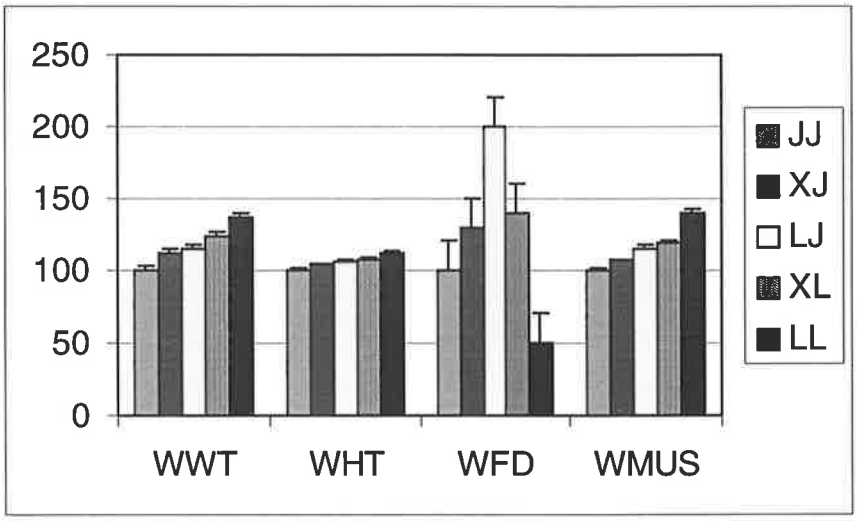


Figure 5.2. Breed means as a proportion (%) of purebred Jersey genes for weaning traits.
Bars- indicates standard errors.
WWT= Weaning weight, WHT= Weaning height, WFD= Weaning fat depth, WMUS= Weaning muscularity.
JJ, XJ, LJ, XL, LL, as in Figure 5.1.

b. Weaning traits: At weaning, breed means for weight, height and girth were the same rankings as at birth (Table 5.2). In addition and as expected, the purebred Limousin was more muscular with the purebred Jersey at the other extreme (Figure 5.2). However, some combinations were the same for length at weaning (Table 5.2). Basically, Jersey (JJ) calves were 3% shorter than the average of other breeds (Table 5.2). However, none of the genetic effects were significant for length (Table 5.3). The F_1 calves had the greatest fat depth with the two purebreds having the least, an indication of a large heterosis effect. Direct breed differences were significant for all the traits at weaning with the exception of length (Table 5.3). The Jersey direct genetic effect resulted in calves with far less weight, height, girth and muscle. There was also a small positive direct effect of the Jersey genes on fat depth. Jersey maternal effects were expressed to a large extent on girth and muscle with a smaller effect on weight and no effects on length, height or fat depth. Heterosis effects, though, were negative for weight, girth and muscle, and positive for fat depth, but not significant for length or

height. Epistatic effects were not significant for any of the traits. Breed effects for pre-weaning gains were the same as for weaning with one exception. This exception was for height where the maternal effect of the Jersey increased daily gain in height but was not significant for weaning height (Table 5.3).

Table 5.2. Least square means for the fixed effect of breed for pre-weaning and weaning traits

Trait	Breed				
	Jersey (JJ)	LJ x JJ (XJ)	LL x JJ (LJ)	LJ x LL (XL)	Limousin (LL)
Birth:					
Wt (kg)	19.6±0.7	23.4±0.6	25.2±0.8	31.8±0.6	35.0±0.8
Ht (mm)	659±7	686±6	689±9	730±6	744±9
Lh (mm)	503±7	523±6	536±8	559±6	564±8
Gh (mm)	633±5	663±5	687±7	735±5	759±7
Weaning:					
Wt (kg)	197.8±6.0	220.9±5.1	226.7±7.0	245.9±5.2	269.6±6.8
Ht (mm)	1047±11	1086±9	1105±12	1134±9	1167±12
Lh (mm)	1120±14	1145±12	1136±16	1162±12	1158±16
Gh (mm)	1383±11	1443±10	1444±14	1473±10	1517±14
Fd (mm)	1.0±0.2	1.3±0.2	2.0±0.2	1.4±0.2	0.5±0.2
Mus. (%)	71.6±1.0	77.4±0.7	82.9±1.5	86.2±0.7	101.3±1.4
400 days:					
Wt (kg)	220.2±5.7	254.2±5.0	258.4±7.0	281.2±5.1	304.8±6.7
Ht (mm)	1101±12	1159±10	1179±14	1205±10	1238±13
Lh (mm)	1222±12	1253±11	1254±16	1267±11	1263±15
Gh (mm)	1502±11	1546±10	1564±14	1590±10	1626±13
Fd (mm)	1.3±0.1	1.7±0.1	1.8±0.2	1.6±0.1	1.0±0.2
Mus. (%)	72.8±1.0	70.1±0.6	82.8±0.9	79.0±0.7	98.3±0.8
600 days:					
Wt (kg)	328.7±9.1	358.1±7.8	400.7±10.6	407.2±7.9	458.3±10.3
Ht (mm)	1177±14	1248±11	1262±16	1308±12	1322±15
Lh (mm)	1290±12	1309±10	1319±16	1342±10	1369±15
Gh (mm)	1704±15	1721±12	1812±19	1774±12	1878±18
Fd (mm)	2.4±0.4	3.2±0.4	5.5±0.5	3.1±0.4	4.4±0.5
Mus. (%)	73.1±1.1	80.2±1.1	75.4±1.7	89.3±1.1	80.3±1.6
ADG1:					
Wt (g/d)	614.1±19.8	693.1±17.1	698.3±23.3	755.8±17.4	811.9±22.7
Ht (mm/d)	134.3±3.3	140.4±2.9	145.1±4.0	141.6±2.9	148.6±3.9
Lh (mm/d)	214.2±3.9	217.5±3.5	210.0±4.8	211.5±3.5	207.9±4.7
Gh (mm/d)	259.2±3.3	270.6±3.0	264.4±4.5	258.1±3.1	265.7±4.3
Fd (µm/d)	3.3±0.7	4.5±0.6	6.7±0.9	4.7±0.9	1.8±0.9
ADG2:					
Wt (g/d)	138.9±14.6	195.9±13.9	163.7±21.4	208.8±14.0	196.3±20.0
Ht (mm/d)	41.1±3.7	50.2±3.5	53.4±5.3	48.6±3.5	54.0±5.0
Lh (mm/d)	68.3±9.3	73.0±8.5	79.7±12.5	69.8±8.5	68.1±11.9
Gh (mm/d)	312.1±6.5	312.2±5.9	312.5±8.6	308.3±6.0	310.3±8.2
Fd (µm/d)	1.0±1.3	2.3±1.2	-4.3±1.7	0.3±1.2	2.9±1.2
Mus. (%/dx10^{-3})	-2.9±1.0	-4.7±0.4	-4.7±0.9	-4.8±0.5	-7.2±0.8
ADG3:					
Wt (g/d)	725.9±32.7	732.4±29.0	970.0±41.4	842.8±29.0	1186.6±39.9
Ht (mm/d)	46.6±4.4	56.5±3.6	44.3±6.4	62.4±3.6	57.5±6.0
Lh (mm/d)	49.3±7.2	44.6±5.7	38.0±10.7	53.5±5.8	77.9±9.9
Gh (mm/d)	140.2±6.4	118.1±5.2	165.7±9.5	122.4±5.2	181.5±8.8
Fd (µm/d)	10.9±2.5	13.1±2.2	31.7±3.3	13.2±2.3	28.9±3.1
Mus. (%/dx10^{-3})	12.4±1.2	-0.6±0.6	6.4±1.2	-0.8±0.8	-4.1±1.0

ADG (1, 2 & 3) = Pre- and post-weaning dry & wet season average daily gains, ± = S.E

Table 5.3. Genetic effects and tests of significance (difference from zero) for pre- and post- weaning traits

Trait	Genetic Effect			
	Jersey Direct	Jersey Maternal	Heterosis	Epistasis
Birth:				
Wt (kg)	-6.9±1.0***	-0.8±0.6	-1.3±0.7	1.8±2.0
Ht (mm)	-41±10***	-2±6	-10±7	23±21
Lh (mm)	-25±10**	-6±6	9±6	6±19
Gh (mm)	-54±7***	-9±5*	0±6	7±16
Weaning:				
Wt (kg)	-46.8±8.5***	10.9±4.9*	-17.9±5.1***	17.3±16.1
Ht (mm)	-72±15***	12±9	-14±8	20±28
Lh (mm)	-21±20	2±11	-6±11	35±37
Gh (mm)	-104±16***	37±10***	-43±12***	59±34
Fd (mm)	0.5±0.3*	-0.3±0.2	1.5±0.2***	-0.4±0.6
Mus. (%)	-20.8±1.5***	6.0±0.9***	-9.6±1.6***	0.3±3.0
400 days:				
Wt (kg)	-57.6±8.3***	15.3±4.8**	-19.3±5.3***	29.7±15.9
Ht (mm)	-91±18***	22±10*	-12±9	37±31
Lh (mm)	-28±18	7±11	5±14	30±38
Gh (mm)	-81±16***	19±10	-18±12	25±33
Fd (mm)	0.1±0.2	0.0±0.1	0.6±0.2***	0.4±0.4
Mus. (%)	-16.5±1.4***	3.8±0.9***	-6.5±1.1***	- - -
600 days:				
Wt (kg)	-80.5±13.2***	15.7±7.3*	-8.6±7.1	-13.1±23.7
Ht (mm)	-85±20***	13±11	0±9	58±34
Lh (mm)	-45±17**	6±10	-16±13	8±34
Gh (mm)	-121±22***	33±13**	-13±15	-74±42
Fd (mm)	-2.1±0.6***	1.1±0.4**	1.0±0.4*	-1.5±1.2
Mus. (%)	1.9±1.7	-5.5±1.1***	4.2±1.7**	12.0±4.0**
ADG1:				
Wt (g/d)	-135.1±28.4***	36.2±16.2*	-50.9±16.4**	73.9±53.2
Ht (mm/d)	-13.1±4.9**	6.0±2.8*	-2.3±3.0	1.4±9.3
Lh (mm/d)	0.3±5.7	2.9±3.4	-4.0±4.0	10.9±11.5
Gh (mm/d)	-19.0±4.9***	15.8±3.1***	-13.8±4.1***	17.6±10.7
ADG2:				
Wt (g/d)	-44.6±22.3*	15.9±14.7	-19.7±21.5	89.3±52.1
Ht (mm/d)	-14.5±5.5**	8.0±3.6*	-2.2±5.2	5.9±12.9
Lh (mm/d)	-3.1±14.0	3.1±8.7	8.4±11.4	-1.9±29.9
Gh (mm/d)	-2.2±9.5	3.1±5.9	3.1±9.5	-1.8±7.7
Fd (µm/d)	-3.9±1.9*	3.0±1.2*	-9.2±1.6***	7.9±4.2
Mus. (%/dx10^{-3})	43.0±13.9**	-21.2±8.8*	24.8±13.2	- - -
ADG3:				
Wt (g/d)	-282.4±48.8***	86.0±28.6**	-38.5±34.2	230.8±95.5*
Ht (mm/d)	-5.0±6.7	-0.5±4.1	-7.3±5.7	22.1±13.8
Lh (mm/d)	-19.7±10.9	5.4±6.7	-31.0±9.6***	1.9±23.0
Gh (mm/d)	-37.0±9.7***	16.4±6.0**	-11.5±8.6	-69.7±20.7***
Fd (µm/d)	-17.9±3.7***	8.9±2.3***	2.9±2.9	-16.4±7.7*
Mus. (%/dx10^{-3})	16.2±1.8***	-8.0±1.2***	10.3±1.7***	- - -

*P<0.05, **P<0.01, ***P<0.001, ADG (1, 2 & 3) = Pre- and post-weaning dry & wet season average daily gains, ± = Standard errors

c. 400- and 600-day performance: Breed effects were highly significant ($P<0.01$) for all the traits measured at 400- and 600-days postpartum except for height, which had a lower significance ($P<0.05$) at 400-days of age (Table 5.1). The variation due to sire and dam were generally small compared to that of the residual variation.

Breed rankings for 400-day postpartum weight, height, girth and muscle were the same as at weaning. Size increased as the proportion of Limousin genes increased (Table 5.2). In length, however, LL and XL were the same but higher than LJ = XJ and JJ respectively. At 400 days, crossbred calves (XJ, LJ and XL) were similar in fat depth and higher than the two purebreds (JJ or LL). The direct Jersey effect resulted in calves significantly ($P<0.01$) lower in weight, height, girth and muscle but this effect was not significant for length or fat depth. However, the Jersey maternal effects resulted in increased weight, muscle ($P<0.01$) and height ($P<0.05$) but not for length, girth or fat depth. Large and positive heterotic effects were observed for fat depth ($P<0.01$). Negative heterosis was observed for weight and muscle ($P<0.01$) but not for height, length and girth ($P>0.05$). At 400 days, no epistatic effects were observed for the traits (Table 5.3).

The effect due to breed differences was highly significant ($P<0.01$) for all the traits at 600-day postpartum. The pattern was similar to that obtained at 400-day postpartum and the ranking of the breeds were consistent for many of the measured traits. Breed means (Table 5.2) show that the purebred Limousin was the heaviest (weight) and biggest (height, length and girth) with the purebred Jersey at the other extreme. There was a gradual increase in weight, height, length and girth as the proportion of Limousin genes increased (Table 5.2). In contrast to observation for muscle at 400-day, XL calves were more muscular than XJ = LL and LJ = JJ, respectively. At this age, the F_1 (LJ) calves were still fatter than any other genotypes.

At 600 days postpartum, the Jersey direct genetic effect was highly significant ($P<0.01$) for all the traits with the exception of muscle (Table 5.3). The direct effects resulted in calves with less weight, height, length, girth and fat depth. Large Jersey maternal effects were also observed on girth, fat depth and muscle with a smaller effect on weight. In contrast to the direct effects, however, maternal effects due to Jersey genes produced slightly heavier ($P<0.05$) but fatter ($P<0.01$) calves with large girth ($P<0.01$) and far less muscle ($P<0.01$). No significant maternal effects were observed on height or length at 600 days. Heterotic effects were significant but lower for fat depth ($P<0.05$) and positively higher ($P<0.01$) for muscle at this age as compared to 400-day postpartum. At 600-day postpartum, the negative heterotic effects on weight was no longer significant but there was significant and positive heterosis on muscle. Also, a strong and positive epistatic effect was observed on muscle at this age.

d. Dry and wet season post-weaning gains: As expected, breed differences in daily gain were significant for most traits in the dry season (ADG2=weaning to 400 day). XL calves had the highest weight gain, followed by XJ = LL, LJ and JJ (Table 5.2). The ranking order for height was similar to pre-weaning. Muscle also followed the same trend (Figure 5.3). However, there was significant fat depth loss in the F_1 (LJ), and the XJ and XL gained less fat than the purebred mean (Figure 5.3). The direct Jersey effects resulted in increased muscle gain but reduced weight and fat depth gain. There was a positive but low Jersey maternal effect on height and fat depth, and a negative and low maternal effect on muscle. Heterotic and epistatic effects were the same as for pre-weaning.

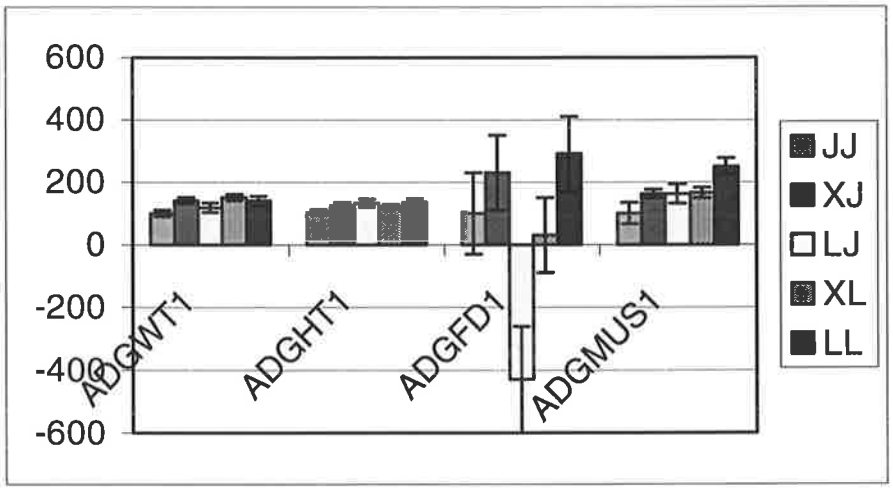


Figure 5.3. Breed means as a percentage of pure Jersey mean for dry season gain
Bars- Indicate standard errors. ADG WT1, HT1, FD1, MUS1= Dry season gains in weight, height, fat depth and muscle.
JJ, XJ, LJ, XL, LL, as in Figure 5.1

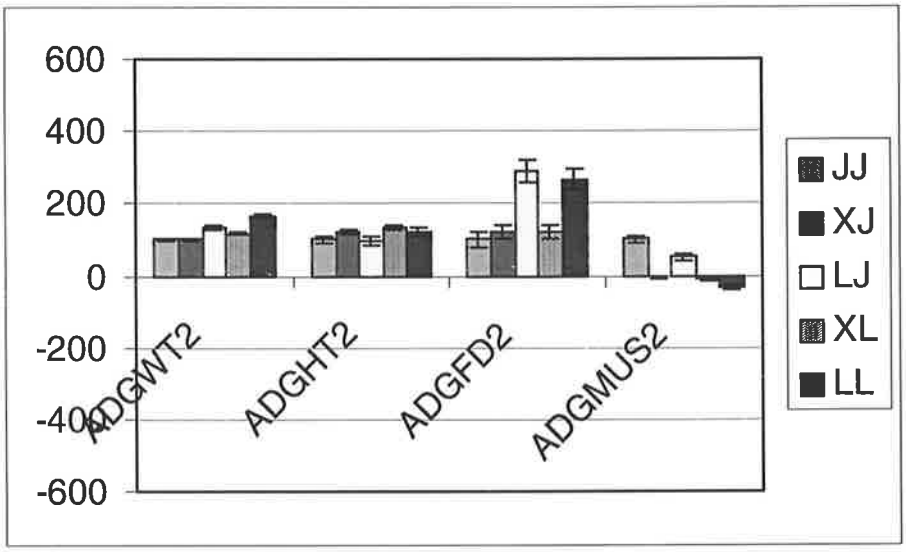


Figure 5.4. Breed means as a percentage of pure Jersey mean for wet season gain
Bars- Indicate standard errors. ADG WT2, HT2, FD2, MUS2= Wet season gains in weight, height, fat depth and muscle.
JJ, XJ, LJ, XL, LL same as in Table 5.1.

In the wet season (400day to 600day), the gains in all the traits were faster than the dry season for all the genotypes. The ranking was similar to the dry season performance. However, the amount of fat depth and muscle lost in the dry season by genotypes affected the level of the wet season gain (Figure 5.4). The direct Jersey effects in the wet- and dry- season were similar for gain in weight, fat depth and muscle (Table 5.4). However, the wet season as compared to the dry season led to greater breed effects on weight, fat depth and muscle. Also, the significant direct effect on dry season height was no longer apparent in the wet season, while the direct effect on girth which was not apparent in dry became highly significant ($P<0.01$) in the wet season. The Jersey maternal effect (Table 5.3) on weight and girth was significant and was greater for fat depth and muscle in the wet season (ADG3) compared to the dry season (ADG2). However, the maternal effect apparent on height in dry season was no longer significant in the wet season. The Jersey maternal effect resulted in calves with increased weight, additional fat depth and less muscle gain. The heterotic effect was significant and positive for muscle with calves gaining more muscle. However, the significant negative heterosis on fat depth gain in the dry season was not evident in the wet season. Although no epistatic effects were observed for any of the dry season traits, there was a positive epistatic effect for weight and negative epistatic effects for girth and fat depth during the following wet season.

5.4 Discussion

5.4.1 Non-genetic effects

The links across the years through common dams helped address the partial confounding between year and breed. Calves born in 1995 were bigger in birth-weight and skeletal growth performance compared to other years. These observed effects are due to environmental conditions such as pasture availability, which to a large extent cannot be controlled. Seasonal pasture productivity induced by climatic environment was an evidence of pasture availability (Wheeler and Freer, 1986), with pasture quality and quantity being

better in the higher rainfall months than in the drier months. During the experiment, 1995 was the best season with good rains into spring.

As expected, similar patterns of growth were observed for pre-weaning and weaning performance in weight, height, length girth, fat depth and muscularity. Gilbert *et al.* (1993) observed a significant influence of year on body dimensional traits with calves born in one year being shorter at withers, longer in body and cannon bone circumference than calves born in another year. However, if the difference between the largest (271kg) and the smallest (202kg) weaning weights are examined herein, then it can be concluded that year effects at weaning are larger for weight (34%) than body dimensions [e.g. height (2%)]. While growth as a whole can be considered as an increase in mass, it includes not only cell division and enlargement but also changes in body composition (e.g. fat deposition) (Owen *et al.*, 1993). Different body tissues respond differently depending upon the stage of cell maturity and feed availability. Thus, although there was a large year effect on weight relative to height, the animals also changed shape as well as being larger overall in 1995.

There was also evidence of an impact of the quality and quantity of pasture available for grazing between years on the magnitude and direction of post-weaning growth of weight and body dimension traits of pure and crossbred calves in this study. Comparable results were obtained previously with post weaning growth of steer (Arthur *et al.*, 1994b) and heifer (Hearnshaw *et al.*, 1994) calves from Hereford, Brahman and their crosses.

At birth, female calves were significantly lighter in weight and shorter in body dimensions than the male calves. Earlier reports have also acknowledged that male calves are bigger than female calves at birth (Gregory *et al.*, 1978; Gregory *et al.*, 1979). However, the maintenance of birth weight advantage to weaning age, as observed herein, is an indication of differences in maternal ability of cows when suckling heavier calves, which tend to be male

(Newman *et al.*, 1993) or of calf's ability to eat grass. The differences between male and female calves on weight, height, length, girth and muscle at weaning were similar to the results reported by Gilbert, *et al.* (1993). In that report, steers were larger than heifers in height at withers, body and head length, head and muzzle width and cannon bone circumference but not in height and width at hips and frame score. In general, the female calves were fatter than the male calves at all stages of growth.

A limitation of this study is the confounding between age of calves and season of growth most especially at the post-weaning growing phases. However, higher growth performance was observed in older growing calves, a period which was during the wet season, compared to when calves were younger in the dry season. The findings indicated that weight gain was almost five times greater in the wet season (i.e. older age) than the dry season (i.e. younger age). The expectation would have been for the older animal to grow slower. Thus, the seasonal effect rather than age was assumed to be the primary cause of the differences in growth performance of the growing calves within the two post-weaning growing phases in this study.

5.4.2 Breed and genetic effects

a. Breed effect: In general, the gradual trend in increased weight gains and many of the body dimensions at all stages of growth as the amount of Jersey genes decreased was expected. This was because the two breeds used in this study are at opposite extremes for many beef and dairy traits. In a crossbreeding experiment involving Brahman and Hereford, there was a similar increase in wither height as the amount of Brahman genes increased (Long *et al.*, 1979a; 1979b; Stewart, *et al.*, 1980; Bolton *et al.*, 1987; 1987b; Comerford *et al.*, 1988; Hearnshaw *et al.*, 1994). However, the greater level of heterozygosity in the F_1 and backcross progeny in some of the traits brings to focus the additive and non-additive gene action associated with crossbreeding.

b. Direct effects: The direct genetic effect of the Jersey genes that resulted in decreased birth weight was similar to some earlier findings on pure and crossbred cattle (Cunningham and Magee, 1988; Newman *et al.*, 1993; Davis *et al.*, 1998a). The lack of a significant maternal effect on birth weight in this study supported the results of Pitchford *et al.* (1993) on calves from Brahman and Hereford crosses. However, the observation was contrary to the significant effect obtained by Cunningham and Magee (1988) with Angus, Charolais, Holstein-Friesian and Simmental crosses and by Alenda *et al.* (1980) with Angus, Charolais and Hereford crosses. The result herein suggests that mothering ability and/or post-natal nutrient supply is a more important component of the maternal effect than pre-natal nutrient supply. Heterotic or epistatic effects, which were not significant for any of the birth traits, strengthen the findings that non-additive genetic effects are not a source of variation in birth weight (Dillard, *et al.*, 1980).

The direct genetic effect was the largest genetic effect compared to other genetic effects for most traits (muscle and bone) at all stages of growth. This indicates that the individual breed genetic effects influence the performance of animals at any age since this effect was consistent across ages for most of the traits under consideration. However, at post-weaning phases the results were not consistent for length, fat depth and muscle.

The direct effect of Jersey relative to Limousin on weaning traits resulted in smaller calves with much less muscle. In previous studies, both Jersey and Limousin breeds had low subcutaneous fat levels (Cundiff, *et al.*, 1988), but in the study herein, the Jersey had slightly more fat than Limousin (Table 5.2). The positive and significant ($P<0.05$) impact of Jersey genes on fat depth at weaning was at 400 days and negative at 600 days (Table 5.3). In contrast but as expected, there was a large significant negative impact of Jersey genes on muscularity at weaning and 400 days, which disappeared by 600 days presumably because of

compensatory growth. A Jersey breed effect on length was not noticed at weaning but became pronounced at 600 days of age.

The genetic effects on growth were smaller in the dry season compared to the wet season due to improved nutrition. Arthur *et al.* (1994c) acknowledged the significance of the influence of post-weaning environment on the magnitude and direction of the genetic effect on a trait. Jersey direct effects were consistent in both seasons for weight, height, girth and fat depth but not for muscle. For example, the Jersey direct effect led to low weight, height, girth and fat depth gain but higher post-weaning muscle gain. This is in agreement with Koch *et al.* (1994) suggesting that the post-weaning muscle score is influenced primarily by direct effect. The positive direct effect of Jersey on muscle gain at older ages was unexpected, since the effect was negative at weaning (-21%) and even at 400 days (-16%). This may be due to faster physiological maturation of Jersey relative to Limousin at these ages.

c. Maternal effects: The impact of Jersey genes on progeny due to large milk production of this breed had no effect on height or length at weaning. However, the calves with Jersey dams were 3% bigger in girth, 5% heavier and well muscled (7%). This suggests that while milk supply (Jersey dam) is important for muscle development, Limousin dams obviously had sufficient milk supply for bone development but may be not for muscle development. Some earlier studies reported high and positive estimates of maternal effects for weaning weight of Angus (Neville *et al.* 1984) and of Charolais and Simmental breeds (Cunningham and Magee (1988). Although, Kress *et al.* (1996) observed no significant maternal effects for early calf weight (40-day), but at 120 days, significant differences due to maternal effects were found. The results herein also indicate a strong and positive maternal effect on pre- and post-weaning girth and muscularity not commonly found in earlier studies.

The positive Jersey maternal effects for weight, height, girth, fat depth and muscle at 400- or 600-days of age is an indication of the importance of the carry-over effects of post-natal nutrition from Jersey cows relative to Limousin cows. The Jersey is a dairy breed and has a high milk supply. However, the decrease in the level of its significance for weight and height, as well as the significant but negative effect for muscle as post weaning age progresses, suggested that the influence of the dam on post-weaning performance of progeny is minimal relative to pre-weaning performance. For example, the initial 7% increase in muscle development (weaning) due to high milk supply from Jersey dams decreased to 4% at 400 days of age. Also, the initial positive Jersey maternal effects on muscle at 400 days but positive Limousin maternal effects at 600 days may suggest an attribute of compensatory growth exhibited by calves born and nursed by Limousin dams. In addition, maternal effects for growth may vary with nutrition, which was confounded with age in this study.

The positive Jersey maternal effects on most daily gain traits were due to high milk production of this breed and had a large effect on progeny even at older ages when exposed to a good post-weaning environment. However, there was a negative effect on post-weaning muscle gain. Again, this may be due to compensatory growth in calves with Limousin dams relative to Jersey dams. This is further demonstrated in the genotype by seasonal re-ranking in weight (Dry: JJ<LJ<XJ=LL<XL Vs Wet: JJ<XJ<XL<LJ<LL) and height (Dry: JJ<XL<XJ<LJ<LL Vs Wet: LJ<JJ<XJ<LL<XL). However, the result of this study contradicts the lack of significant maternal additive effect for post-weaning average daily gain and live-weight observed by Arthur *et al.* (1994c) in *Bos indicus* and *Bos taurus* crosses. This might be due to large breed difference between Jersey and Limousin.

d. Heterotic effects: The observed decrease in weight and muscle as well as a large increase in fatness due to heterotic effects at weaning was unexpected. Rarely has heterosis been estimated to have a negative effect on growth as in this study (-7%). Dillard *et al.* (1980)

observed positive specific individual heterotic effects on weight among Angus, Charolais, and Hereford crosses. Cunningham and Magee (1988) also found a positive and significant influence of individual heterotic effects on weaning weight among Angus, Charolais, Hereford, Holstein-Friesian, and Simmental crosses. When the breed means are plotted relative to purebred Jersey (Figure 5.2), the huge effect of heterosis on fat depth is obvious in the F_1 calves. This trend continued until these calves were slaughtered, where the F_1 progeny were much fatter than the purebreds in this study (Pitchford *et al.*, 1998).

Many studies have reported heterotic effects on growth but only a few examined the effects on fat depth and fewer on muscularity. The estimates of heterotic effects in this study, which were positive for fat depth and negative for muscle, support earlier reports of Gregory *et al.* (1994) and Pitchford *et al.* (1993). In 1994, Gregory et al. reported that heterosis levels were retained in three composite lines. Among the three lines, two (MARCII and MARCIII) had significantly lower percentage lean meat and higher percentage fat trim than the mean of the contributing purebreds. In part of the study on Brahman-Hereford crosses (Pitchford *et al.*, 1993), there was also positive heterosis for condition score (Hearnshaw *et al.*, 1994).

The large fatness of the F_1 (LJ) calves compared to other genotypes at all ages was predominantly due to heterotic effects but was also partly due to the maternal effect. The F_1 progeny were clearly fatter with less muscle than expected. However, the negative heterosis on dry season gain (Table 3; Figure 2) is just an indication of the loss of the pre-weaning effect. The significant negative heterosis on weight is contrary to earlier reports. Koch *et al.* (1985) obtained a greater than expected retained heterosis for post-weaning gain and final weight. Also, Pitchford *et al.* (1993) found that heterosis effects were 1-21% for mature weight and 0-4% for mature height depending on the pre-weaning environment. In male and female lines of three composite populations (MARC I, II and III), heterosis was important for

average daily gain from weaning to 368-day, 368-day weight, and 368-day condition score (Gregory *et al.* 1991).

The observed deviation of negative heterosis on weight at 400 days and no effect on post weaning weight gains might partly be due to the limited number of sires per breed (2-3) in this study. However, while sires were poorly represented, there were large numbers of dams from wide range of sources. Also, the phenotypic difference between the breeds (Limousin and Jersey), especially for carcass traits, is larger than for most other studies. The highly significant heterotic effect on muscle at post-weaning ages herein was in contrast to the previous findings of no significance heterotic effects on this trait (Gregory *et al.*, 1991).

e. Epistatic effects: At weaning, there was no epistatic effect on any of the traits. However, the positive epistatic effects on some post-weaning traits (weight and muscle) and negative effects on others (girth and fat depth) herein indicate that epistatic effects are important in older ages of growing calves. Thus, non-additive genetic attributes hidden in the recombinants at pre-weaning growing phase are revealed at post-weaning growing phase probably because of the change in nutrition or post-weaning environment. A study in mice has shown that there are different quantitative trait loci (QTL) affecting early and late growth (Vaughn *et al.,* 1999). In that study, QTL were mapped to separate chromosome locations. Major gene additive effects or smaller genes with major effect are speculated for many growth traits. However, the effect due to non-additive gene action may not be ruled out mostly especially at older ages. The breed re-ranking in most of the body dimension traits in the current study was a function of non-additive (heterosis and epistasis) genetic effects.

5.5 Conclusions

This study has demonstrated a strong and positive maternal effect (6%) of the Jersey (relative to Limousin) on muscularity due to high milk supply of the Jersey dam. Also, the

crossbred calves (LJ, XJ and XL) were fatter than the mean of their purebred parents because of the strong and positive heterosis on fat depth. It is, therefore, possible to exploit the positive heterosis and maternal effects in both fat depth and muscularity to meet specific consumer demands for high quality and quantity meat. However, the two breeds utilized herein may not be the most representative models in a crossbreeding program to meet various demands. There is a need to further explore the potential derivable from other diverse breeds. Furthermore, the impact from crossbreeding of this type, strengthened the possibility of post-weaning compensatory growth (thereby weakening the non-additive genetic effect at older age) for the pre-weaning disadvantaged calves. Those calves that were lacking in growth pre-weaning, probably due to the short milk supply from Limousin dam, were compensated when exposed to good post-weaning environment.

This study has also indicated that there were different significant genetic effects for post-weaning compared to pre-weaning growth of growing calves. The non-additive genetic effects of epistasis (apart from maternal and heterotic effects) could probably be exploited in this type of crossbreeding program in older calves that are heavily dependent on forage rather than milk. This finding may support the hypothesis that different QTL are affecting growth at younger and older ages as reported in mice (Vaughn *et al.,* 1999). Therefore, the aspects of different QTL effects for growth at pre- and post-weaning ages would be examined in the following experiment (Chapter six).

Chapter 6

QTL effects on growth and development

6.1 Introduction

The development of genetic marker technology is a new and recent approach at targeting genetic improvement of economically important traits at the genome level. It involves identifying relationship between specific quantitative trait loci (QTL) or genes with their positions on various autosomal or sex chromosomes and the phenotypic performance of different animal species or breeds. QTL identification is an ideal first step in finding specific chromosomal regions where genes controlling the expression of performance in economic traits are located. By identifying these genes, introgression approaches can be adopted to establish the favourable gene(s) in livestock. This technology is also of extreme importance to seed-stock producers to aid improvement in traits that are difficult or expensive to measure in commercial or domestic stock.

Among the traits identified as difficult and/or expensive to measure in beef cattle breeds are the carcass and meat quality characters (Wheeler et al., 1997). Genetic improvement programs for meat quality and quantity traits could be enhanced if methods to assess differences in genetic potential for carcass merit prior to processing could be utilized. The strong link between predicted and actual carcass traits (Figures 3.1 and 3.2) could be indicative of the reliability on QTL mapping for the actual traits based on the predicted traits. Thus, the ability to accurately predict segregating QTL alleles having major economic effects on carcass characteristics early in life could reduce genetic evaluation costs by reducing lengthy and expensive data collection in many cattle populations. QTL have been mapped for growth and carcass traits in several studies involving beef cattle (Davies et al., 1998a; Stone et al., 1999; Casas et al., 2000; Li et al., 2002). The objective of this study was to identify chromosomal regions representing QTL influencing growth and developmental traits by genotyping micro-satellite markers on backcross progeny from Limousin x Jersey sires.

6.2 Materials and methods

6.2.1 Animal

The animals used in this study were the 370 back-cross calves produced in the second phase (1996-1998) of the Davies Gene Mapping Project (DGM). As stated in Chapter 2, part of the design was to generate two backcross families (3/4 Jersey and 3/4 Limousin) using three first-cross sires L x J (F_1) mated to purebred Jersey or Limousin cows. Of the total, 205 were 3/4 Jersey and 165 were 3/4 Limousin. The detailed description of the design, management and live-traits measured is provided in Chapter 2.

6.2.2 Markers and genomic screen used

Sire-derived alleles were determined for a total of 246 informative micro-satellite loci (an average >150 loci per sire group) spread across the whole genome, except for the X- and Y-chromosomes. Informative markers in the sires were chosen from available maps on all the 29 autosomal chromosomes with an aim of over 90% genome coverage of the F_1 sire families. The three F_1 sires were tested for heterozygousity at every marker loci, so approximately half the alternative marker allele from either the Limousin or Jersey grandsire was inherited by the progeny through the sire, with the other allele inherited from their respective dams. Amplification reactions for markers were done with purified DNA extractions obtained from blood samples collected in sterile tubes containing ACD as anticoagulant. Genotyping based on markers of the F_1 sires and their backcross progeny was performed at AgResearch, New Zealand. The fragments were visualized by autoradiography after electrophoresis of stained polyacrylamide gels.

6.2.3 Data and statistical analyses

Traits analysed were live animal measurements between different ages as reported in Chapter 2. Phenotypes for all traits (Table 6.1) were pre-adjusted to account for known fixed effects of year of birth (1996-98), day of birth (5 classes with each comprising 20% of animal

born in succession), sex (heifer or steer), breed (3/4 Jersey and 3/4 Limousin) and year of birth by sex interaction as described in Chapter 5. Residuals were stored after standardisation by dividing by the phenotypic (residual) standard deviation (σ_P). In view of the close relationships between traits observed in the cluster analysis of genetic correlations in the earlier experiments (Chapter 4), principal components (PC) were calculated for the group of clustered traits using Proc Princomp (SAS, 1992). The first PC for each group of clustered traits, which accounted for at least 47% of variance in all cases, is as defined below:

1. Birth-trait (Bwt, Bht, Blh, Bgh)
2. Growth-trait (Wwt, 400-d wt, 600-d wt, Wlh, 400-d lh, 600-d lh)
3. Height-trait (Wht, 400-d ht, 600-d ht)
4. Girth-trait (Wgh, 400-d gh, 600-d gh)
5. Muscle-trait (Wmus, 400-d mus, 600-d mus)
6. Fat-trait (Wfd, 400-d fd, 600-d fd)

Linkage between each marker per chromosome and each standardised trait or PC group was tested using Knott et al. (1996) regression procedures, with "QTL Express" software (Sealey et al., 2001). For each progeny, the probability of inheriting the sire haplotype in a linkage group was calculated at fixed intervals (e.g. 4-cM) conditional on its marker genotype. Subsequently, a QTL is fitted at the fixed intervals along the linkage group by regression of phenotype on the probability of inheriting the haplotype of the parent. The analysis was nested within families and the residuals pooled across families to calculate a test statistic that was considered suggestive of linkage if it exceeded a value of F >4. When mapping QTL, a significantly linked marker ($P< 0.05$, genome-wide test) was required to have an F-test statistic > 10.1 (within a single sire tested separately) or > 5.2 (across all three sires together), using the criteria of Lander and Kruglyak (1995). The regression model for every chromosome is as follows:

$$Y_{ijk} = a_i + b_{ij}X_{ij} + e_{ijk}$$

Where Y_{ijk} is the standardised trait value of individual j, half-sib progeny from parent i, a is the polygenic effect for half sib family i, b is the regression coefficient within family i (i.e., allele substitution for a putative QTL); X_{ij} is the conditional probability for individual j of inheriting the first haplotype from parent i, and e_{ijk} is the residual effect. For every linkage group (chromosome), the most likely position of a QTL is calculated as the position associated with the maximum F-value. Candidate regions are identified based on significance levels from permutation tests on individual chromosomes as described by Churchill and Doerge (1994). The two-QTL model (Sealey et al., 2001) option was also tested, where there is an initial indication for two QTL on the test of significance curves of a chromosome.

Table 6.1. Main and gain traits of growth and development for mapping animals

Trait	Abbreviation	N	Mean	σ_P	CV (%)
Birth:					
Weight (kg)	Bwt	409	26.1	3.9	14.9
Height (cm)	Bht	409	68.7	3.8	5.5
Length (cm)	Blh	409	53.3	3.3	6.1
Girth (cm)	Bgh	409	69.5	3.9	5.6
Weaning:					
Weight (kg)	Wwt	370	228.7	26.0	11.4
Height (cm)	Wht	363	110.0	3.9	3.5
Length (cm)	Wlh	369	114.2	6.0	5.2
Girth (cm)	Wgh	370	146.6	6.1	4.2
Muscle (%)	Wmus	370	81.1	5.5	6.7
Fat depth (mm)	Wfd	369	0.5	1.1	228.6
400-day:					
Weight (kg)	400-d wt	370	252.6	25.3	10.0
Height (cm)	400-d ht	369	119.5	4.4	3.7
Length (cm)	400-d lh	369	125.9	7.6	6.1
Girth (cm)	400-d gh	369	157.5	5.9	3.7
Muscle (%)	400-d mus	289	74.0	5.0	6.8
Fat depth (mm)	400-d fd	369	1.0	0.7	65.4
600-day:					
Weight (kg)	600-d wt	367	361.6	31.0	8.6
Height (cm)	600-d ht	367	126.1	3.7	3.0
Length (cm)	600-d lh	367	129.8	6.0	4.6
Girth (cm)	600-d gh	363	174.1	6.6	3.8
Muscle (%)	600-d mus	287	74.4	4.8	6.5
Fat depth (mm)	600-d fd	366	1.6	1.8	110.0
ADG1:					
Weight (g/d)	Adgwt1	370	711.5	84.1	11.8
Height (mm/d)	Adght1	363	145.1	14.0	9.6
Length (mm/d)	Adglh1	369	214.0	20.1	9.4
Girth (mm/d)	Adggh1	370	269.3	20.2	7.5
Fat depth (μm/d)	Adgfd1	369	1.7	4.0	229.7
ADG2:					
Weight (g/d)	Adgwt2	370	161.0	93.0	57.8
Height (mm/d)	Adght2	362	65.7	26.5	40.4
Length (mm/d)	Adglh2	368	83.6	61.2	73.2
Girth (mm/d)	Adggh2	362	327.8	38.1	11.6
Muscle (%/dx10^{-3})	Adgmus2	289	-47.0	48.9	104.0
Fat depth (μm/d)	Adgfd2	268	4.6	7.4	160.2
ADG3:					
Weight (g/d)	Adgwt3	367	572.5	88.3	15.4
Height (mm/d)	Adght3	367	34.5	19.3	56.0
Length (mm/d)	Adglh3	367	23.4	43.1	183.9
Girth (mm/d)	Adggh3	363	87.1	33.7	38.7
Muscle (%/dx10^{-3})	Adgmus3	287	-5.6	27.1	480.7
Fat depth (μm/d)	Adgp83	366	5.8	10.7	182.4

6.3 Results and Discussion

A genome scan for the chromosomal regions affecting pre- and/or post-natal growth and development was undertaken using over 200 informative microsattelite markers spanning about 25 Morgans on 29 bovine autosomal chromosomes. Several regions on specific chromosomes that achieved genome-wide significance for different traits (animal weight, skeletal size and muscular composition) were identified. Seventeen out of the 29 autosomes were shown to contain regions with QTL effects for individual traits of weight, skeletal dimensions (height, length and girth), muscularity (hip by stifle ratio) and P8 fat depth measurements at birth, weaning (250-days), 400- and 600-day postpartum. QTL were also mapped for average daily gains in all traits between different ages (Appendix 5a and 5b).

Genetically correlated cluster traits were used for principal component (PC) analysis to determine the major QTL regions. The use of the principal component method extracts more information from the measured traits across ages than the conventional linkage analysis based on individual traits, thus having the potential to enhance power of detected QTL. This type of hierarchical clustering step offers a way to select functionally distinct chromosomes for detailed molecular analysis, or to measure the extent of genetic variation across chromosomes for specific traits in the population of interest, thereby potentially revealing the signature of possible selection effects (Kim and Georges, 2002). Only eight chromosomes had principal component regions that reached genome-wide significance.

Genome-wide screening of progeny (370) from the F_1 sires provided a significant indicative evidence of QTL effects initially segregating on regions of most chromosomes (1, 2, 4, 5, 6, 7, 8, 9, 13, 14, 16, 17, 19, 21, 22, 23 and 25) (Appendix 5a and 5b). Most QTL had genome-wide permutation test with up to the 99% confidence limit ($P<0.01$).

As shown in Table 6.2, only the first PC (PC1) component had an eigenvalue greater than 1, accounting for over 50% of the total variation for all groups except for PC on muscularity where only 47% of variation was determined by PC1. The second PC (PC2) on muscularity accounted for an additional 27% variation with an eigenvalue close to 1. The second, third, fourth, fifth and sixth principal components (Table 6.2) were not considered for many of the traits because the eigenvalues were generally less than 1 (Gutierrez and Goyache, 2002). The interpretation of the first two PC (described as Factors 1 and 2) was possible taking into account the sign and magnitude of the eigenvectors. The eigenvectors for the first PC, which was ≥0.5 in many instances, was best in describing the animal for birth (size), growth, height, girth (skeletal development), muscle and fat (shape) traits across ages (Table 6.3).

Table 6.2. Eigenvalue and proportion of total phenotypic variance explained (in percentage) by principal component on groups of clustered traits

Trait (Component)	Principal component (PC)	Eigenvalue	Proportion of total variance	Cumulative proportion
Birth-trait: (Bwt, Bht, Blh, Bgh)	1	3.03	76	76
	2	0.43	11	87
	3	0.37	9	96
	4	0.17	4	100
Growth-trait: (Wwt, 400-dwt, 600-dwt, Wlh, 400-dlh, 600-d lh)	1	3.72	62	62
	2	0.80	13	75
	3	0.61	10	85
	4	0.54	9	94
	5	0.21	4	98
	6	0.13	2	100
Height-trait: (Wht, 400-dht, 600-dht)	1	2.21	74	74
	2	0.41	14	87
	3	0.39	13	100
Girth-trait: (Wgh, 400-dgh, 600-dgh)	1	2.10	70	70
	2	0.54	18	88
	3	0.37	12	100
Muscle-trait: (Wmus, 400-d mus, 600-d mus)	1	1.42	47	47
	2	0.81	27	74
	3	0.78	26	100
Fatness-trait: (Wfd, 400-d fd, 600-d fd)	1	1.62	54	54
	2	0.81	27	81
	3	0.57	19	100

Table 6.3. Eigenvectors of the first two principal components on group of clustered traits

Cluster trait	PC1 (Factor 1)	PC2 (Factor 2)
Group1 (Birth-trait):		
Bwt	0.53	-0.20
Bht	0.47	-0.40
Blh	0.48	0.87
Bgh	0.52	-0.21
Group2 (Growth-trait):		
Wwt	0.47	-0.12
400-d wt	0.48	-0.09
600-d wt	0.46	-0.06
Wlh	0.38	-0.21
400-d lh	0.27	0.95
600-d lh	0.36	-0.13
Group3 (Height-trait):		
Wht	0.58	-0.22
400-d ht	0.58	0.79
600-d ht	0.58	-0.57
Group4 traits:		
Wgh	0.57	-0.69
400-d gh	0.61	-0.03
600-d gh	0.56	0.73
Group5 traits:		
Wmus	0.57	0.80
400-d mus	0.59	-0.23
600-d mus	0.58	-0.55
Group6 traits:		
Wfd	0.63	-0.20
400-d fd	0.59	-0.50
600-d fd	0.50	0.84

As in this study, some earlier studies describing animals in dairy herds for size, skeletal and muscular development utilised only the principal components with eigenvalue ≥1 (Vuksinovic et al, 1997; Roughsedge et al., 2000). In a recent study involving Asturiana de los Valles beef cattle in Spain, Gutierrez and Goyache (2002) retained two principal components showing an eigenvalue >1, accounting for 50% of the phenotypic variance in a combination of 10 type traits.

The application of animal size and shape classification based on principal components (PC) obtained from a clustered group of main traits reduced the chromosomal number with QTL effects from 17 to 8. Significant evidence of QTL effects based on the first PC on trait for body growth and development were observed on BTA2 (early and late postnatal

muscularity), BTA5 (birth-trait), BTA6 (postnatal growth), BTA13 (early and late postnatal muscularity), BTA14 (pre- and post-natal growth), BTA16 (late postnatal growth), BTA21 (early and late postnatal fatness) and BTA23 (postnatal growth) (Table 6.4). There was also significant evidence of a QTL effect on BTA24 for PC2 on muscularity that defined early postnatal muscular development.

Table 6.4. QTL effects on first principal components of growth and development traits

Chr.	(M)	Trait	QTL effect±S.E F_1 Sire per family 1(361)	2(368)	3(398)	F	Loc. (cM)	Prob.
			Single QTL model					
2	**(10)**	PC1MUS	-0.93±0.29***	-0.30±0.28	1.03±0.32***	7.3	8	0.01
5	**(9)**	PC1BT	0.08±0.31	-0.52±0.47	1.36±0.36***	5.1	32	0.05
6	**(8)**	PC1GT	0.82±0.39*	0.51±0.38	1.79±0.75**	4.0	112	0.05
13	**(9)**	PC1MUS	0.55±0.26*	0.66±0.24***	-0.18±0.27	4.2	0	0.05
14	**(9)**	PC1BT	-1.22±0.31***	-0.29±0.32	-0.24±0.32	5.5	28	0.01
		PC1GT	-1.23±0.38***	0.04±0.36	-0.28±0.38	3.7	24	0.05
		PC1HT	-1.26±0.30***	0.00±0.30	-0.78±0.30***	8.3	12	0.01
		PC1GH	-0.92±0.29***	-0.13±0.28	-0.03±0.29	3.4	24	0.05
16	**(9)**	PC1GT	-0.57±0.37	-0.39±0.19	-1.03±0.38***	3.7	72	0.05
21	**(9)**	PC1FD	-0.99±0.27***	-0.51±0.23*	-0.06±0.28	6.0	48	0.01
23	**(6)**	PC1GT	1.46±0.54***	-1.21±0.66	-0.71±0.66	3.9	16	0.05
24	**(4)**	PC2MUS[a]	0.52±0.21**	-0.12±0.20	-0.57±0.23**	4.2	16	0.01
			Two QTL model					
2	**(10)**	PC1MUS						
		QTL1 (2aMus)	-0.84±0.30***	-0.19±0.27	1.04±0.34***	5.4	4	0.01
		QTL2 (2bMus)	-0.15±0.32	-0.56±0.29**	0.71±0.29**	3.4	80	0.05

PC1= Principal component 1, [a]PC2= Principal component 2, MUS= Postnatal muscle-trait, BT= Birth-trait, GT= Postnatal growth-trait, HT= Postnatal height-trait, GH= postnatal girth-trait, FD= postnatal fat-trait, M= # markers/chromosome

In general, separate genes or QTL control of prenatal growth of weight and body dimensional traits (eg. animal size at birth) could not be established. In this study, the control of animal size at birth could be attributed to regions of the genome that were distinct from the regions controlling post-natal growth. Apart from a region on chromosome 14 which influences early and late growth, the results herein suggest that different regions of the

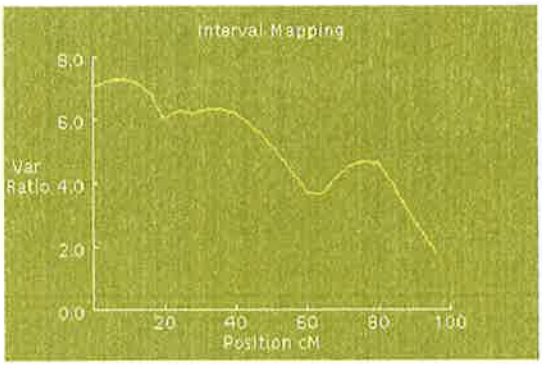
genome might be responsible for the expression of pre- versus post-natal body growth and composition in beef cattle breeds. Furthermore, the postnatal measure of muscularity was influenced by QTL distinct from the fatness QTL. This might allow effective and early genomic introgression to meet specific meat quality specifications for future stock.

The fact that post-natal growth traits such as the height of an animal may be significantly influenced separately higher than weight or other body dimensional traits (e.g. animal length and girth) by the same region is a key finding herein (Table 6.4). There was also indication of specific locational control for most of the constituent traits of growth and development (Appendix 5a and 5b). While postnatal growth of girth and length in combination with animal weight is important in improving the localization of QTL for growth, the impact of the QTL for postnatal height growth was observed to be different in phenotypic expression. This is an indication that some specific QTL (e.g. BTA 14) has an independent action on post-natal growth of animal height (Table 6.4).

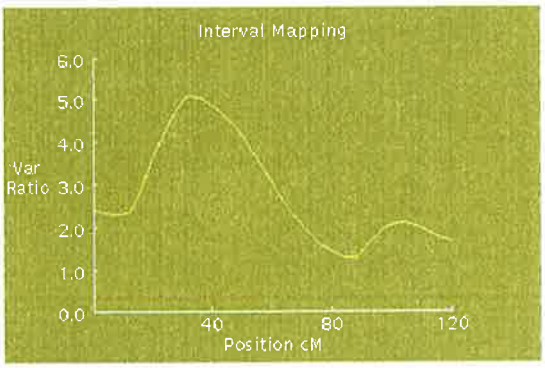
6.3.1 Significant QTL on chromosome 2: Two significant DNA regions were identified on BTA2 influencing PC1 on muscularity. The first QTL (QTL1) was between micro-satellites BM2113 and BMS356 (same region of TGLA44 and INRA40), situated from approximately 0 to 5cM. The second QTL (QTL2) was between markers OAFCB20 and ILSTS30 (close to another marker BMS2626) from approximately 65 to 85cM (Figure 6.1). Effect associated with the second QTL (mapped more than 70cM away from the first QTL) was independent of the first QTL, since the F-statistic remained significant ($P<0.05$) after accounting for the first QTL. This result suggests the likelihood of another QTL affecting post-weaning muscular development on BTA 2.

The differences between the L-derived and J-derived alleles from the sire for QTL1 (at approximately 4cM) or QTL2 (at approximately 80cM) were significant ($P<0.01$) in two

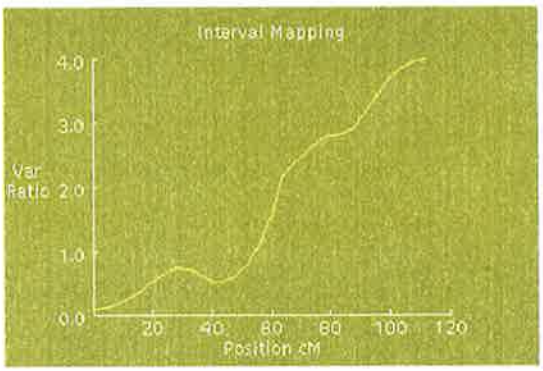
sire families for QTL1 and one sire family for QTL2 (Table 6.4). PC1 for muscularity accounted for 47% (Table 6.2) of the variance in 3 traits (muscularity at weaning, 400- and 600-day). As an average across the two significant sire families, the estimated QTL effect as a percentage of the standard deviation was over 60% for the first QTL (Figure 6.2). Interestingly, J-derived alleles significantly ($P<0.01$) increased muscularity phenotype in one sire family (361) and the L-derived alleles increased muscularity in another sire family (398) (Table 6.4).



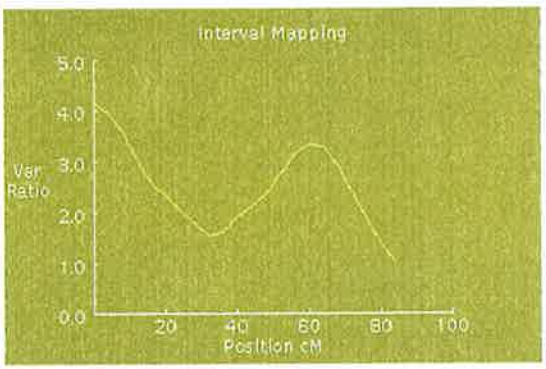
PC1 of muscularity on BTA2



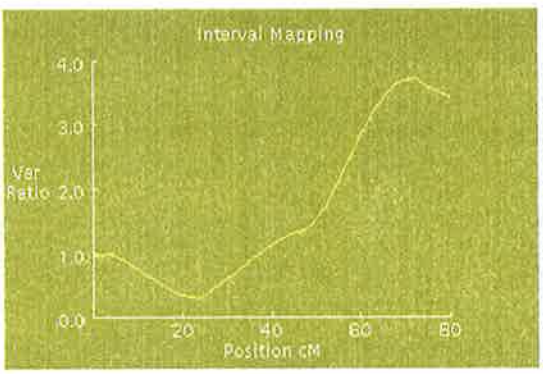
PC1 of birth-trait on BTA5



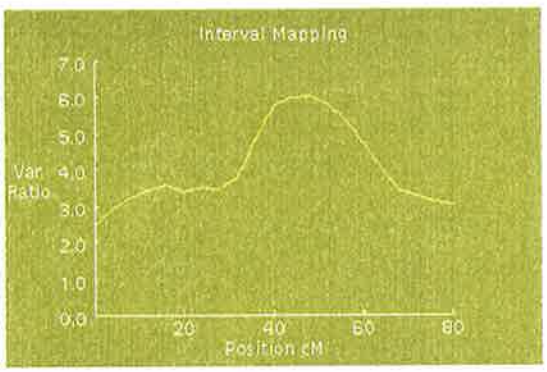
PC1 of growth-trait on BTA6



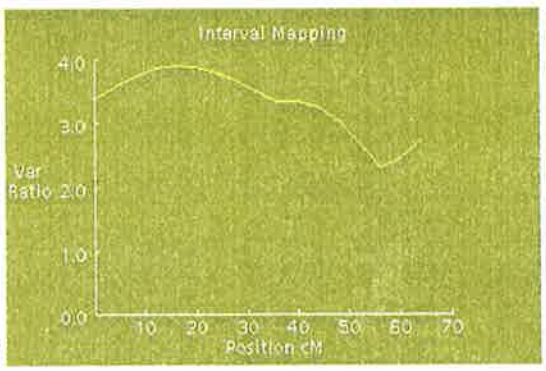
PC1 of muscularity on BTA13



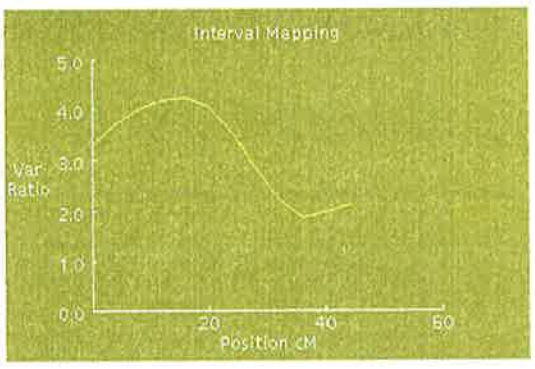
PC1 of growth trait on BTA16



PC1 of fat trait on BTA21



PC1 of growth trait on BTA23



PC2 of muscularity on BTA24

Figure 6.1. Test of significance of QTL for growth and development traits

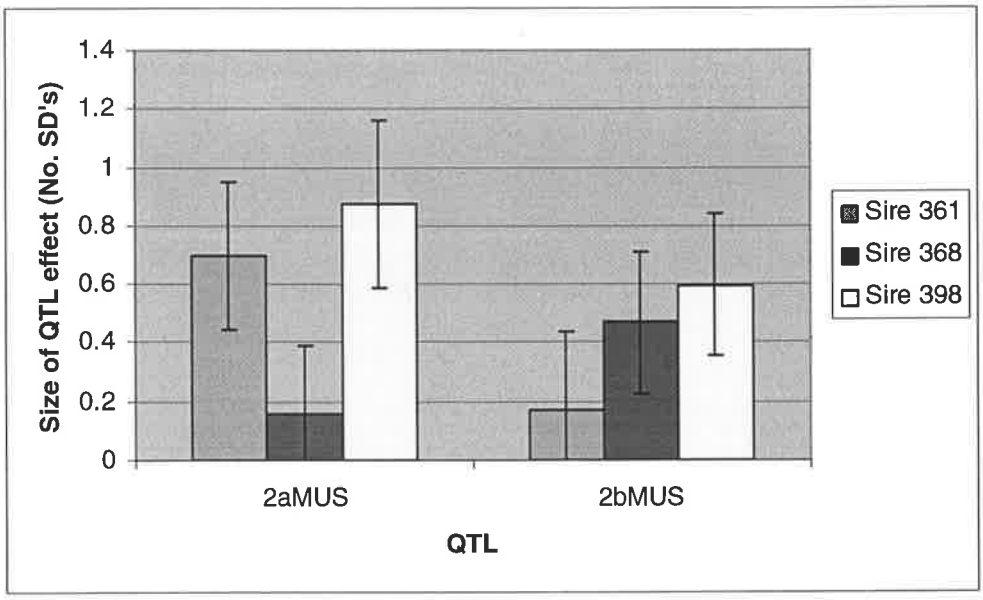


Figure 6.2. Size of QTL effects of PC1 on muscularity: Two QTL model

The position of the first QTL segregating on the measure of muscularity (PC1) in this study on BTA2 coincides with the position of mh locus containing the myostatin gene. Individual component traits that make up the PC1 muscularity were also significant at this position at the suggestive level. The myostatin gene is a strong positional candidate gene with five mutants identified to be responsible for double-muscling or muscular hypertrophy in mice (McPherron et al., 1997) and in cattle (Smith, et al., 1997; Casas et al., 1998). This gene is located at the centrometric end of bovine chromosome 2 (McPherron and Lee, 1997; Smith et al., 1997; Grobet et al., 1998). The studies of Charlier et al. (1995) and Dunner et al. (1997) also mapped the *mh* locus to BTA2 between TGLA44 and the centromere at position of 2 and 3.1 cM respectively, on the linkage map.

The study herein confirms the historical evidence that myostatin must be a major gene in beef cattle causing similar physiological events in all breeds with specific allelic variants (Menissier, 1982; Arthur, 1995). A comparison of the families generated by the three F_1 sires indicated that at least two of the sire families were heterozygote for the observed condition. Also, the F-statistics were high for the first QTL, giving a level of confidence that the result would be real in this population. The inheritance of the allele from Jersey origin led to an

increase in muscularity relative to Limousin allele for the QTL. This finding between the alternative allele was similar to that previously reported in which individual inheriting the *mh* allele, from either the Belgian Blue or Piedmontese sire, had a higher proportion of muscle mass and were leaner (Casas et al., 1998).

Stone et al. (1999) also detected a QTL for marbling on chromosome 2, but the locus was unrelated to the myostatin gene (distance >60cM apart). Contrary to the study of Stone et al. (1999), no significant QTL at the chosen level of F-statistics was observed on BTA2 for any sire family for the measure of fatness (P8 fat depth) in this study.

In contrast to the single QTL effect on muscularity reported by many earlier studies, the present result has indicated that apart from the myostatin gene (or a gene close by), there could be another QTL segregating on BTA2 which is responsible for variation in the degree of post-weaning muscularity in the Limousin x Jersey cross population. Since the first QTL mapped between 4 to 8cM, it could be related to the double muscling (*mh)* locus, which is at 4cM (Smith et al., 1997; Casas et al., 1998). However, a possible candidate gene for the position of the second QTL at 75-80cM is yet to be determined. Since more than one region within or between chromosomes (i.e. BTA13) with significant QTL effects were detected, the results suggest that there may be more than one QTL on postnatal muscularity. These QTL may be working additively or epistatically.

6.3.2 Significant QTL on chromosome 5: A single DNA region on BTA5 was found to have a significant association with the PC1 for birth-traits. The region of the QTL was between microsatellites AGLA293 and OARFCB05, situated at approximately 32cM (Figure 6.3). The differences between the L-derived and J-derived alleles from the sire for the QTL was significant as a t-test at $P<0.001$ for one sire family (398) (Table 6.4). PC1 for birth-traits, which represents average size description based on weight and body dimension at birth

(Table 6.2), accounted for 76% of the variance based on the PC analysis of the constituent traits (Bwt, Bht, Blh and Bgh). The QTL was significant at P<0.05 (Table 6.2). The only sire (398) with significantly linked phenotypes in the progeny had over 60% of the PC1 deviation accounted for by the QTL effect (Table 6.3) with J-derived allele increasing birth-traits and the L-derived allele decreasing the birth-traits.

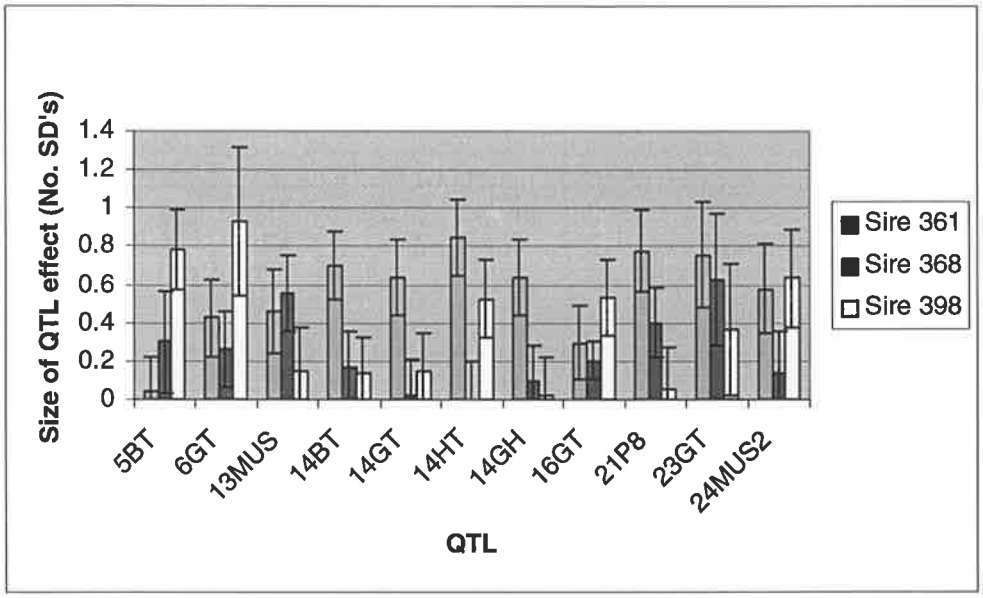


Figure 6.3. Size of QTL effects of PC: One QTL model

The QTL for birth-traits that was mapped to the region of 32cM on bovine chromosome 5 was similar to some earlier studies. Li et al. (2002) detected a region between 10 to 30cM from centromere that affected birth weight, preweaning average daily gain and average daily gain on feed in an M1 line cattle. This M1 line was developed from an Angus base and is a medium-framed, maternal strain selected for fertility, mothering ability, and pre-weaning gain. The position for birthweight QTL herein was also close to the 50-85cM QTL found by Stone et al. (1999) and the 65-75cM QTL found by Li et al. (2002) in M3 cattle on BTA5. The M3 line is a small-framed, maternal strain developed from small cows of various breeds that have no difficulty calving. In the report of Davies et al. (1998a), however, the observed QTL for birth weight on chromosome 5 using families obtained from a *Bos indicus x Bos taurus* cross was in the region of 70 to 110cM. The position of the QTL in that report

(Davies et al., 1998a) was over 50cM apart from the QTL reported herein and may suggest different QTL in the two studies.

Other studies have identified closely linked candidate genes that may be responsible for growth and carcass composition in bovine at the position of the QTL found on BTA5 in this study. Casas et al. (2000) observed a QTL for carcass traits located near the *insulin-like growth factor I* gene (IGF1) on chromosome 5. Also, an association between IGF1 and growth in Hereford cattle has been reported which suggests that IGF1 or a neighbouring gene could be associated with growth (Moody et al., 1996). In another study by Stone et al. (1999), there was compelling evidence for a QTL on BTA5 that increases the amount of bone in wholesale ribs and decreases dressing percentage in progeny inheriting the Brahman allele compared with the Hereford allele. In the homologous region of chromosome 5 in mice, there was also a reported QTL associated with growth using markers closely linked with IGF1 (Collins et al., 1993). The study of Horvat and Medrano (1995) using a population of mice segregating for the high growth (*hg*) locus mapped the gene to a region near IGF1. However, the 500-kb deletion, presumably responsible for the high growth phenotype, did not include IGF1.

In the cattle population studied herein, a large proportion of the genetic variation in birth-trait PC1 was accounted for by the QTL on BTA5. The opposing relationship observed between the two alleles (J- and L-derived) is of great interest. The L-derived allele that decreases the size of animals at birth may be desirable in a breeding scheme to reduce the incidence of dystocia or difficult births since the same allelic effect on BTA 14 was found to increase late growth (Morris et al., 2002). Li et al. (2002) also reported an haplotype associated with lower birth weight and higher average daily gain in later life in the same genomic region (BTA5) in commercial lines of *Bos taurus* breeds.

6.3.3 Significant QTL on chromosome 6: The maximum F-statistics for postnatal growth-trait PC1 (clustered of weight and length) QTL was detected at 112cM in two sire families (Figure 6.1). The effect of the same QTL was near significance (F-value = 3.03) for the girth PC1 of sire 361 at the same location. Microsatellite BM2320 is close to the DNA region containing the QTL (112.5cM). The differences between the L-derived and J-derived alleles for this QTL were significant for the growth phenotypes of progeny from sires of 361 ($P<0.05$) and 398 ($P<0.01$) (Table 6.4). The estimated effect on the PC1 accounted for 62% of the phenotypic variance in the 6 constitutive traits (postnatal weights and longitudinal skeletal traits) (Table 6.2). For the most significantly linked sire (398), the QTL effect on the trait accounted for 80% of the deviation (Figure 6.3).

Very few studies have identified QTL for growth on cattle chromosome 6, especially at the region reported in this study. In a Belgian Blue family, Casas et al. (2000) found evidence of a QTL on chromosome 6 for growth traits such as birth weight and weight at one year of age. The same authors also observed an influence of the QTL on carcass traits such as Longissimus dorsi muscle area and hot carcass weight as well. The findings by these authors may support the study herein, where a QTL for weight at weaning (approximately 250 days) and pre-weaning weight was observed in the region between 108 to 112cM but not at birth (AT. 4a). Also, similar to Casas et al. (2001), this study identified differences in early weight traits due to an alternative allele inheritance. The J-derived rather than L-derived allele increased early weight traits in the two significant sire families, which could be an indication that the J-allele may be associated with early growth only.

Davies et al. (1998a) conducted a study that was focussed mainly on birth weight and they also observed a QTL on cattle chromosome 6. However, in this study (herein), there was no significant association between the detected QTL and birth-traits (either individually or as clustered trait). For the PC1 on postnatal growth, the magnitude of the identified QTL effects

was only suggestive on a genome-wide level, indicating that the effects of the loci may be small in the population herein. Although the present results suggest that this region of chromosome 6 may be associated with early postnatal growth, this should be confirmed in another population with more progeny.

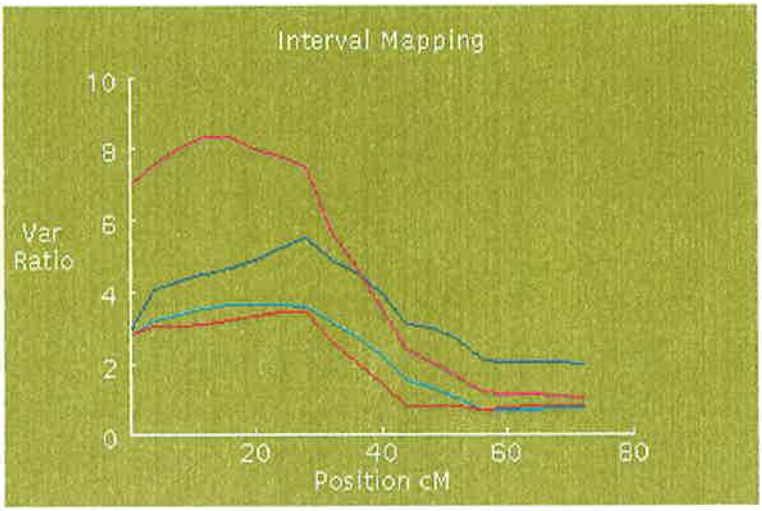
6.3.4 Significant QTL on chromosome 13: A suggestive F-statistic peak (F = 4.15) at 0cM on BTA13 for a significant DNA region for the PC1 on muscularity was observed (Figure 6.1). The microsatellite marker identified at this region was TLGA23. A significant difference between L- and J-derived alleles was observed for sire 361 ($P<0.05$) and sire 368 ($P<0.01$) (Table 6.4). The percent estimated effect of QTL on standard deviation of PC1 on muscularity using the most significant sire family was over 50% for this region of chromosome (Figure 6.3). The L-derive allele increased muscularity in the most significant ($P<0.01$) family (368) in contrast to the J-derived allele but the reverse was the case for the other family (361, $P<0.05$) (Table 6.4).

The results of the present study provide support for a significant muscularity QTL on BTA13 that has not been reported in any study. However, in one earlier study, Casas et al. (2000) identify a putative QTL on fat depth and retail product in a Piedmontese family on BTA13. This family was also segregating alternative forms of myostatin on BTA2. Interestingly, an earlier report of Stone et al. (1999) also observed a QTL which decreased dressing percentage and rib-fat weight (Brahman relative to Hereford) with a corresponding increase in rib muscle and retail product yield on BTA13, just below the significance threshold level.

In the present study, the J-derived allele was found to increase muscularity relative to the L-derived allele in both sire families with a significant QTL effect as observed on BTA2. Unlike the study of Stone et al. (1999), which reported an alternative effect of the QTL on muscling and fat, the study herein found no effect of the same QTL on measurement of fatness on BTA13.

Although the candidate gene GHR (growth hormone receptor) from the GH-IGF endocrine axis is at approximately 65cM on BTA13 (Barendse et al., 1994), this position is quite distant from the 0cM position of the significant QTL for PC1 on muscularity mapped in the present study. The huge gap between the DNA regions in the study herein and that reported by Barendse et al. (1994) suggested that the QTL are unrelated. However, there was an indication of a QTL, near significant for PC1 on muscularity (Figure 6.1), and significant for muscularity at 600-day (Appendix 5a) at approx. 60cM (close to 65cM) next to that reported by Barendse et al. (1994).

6.3.5 Significant QTL on chromosome 14: Marker information suggested a pronounced influence of a single QTL on the birth-trait PC1 (at approximately 28cM, F=5.52) and PC1 for post-natal height-trait (at approximately 12cM, F=8.31) on chromosome 14 (Figure 6.4).



__ PC1 Height, __ PC1 Birth, __ PC1 Growth, __ PC1 Girth

Figure 6.4. Test of significance of QTL for pre- and post-weaning growth traits on BTA 14

The PC1 for birth-traits and postnatal height-traits were 76% and 74% of the phenotypic variance of their respective constituents (Table 6.2). The QTL was between microsatellites ILSTS011 and ILSTS008, situated from approximately 10-30cM. Birth height as a single trait was not influenced by the QTL at this region (Appendix 5b). The effect of the same QTL on other PC1 traits of post-natal growth (defined by postnatal weights and length measures) (F=3.67) and postnatal girth (F=3.41) did not reach significance at the chosen level of F-statistic (F=4) (Table 6.4). However, genome-wide permutation tests indicated significant ($P<0.05$) QTL effects for both pre- and post-natal growth in this same region (10-30cM).

The differences between the L-derived and J-derived alleles from the sire for the QTL were significant at $P<0.01$ for birth and post-weaning height and growth phenotypes (Table 6.4). Sire 361 was the only one with phenotypic significant ($P<0.01$) linkage for birth-trait, while the same sire ($P<0.01$) together with sire 398 ($P<0.01$) had significant linkage with the postnatal height PC1 on BTA14 (Table 6.4). Also, as with single individual traits, most phenotypes under the control of the same QTL showed a distinction between L- and J-derived alleles ($P<0.01$, Appendix 5b). The percent estimated QTL effect using the only significant sire on birth-trait PC1 was over 60% and average across the 2 significant sires for PC1 on

postnatal height was over 50% (Figure 6.3). The J-derived allele in contrast to the L-derived allele decreased both pre- and post-natal growth traits.

The evidence of a QTL on BTA14 segregating in the population herein which affects pre- and post-natal growth supports a number of published papers. Davies et al. (1998a) detected and mapped QTL for birth weight on bovine chromosome 14 in three Charolais x Brahman paternal half-sib families at 0cM and at 42cM. Stone et al. (1999) reported on a Brahman paternal half-sib family with suggestive evidence of a QTL for carcass and growth traits at 19cM. A study by Casas et al. (2000) also suggested that a QTL was segregating in a region of 15cM on BTA14 for carcass composition and growth in a Piedmontese paternal half-sib family and in a Belgian Blue family. Other reported studies of QTL on BTA14 include that of Spelman et al. (1999) for stature (36cM) and that of Kim and Georges (2002) for milk composition (1cM) in dairy cattle and Buchanan et al. (2000) for growth in cattle at both 0cM and 67cM. Growth QTL was also reported in the same syntenic region of pigs (Andersson et al., 1994; Wang et al., 1998; Walling et al., 2000).

Some important and possible candidate gene in the region of the identified QTL in this study include *myc*. *myc* is a transcription factor known to activate growth promoting genes and repress growth arresting genes (Morris et al., 2002). Another possible candidate gene in the observed region could be thyroglobulin gene (*TG*), which also has been reported to be associated with marbling in cattle (Barendse, 1997). In pigs, Yu et al. (1999) linked PIT1 gene to the same syntenic region with significant effect on birth weight.

The QTL on chromosome 14 herein is singular in its effect on both early and late growth. The pleiotropic significance of the QTL on BTA14 on early and late growth needs further investigation. Apart from its influence on growth traits, the QTL on BTA14 has also been significantly linked with important carcass traits (Stones et al., 1999; Casas et al., 2000;

Morris et al., 2002). The fact that several traits were apparently associated with the same chromosomal region increases the confidence that more than one haplotype of a gene or cluster of genes affecting growth and possibly carcass traits resides in the region. The role of this QTL in relation to other QTL within the genome for growth and production traits in different populations should therefore be ascertained.

6.3.6 Significant QTL on chromosome 16: There was an indication of a QTL for PC1 on growth (defined by postnatal weights and length measures) at position 72cM (Figure 6.1) on chromosome 16. The DNA region was between microsatellites BM719 (at approximately 71cM) and BM3509 (at approximately 77cM). Genome-wide permutation test was significant at $P<0.05$ ($F= 3.75$) with one sire (398) showing highly significant ($P<0.01$) differences between the L-derived and J-derived alleles (Table 6.4). The percentage estimated effect due to the QTL on the standard deviation in this sire family was 55%. The suggestive QTL effect at 72cM on chromosome 16 influencing growth was not supported by any earlier studies. The fact that the permutation test on this QTL was significant only at $P<0.05$ in one sire family calls for further investigation to determine the authenticity of the QTL in other populations with more progeny.

6.3.7 Significant QTL on chromosome 21: A suggestive QTL affecting fat depth PC1 was identified on a region of chromosome 21 at a distance of 48cM ($F=6.02$). The observed QTL was between microsatellites BMC4228 (at approximately 40cM) and ILSTS016 (at approximately 50cM) (Figure 6.1). Genome-wide permutation was highly significant ($P<0.01$) for the QTL and 2 sires families [361 ($P<0.01$ and 368 ($P<0.05$)] were significantly segregating differences between the Jersey and Limousin inherited alleles (Table 6.4). The PC1 for fat depth (Table 6.2), which represents proportionate fat content through weaning to 600-day age, accounted for 54% of the variance in 3 traits (Wfd, 400-d fd and 600-d fd). Sire 361 had the most significantly linked progeny phenotypes and the estimated QTL effect was

70% of the standard deviation unit (Figure 6.3). However, on an average across the two significantly sires families, the percent estimated effect of QTL on the PC1 variance was reduced to 55%. The J-derived allele in contrast to L-derived allele resulted in fat reduction in the most significant family.

One peak at the centromeric position of chromosome 21 achieved genome-wide significance (P<0.01) on the measure of fatness (P8 fat depth) around 48cM (F=6.02). No other reported QTL effect on fatness has been reported on BTA21, suggesting that the observed result requires further investigation in larger cattle populations. In a family of Belgian Blue cattle, evidence suggesting the presence of a QTL that affects fat depth and marbling score was identified on chromosome 8 (Casas et al., 2001). In earlie studies, a QTL for fat traits was detected on chromosome 2 in a family with a *Bos taurus* x *Bos indicus* sire (Stone et al., 1999) and on chromosome 5 and 14 in a Piedmontese x Angus sire family (Casas et al., 2000).

In the present study, there was also a genome-wide close to significant (P<0.05) QTL on 400-d fat depth in one sire family at 28cM position on chromosome 8 (Appendix 5a). The QTL for fat depth on region of BTA8 was similar to that reported (Casas et al., 2001). Although epistatic interactions between loci have been postulated to exist for QTL (Falconer, 1989), these interactions were not shown herein. Casas et al. (2001) observed evidence of an interaction of the QTL on BTA8 with the myostatin gene on chromosome 2. In that study, Casas et al. (2001) showed individuals inheriting the allele from the double-muscled grandsire deposited greater amounts of fat than those individuals inheriting the active myostatin allele from the grandam. The possibility of this kind of interaction between the QTL obtained on chromosome 2 and the specific region associated with fat metabolism (e.g. region on BTA8 or BTA21) was not investigated herein and cannot be ruled out.

6.3.8 Significant QTL on chromosome 23: A suggestive QTL affecting PC1 on postnatal growth was identified on a region of chromosome 23. The position of the QTL by genome-wide permutation ($P<0.05$) was 16cM (Figure 6.1) between microsatellite INRA132 (at approximately 0cM) and CYP21 (at approximately 36cM). There was a significant difference between the J- and L-derived alleles of the QTL as a t-test ($P<0.01$) in one sire family (361) (Table 6.4). The QTL effect was over 70% of a standard deviation unit in the single significant sire family. The J-derived allele increased the postnatal growth in the significant family in contrast to L-derived allele.

There was no reported QTL effect for the growth traits on BTA23 in any earlier studies except in Finnish Ayrshire dairy cattle (Elo et al., 1999). In that study, a QTL for live weight was detected using six microsatellite loci on BTA23 between markers BM1258 (at approximately 21cM) and BoLA DRBP1 (at approximately 31cM). Since there is a limited study for comparison, the significant QTL on growth observed on BTA23 could be an artifact rather than definitive. This is partly because of the limited markers (6) on this chromosome and partly because of the wide gap between adjacent markers at the telomeric end. When using data from extreme animals for a seleted trait, widely spaced markers (i.e. 10 – 20cM) could result in esitimated QTL effects that are biased in absolute value (Stone et al., 1999). Although, genome-wide test of significant was obtained for the QTL on a single sire family, considerable caution should be used in accepting the informativeness of the markers because of the earlier enumerated limitations. In essence, further studies involving additional animals and markers may be required to ascertain the validity of the QTL indicated by the suggestive F-statistic peak in this study on BTA23.

6.3.9 Significant QTL on chromosome 24: There was evidence supporting the presence of a QTL for PC2 on muscularity on BTA24. The DNA region was situated at 16cM (F=4.23) (Figure 6.1) and was flanked by microsatellites BM7151 (at approximately 0cM) and CSSM31 (at approximately 19cM). PC2 (mainly define muscularity at weaning) accounted for 27% of the variability in muscularity in the three traits (Wmus, 400-dmus and 600-dmus) (Table 6.2). Two sire families (361 and 398) had highly significant (P<0.01) differences between the L-derived and J-derived alleles for this QTL (Table 6.4). The estimated QTL effect from averaging the two sire families was over 40% of a standard deviation unit (Figure 6.3). In one sire family (361), the J-derived allele was involved in decreasing the weaning muscularity in contrast to L-derived allele but the reverse situation occurred in the other significant family (398).

The map position of a QTL for PC2 on muscularity (defined as early muscling) in BTA24 has not been previously reported. The fact that two sire families were significantly informative at the genome-wide level provides strong suggestive evidence of a segregating QTL for early muscularity development. However, the result of this study indicates that the impact of the alternative allele inherited from sire in each significant family were in opposite direction. Although the role of the alternative inherited allele was complementary for the QTL effect, the reason for this relationship cannot be established at this stage.

6.4 Conclusions

This study found strong evidence of separate associations between markers and QTL for pre-natal and postnatal growth and development. These results indicate that chromosome 2 may have two QTL with effects on postnatal muscularity, chromosome 5 may have one QTL with effects on birth-traits, chromosome 6 may have one QTL with effects on postnatal growth, and chromosome 21 may have one QTL with effects on fat depth. There could be a unique QTL, working independently or in association with other QTL, on chromosome 14

with effects on both pre- and post-natal growth. These findings provide important information for further studies to discover the genes affecting specific growth and development traits, identifying useful markers, and applying marker-assisted selection for these traits in various cattle populations.

Chapter 7

General Discussion

7.1 Introduction

Being able to better match the expected economic gain on product end-points with the realised genetic improvement in finishing programs is one of the most formidable tasks facing the beef production industry. The satisfaction of the ever-increasing demand of consumers for high quality meat, in the long term, depends largely on the incentive of beef producers to remain in production. Value-based marketing of beef products that would reward the producers should originate from their ability to link with seed stock breeders to accurately determine the amount and quality of carcasses from live cattle measurements. Unless accurate and practical live cattle measurements of carcass merit are developed, the economic advantage of genetic improvement will only benefit the processors rather than the producers.

In order to make rapid genetic progress for carcass value, the live measurements that could contribute to carcass merit must be heritable and measured with reasonable repeatability (Herring et al., 1994). Moreover, indirectly measured traits is also expected be favourably correlated to the breeding objective traits. The amount of saleable product, affected by the proportion of fat, bone and muscle (Tatum et al., 1986b), is influenced by animal growth and development. Thus, live cattle measurements that can adequately predict not only animal growth but also the rate of fat and muscle development will improve carcass quality. Since carcass value traits are difficult or expensive to measure, Stone et al. (1999) proposed the use of selection indices that included QTL with accurately estimated effects on carcass characteristics. Carcass traits cannot be measured generally on breeding animals and hence require indirect traits and/or link QTL. This practice could reduce the amount of lengthy and costly data collection by providing a means of genetic evaluation early in life. Also, for populations segregating QTL alleles having major effects, it is conceivable that individuals could be classified early in the production system to match genotypes with market targets (Stone et al., 1999).

7.2 Discussion

The present study involving growth and general body development in beef cattle breeds prior to slaughter is primarily targeted at predicting carcass characteristics that can be determined from live animal growth measurements. This was also an effort to assess differences in genetic potential for carcass merit prior to the processing and distribution phase, which has not been well established previously in beef production (Stone et al., 1999). However, one of the first difficulties in relating growth (usually measured in weight) to carcass traits is the genetic antagonism (or correlation, r_G) between early (eg. birth-weight) and late growth traits (eg. yearling weight) (Koots et al., 1994b; MacNeil et al., 1998), which may be detrimental to genetic progress by selection. This genetic antagonism among direct effects, as observed by Grotz and MacNeil (2001), results in a situation wherein selection based on phenotypes or breeding values for greater yearling weight may also significantly increase birth weight, but potentially increasing the incidence and severity of dystocia (calving difficulty). The converse is also true; selection for lower birth weight is likely to reduce yearling weight (Grotz and MacNeil, 2001), and hence, carcass yields. Thus, while unweighted or weighted r_G is positive (0.48 or 0.55) between birth-weight and subsequent weight (eg. yearling weight) (Koots et al., 1994b), the relationship between calf survival and birth-weight is antagonistic when birth-weight is higher than optimal (Cundiff et al., 1986).

Since the present study was not aimed at the prediction of carcass yield alone, but also other carcass quality characteristics important to prevent cold shortening and drip loss of meat, other developmental traits beside weight were considered. Included in this category were body dimensions (eg. height, length and girth measures), fat depth (P8) and muscularity measurements. These traits were needed to sufficently describe growth and development in relation to most economically important carcass traits (Chapter 4 and 5).

In order to enhance genetic improvement tools, the present study like most recent studies, combined both quantitative and molecular approaches. One of the most powerful tools in resolving the antagonism between economically important traits discussed above would be to identify genes or genomic regions (QTL) affecting early growth (eg. birth-weight) and not affecting subsequent growth (eg. yearling weight) or, conversely, subsequent growth but not birth traits. This practice will allow pre-natal genetic manipulation, and postnatal genetic selection for growth rates to fit populations in specific environments and operations (Grosz and MacNeil, 2001). QTL comprise one or more genes whose allelic variation contributes to a proportion of the genetic variation in a quantitative trait in a particular population (Burrow et al., 2001). Detection of genetic markers that are associated with QTL or genes controlling economic traits are useful to understand the relationship between the traits under consideration and the genetic regulation of physiological characteristics and to identify potential markers for marker-assisted selection of the trait.

7.2.1 Prediction of carcass traits from live animal measurements

The aim of the first experiment in this study (Chapter 3) was to establish whether the objective measurements used herein could predict beef cattle carcass traits. This would justify the use of some of the live measurements (eg. objective muscle score and scanned fat measures) for carcass composition prediction. Other reported studies of estimators of potential carcass yield and quality characteristics differences in live animals have been mainly based on weight, fatness (P8) and subjective muscle scores (Perry et al., 1993a, b;) or ultrasound muscle scores (Herring et al., 1994; Wolcott et al., 2001; Crews and Kemp, 2001; Crews and Kemp, 2002). However, subjective muscle score is often criticised for being easily subject to error depending on the skill of assessors and the inability to separate scores based on yield and muscle from yield and fat (Kempster et al., 1982). On the other hand, ultrasound animal muscle scoring requires specialized equipment and skills, making the use of the technology limited and expensive for many beef producers.

The first experiment found the measure of muscle (percentage ratio stifle to hip) to be negatively correlated (Table 3.3) with the P8 fatness measures, an indication that the measurement may not be biased towards fatter animals. It was also found that in predicting saleable meat yield, the objective body dimension (eg. height) and muscle measurement and scanned P8 fat depths compared favourably with those predicted from ultrasound P8 fat depth and muscle score plus weight (Wolcott et al, 2001) and from weight, visual muscle and P8 fat depth (Perry et al., 1993a,b; Herring et al., 1994). Thus, there could be value in utilizing the alternative muscle measurement herein plus scanned P8 fat depth to define composition with reasonable precision (R^2 = 56%, Table 3.3). Although there was a progressive loss in the predictive power of some measurements as the age between measurements and slaughter increased (data not presented), the strong correlations between measurements at post-weaning ages means that early prediction of carcass composition should still be possible.

7.2.2 Breed effect and genetic parameters on growth and development

In the second experiment (Chapter 4), the main aim was to quantify both between and within breed variation in the live animal measurements to justify using these measurements for selection. Of the body dimensional traits, only the measure of animal height was moderate to highly heritable at all ages including birth. This means that as early as birth, reasonable progress can be attained by selection for animal height compared to weight or other body dimensional traits (length and girth). Thus, if the genetic correlation of height with other production or carcass traits is favourable, then height could be an important early selection parameter.

Good estimates of genetic parameters with low standard errors for growth and developmental traits were obtained for animal measurements at 400-days postpartum as a case study (Chapter 4). At this age, height, though highly heritable (0.53), was less correlated genetically to weight (0.47) than the other skeletal traits of length (0.59) or girth (0.62).

Overall, the morphometric traits such as height, length and girth were still moderately correlated with weight, agreeing with studies on Brahman cattle (Magnabosco et al., 2002). Thus, tall, long and wide animals usually are heavier than compact animals (i.e. big animals are bigger in all dimensions). In practical terms, and under some farm conditions (eg. without weight scales), the selection for morphometric traits, which have strong genetic correlations with weight, could be a useful selection aid because of the opportunity for indirect selection for postnatal weight. However, the study herein indicates the use of girth or length rather than height is better for weight prediction at advanced ages, in contrast to the study of Magnabosco et al. (2002) on Brahman cattle.

Height at 400 days was also moderately positively and genetically correlated with muscularity (0.27), but moderately negatively genetically correlated with fatness (-0.24) (Table 4.4). Muscularity as defined in this study was highly heritable (0.44) at the same age. In another beef cattle study, thigh development at slightly older ages was used as a major score for muscular development with moderate heritability (0.22) and good genetic correlations (0.51-0.88) with traits reflecting skeletal development (Gutierrez and Goyache, 2002). In dairy cattle (British Holsteins), animal shape was reported with a heritability of 0.26 and moderate to high genetic correlations with rump width (0.55) and chest width (0.82) (Brotherstone, 1994). These correlations of animal height with traits for size on linear (skeletal traits) or volumetric scales (weight), muscular development and fatness may be useful for carcass selection.

Since there were no phenotypic relationships between height and muscle or height and fatness in this study, most of the observed genetic correlations may be due to independent gene action. Moreover, while all of the phenotypic correlations estimated between weight and morphometric traits (height, length and girth) were positive, they were smaller than the corresponding genetic correlations at all ages. When cluster analysis of the genetic

correlations of all traits pooled across ages was performed, it provided different groupings for pre- and post-natal growth and development (Chapter 4.3.2). There was a separate clustering across ages for postnatal height, weight with length, girth, muscularity and fatness traits, suggesting the influence of different and specific loci. These loci may contain single or multiple genes. A recent study in rats has suggested measuring additional phenotypes as a method to identify the causal gene in a region that consists of several genes (Jacob and Kwitek, 2002). This approach could also be used to resolve the number of genes per QTL herein.

7.2.3 Genetic effects on growth and development

A limitation of the second experiment (Chapter 4) was the inability to separate the additive from the non-additive genetic effects on growth and developmental traits because a single dam breed was utilised. The third experiment (Chapter 5), therefore, was performed to quantify some genetic effects on the traits under consideration. At birth, the size of animal was essentially determined by the direct genetic effect (Table 5.3). In addition, for most of the postnatal growth and skeletal size across ages, the direct effects were higher in significance compared to any of the non-additive effects. This indicates the importance of additive effects as the primary cause of variation in growth and animal size at any age. However, the genetic clustering of weight with all of the skeletal dimensions at birth (Chapter 4.3.2) suggests that the birth-traits are under the same loci control and any of the four birth traits could be used in selection for animal size at this age.

The maternal effect was significant for some early postnatal growth traits (weight, girth and muscle) but not for the birth traits (Table 5.3). This indicates the importance of mothering ability and/or post-natal nutrient supply rather than pre-natal nutrient supply for the two breeds in this study. Although some other studies support this observation, most studies are based on only weight as a measure of growth (Neville et al., 1984; Cunningham

and Magee, 1988; Kress et al., 1996). Of all of the postnatal growth and size traits, only weight and girth were significantly influenced by the maternal effect through to 600 days of age (Table 5.3). In addition, cluster analysis (SAS, 1992) of genetically correlated traits (Chapter 4) also suggested that, apart from length, girth may be more related to weight than height at postnatal ages. Although there was a significant maternal effect on postnatal muscularity and measure of fatness at 600 days, cluster analysis showed no genetic relationship between muscular and fat traits or any of the growth traits (Chapter 4.3.2). This observation might suggest that additive effects of genes or loci influencing postnatal growth (size) could be different from those loci determining postnatal animal shape (fatness) and muscular development.

There are few reports on postnatal non-additive heterotic effects on fat depth as found herein and even fewer on muscularity. In a study on Brahman-Hereford crosses (Pitchford et al., 1993; Hearnshaw et al., 1994), heterosis was reported to be significant for subjective condition scores. There was also some suggestive evidence of epistatic effects for postnatal weight and muscle in this study. Although these epistatic effects for postnatal growth and developmental traits was postulated to be possibly due to changes in nutrition (Chapter 5), a study in mice suggested that there is independent gene action at different phases of growth which may be responsible (Vaughn et al., 1999). The positive and large size of effects due to heterosis on postnatal fatness and the suggestive evidence of epistatic effects on muscularity at 600 days of age support the possibility of different types of gene action on early and late growth and development.

7.2.4 QTL effects on growth and development

The hypothesis that there are different quantitative trait loci affecting early and late growth in cattle (Chapter 5) similar to those observed in mice (Vaughn et al., 1999) formed the basis of the last experiment (Chapter 6). The fourth experiment was to identify and

quantify the percentage contribution of QTL to the overall phenotypic expression of traits studied herein and the first principal components (PC1) of the clustered traits (Chapter 4). Individual traits across ages had significant QTL identified throughout the genome (Appendix 5a and 5b). Some of the QTL for growth traits have been reported in earlier studies, while many others had not been previously identified (Chapter 6).

As described earlier (Chapter 4), cluster analysis of the genetic correlations of growth and developmental traits pooled across ages identified six groupings. For each of the groupings (birth-traits, height-traits, growth-traits, girth-traits, muscle-traits, fat-traits), the first principal components (PC1) that represented over 50% of the total phenotypic variance were used to screen the genome for QTL. Based on the PC1 traits, strong evidence of separate associations between markers and QTL for prenatal and postnatal growth and development were observed. These results indicate that chromosome 2 has two QTL with effects on postnatal muscularity, chromosome 5 may has a QTL with effects on birth-traits, chromosome 6 has a QTL for postnatal growth, chromosome 13 has another QTL with significant effects on postnatal muscularity and chromosome 21 has a QTL for fat depth. Also, there could be a unique QTL on chromosome 14 with independent or correlated effects with other QTL on both pre- and post-natal growth and development.

There are quite a number of published reports of genome-wide screening for QTL affecting growth and carcass traits in different beef cattle populations. Most QTL herein have been observed in similar locations (Davis et al., 1998a; Stone et al., 1999; Casas et al., 2000) with a few exceptions. The chromosomes with suggestive evidence of QTL regions vary between studies because:

1. The same markers are not used,
2. The animals are reared in various environments,
3. Different methods of analysis are used,

4. Traits are not measured identically between studies,

5. Different populations and breeds of cattle have different allelic variants.

As many as 10 chromosome regions (BTA 5, 6, 7, 13, 14, 17, 19, 22, 27, and 29) influencing carcass composition and growth were reported in a Piedmontese paternal half-sib family and in a Belgian Blue family by Casas et al. (2000). Stone et al. (1999) reported significant evidence of QTL on 4 chromosomes (BTA 1, 2, 5, and 13) and suggestive evidence of QTL on another 5 chromosomes (BTA 7, 11, 14, 18, and 26) that affect carcass and growth in a Brahman paternal half-sib family. Davies et al. (1998a) also detected and mapped QTL for birth weight on 5 bovine chromosomes (BTA 5, 6, 14, 18, and 21). Detected QTL on specific chromosomes were also reported for live weight on BTA23 (Elo et al., 1999) and for growth on BTA5 in a *Bos taurus* line (Li et al., 2002). However, all of these studies on growth involved only measures of weight and weight gain, and most of the weight traits were considered at specific ages. Nevertheless, some of these studies have also examined muscling, retail yield and many carcass quality traits (including fatness) (Dunner et al., 1997; Stone et al., 1999; Casas et al., 2000). It is encouraging that many of these traits overlap with the PC1 traits mapped herein (Table 7.1).

The identification of separate groupings for prenatal growth and postnatal growth and development through cluster analysis (Chapter 4) provide one of the unique features of the present study. The mapping of different QTL responsible for pre-natal growth (involving animal size traits) and for post-natal growth and development (involving animal size and shape) indicates that different genes are controlling these traits. Thus, the problem of genetic correlation antagonism (Koots et al., 1994a; MacNeil et al., 1998) associated with selection for early growth having effects on later growth (vice-visa) can be resolved using marker-assisted selection (Grosz and MacNeil, 2001).

Table 7.1. QTL comparison with some published studies

BTA	QTL (PC1) in this study	QTL in other studies	References
2	Postnatal muscularity	Double-muscling	Charlier et al., 1995; Dunner et al., 1997
		Retail product yield	Stone et al., 1999
5	Birth-trait	Fat depth, retail product yield, USDA yield grade	Casas et al., 2000
		Rib-bone weight, dressing %	Stone et al., 1999
		Birth-weight	Davies et al., 1998a
6	Postnatal growth	Birth & yearling weight, longissimus muscle area & hot carcass weight	Casas et al., 2000
		Birth-weight	Davies et al., 1998a
13	Postnatal muscularity	Retail beef yield	Stone et al., 1999
14	Pre- & post-natal growth	Fat depth	Casas et al., 2000
		Longissimus muscle area	Stone et al., 1999
		Birth-weight	Davies et al., 1998a
21	Postnatal P8 fat depth	Birth-weight	Davies et al., 1998a

Heritability (h^2) values for measured birth-traits (Table 4.4) were moderate to low and the h^2 estimates for the birth-trait PC1 (data not presented) was also very low. This indicates that the QTL effects on BTA 5 accounting for up to 30% of the phenotypic variance (Chapter 6) provides potential for genetic selection against birth-size (less dystocia) using a molecular approach as observed in the study herein. In addition, it was surprising that the QTL allele from the bigger breed (Limousin) decreases birth-trait PC1 compared to the allele from the smaller breed (Jersey) in progeny of the significant sire family. Consequently, the favourable QTL allele affecting birth-traits found at the centomeric end of BTA 5 could be selected to reduce birth-size without negative effects on subsequent growth. In a commercial line of *Bos taurus* cattle, Li et al. (2002) observed relatively higher frequencies of haplotypes on BTA 5 associated with lower birth weights but higher average daily gains. On the same chromosome, Ge et al. (2001) found a mutation in the promoter region of the IGF-I gene (BTA 5) that was significantly associated with higher weight gain during the first 20-d after

weaning and a slight dominance effect on post-weaning gain. Grosz and MacNeil (2001) found evidence of the presence of a gene at the telomeric end of chromosome 2 in the interval between BM2113 and OarFCB11 affecting birth weight, but not subsequent weight.

Interestingly, a region at 10 to 30 cM from the telomeric end of chromosome 14 that affects growth (weight and body dimensional traits) at all ages was found in our population (Appendix 5b). There was no link detected between this QTL and postnatal muscularity or fatness, suggesting that the QTL may only be involved in the description of the animal-size rather than the shape of the animal. The size of the QTL effects (Figure 6.3) in standard deviation units of the PC1 of birth-traits (70%) and the PC1 of subsequent growth traits (64%) on BTA 14, with the individual heritability estimates for these traits (Figure 4.5) suggests that more than 50% of the genetic variation in these traits could be attributed to this QTL. Consequently, if the effect of the allele segregating at this locus for either of the traits is favourable, then selection based on markers would result in reasonable genetic gain. At the position of the QTL on BTA 14 in the present study, alleles for the bigger Limousin breed resulted in increased birth-size and postnatal height compared to the allele derived from smaller Jersey breed. Thus, the Limousin derived allele increased both pre-natal (birth-size) and late postnatal growth. Morris et al. (2002) reported that the New Zealand data supported the findings in the Australian half of the Jersey-Limousin mapping project.

Postnatal height is essentially controlled by a single haplotype on BTA 14 since two families had significant allelic effects for the QTL (Table 6.4). The substitution effects of these families ranged 0.53 - 0.85 standard deviation units. The other genetically correlated postnatal skeletal dimensions (Table 4.4) of length (r_G = 0.49) and girth (r_G = 0.26) at an average age (400 days), had a peak at the same chromosomal position as height, but the test statistic was not significant at the suggestive threshold level (F = 5.2). This might mean that there were no enough meioses to allow for significance for other postnatal growth trait

measurements. The allelic substitution QTL effects on some other specific regions were higher for postnatal growth or length (0.93 on BTA 6; 0.53 on BTA 16 and 0.75 on BTA 23) and the highly correlated girth trait. Interestingly, the J-derived alleles resulted in higher postnatal growth in two families (BTA 6 and 23) and resulted in lower postnatal growth in one (BTA 16). The result of higher non-additive postnatal maternal and heterosis effects (Chapter 5) on weight or girth compared to height trait also supported different gene actions on these traits.

Since the QTL responsible for post-natal muscularity is distinct from the QTL for postnatal fat deposition, genetic manipulation for body composition should be possible. The range of heritabilities for muscularity and fat depth (Chapter 4) were moderate and the size of the QTL effect for the PC1 of both traits, as standard deviation units of the most significant sire family, were 87% (using the single QTL model on BTA 2) and 78% (BTA 21), respectively (Chapter 6). This indicates that close to 90% of the genetic variation in muscularity and about 50% of the variation in fat depth was due to the identified QTL for each specific region. In other words, selection based on markers linked to these QTL should result in rapid genetic progress in body compositional traits.

One of the unique features of this study compared to others for QTL detection on growth and development was the wide disparity between the two breeds used in weight (size) and fatness. The double backcross design further assisted in maximum segregation of QTL or genes in the progeny to allow for differences in J (Jersey) and L (Limousin) allelic effects on grow and development traits. Interestingly, while the Jersey-derived allele increased postnatal muscularity (Figure 6.2) in the first sire family (398), the same allele decreased fat (Figure 6.3) in the other sire family (361). The result of positive Jersey maternal effects on early postnatal muscularity and no effect on fatness is an indication of importance of dam milk supply for muscle development with no consequential effect on excessive fat deposition.

This finding also supported independent gene action on the two important body composition traits (Chapter 5). Moreover, the lack of effect of dam milk supply on bone growth (height or length) indicates that most of the *Bos taurus* beef cows had sufficient milk supply for bone development. Single genes for growth and development traits (eg. muscle and fat depth) with correlated responses in carcass quality attributes provide opportunities for livestock breeders to increase meat quantity, and at the same time, improve carcass quality. With appropriate breeding programs, animals that carry major genes which affect carcass quality attributes also provide opportunities to decrease product variability (Burrow et al., 2001). Thus allowing for the exploitation of within and between breed variations for specific market requirements.

7.3 Future work

A shortcoming of the study herein, was the inability to investigate the epistatic effects due to QTL by QTL interactions that may exist within and between PC1 traits. For example, there could be interactions between the QTL on BTA 14 and any of the QTL affecting specific stages of growth (eg. QTL on BTA 5 or BTA 6). The same could be true for the QTL for the same trait at different loci (e.g. muscularity trait on BTA 2 and BTA 13) or different traits at the same or different loci [e.g. muscularity (BTA 2 or 13) and fatness (BTA21)]. An epistatic interaction between loci, as postulated by Falconer (1989), was reported for fat depth QTL on BTA 8 with the myostatin gene on BTA 2 (Casas et al., 2001). Further analyses are required to quantify QTL by QTL interactions in the current study.

As for future experiments, the contribution of the paternally imprinted or maternally imprinted gene effects on the growth and development of progeny may be worth investigating. This non-Mendelian mode of inheritance is a phenomenon only reported in livestock recently. Cockett et al. (1998) described polar over-dominance inheritance for the calliphyge locus in sheep, where only individuals that inherited the mutated allele from the sire show the doubly muscled phenotype. Two other studies (Jeon et al., 1999; Nezer et al.,

1999) proved the IGF-II gene to be imprinted in pigs and found a QTL linked to this gene with strong effects on muscle mass and fat deposition, but only when inherited from the sire. In more recent studies, imprinting effects have been reported for some beef cattle (Engellandt and Tier, 2002) and dairy cattle (Essl and Voith, 2002) traits.

The other area needed for investigation would be fine mapping of candidate genes for growth and development. This would involve comparative mapping with human or mouse to verify the QTL identified herein. Furtunately, many conserved putative orthologous segments between cattle and human chromosomes are known (Band et al., 2000) and can be exploited to this end.

7.4 Conclusions

The results of this study have shown that different regions of the genome control early growth compared to late growth and development in beef cattle. Specifically, the result of the cluster analysis has identified different groupings for postnatal body composition (muscularity and fatness) from growth (weight and skeletal dimensions). The mapping findings of the first principal components that represent over 50% of the phenotypic variation in body composition also indicated separate regions control for these traits. Thus, important information has been obtained for finding the genes affecting specific growth and development traits, identifying useful markers, and applying marker-assisted selection for these traits in various populations. However, strategies using both marker and phenotypic information especially for growth traits, though more superior, would be more expensive than phenotypic selection alone. On the other hand, the advantage of MAS for growth and development would be the ability to select for pre-natal growth independent of post-natal growth and development. Also, MAS would allow very early selection (eg. embryo or birth) before measurement of the traits is possible or the rapid introgression of the favourable gene into inbred and outbred populations of beef cattle. So while the size of QTL effects herein are

large enough to allow markers close to the region to be used for selection and the relationship between haplotypes or alleles was favourable, the cost-benefit of use of MAS for these traits needs to be considered.

Appendices

Journal Papers

1. **Afolayan, R.A., Pitchford, W.S. and Bottema, C.D.K. (2002).** Genetic variation in growth and body dimension of Jersey and Limousin cross cattle. 1. Pre-weaning and weaning performance. Asian-Aus. J. Anim. Sci. **15 (10)**: 1371-1377.

2. **Afolayan, R.A., Pitchford, W.S. and Bottema, C.D.K. (2002).** Genetic variation in growth and body dimension of Jersey and Limousin cross cattle. 2. Post-weaning dry and wet season performance. Asian-Aus. J. Anim. Sci. **15 (10)**: 1378-1385

Conference Proceedings

1. **Afolayan, R.A., Pitchford, W.S. and Bottema, C.D.K. (2001).** Genetic effects on shape and fatness of calves from diverse crosses. Proceedings Conference Assoc. Advmt. Anim. Breed. Genetics, Queenstown, New Zealand, **14**: 481-484.

2. **Afolayan, R.A., Deland, M.P.B., Rutley, D.L., Bottema, C.D.K., Ewers, A.L., Ponzoni, R.W. and Pitchford, W.S. (2002)**. Prediction of carcass meat, fat and bone yield across diverse cattle genotype using live-animal measurements. In Proceedings Biennial Conference Austr. Soc. Anim. Prod., Adelaide, Australia, Anim Prod. Aust. **24**: 13-16.

3. **Afolayan, R.A., Bottema, C.D.K. and Pitchford, W.S. (2002)**. Evidence of non-additive genetic effects on predicted carcass composition. Proceedings 7th World Congress Genetic Applied Livestock Production, Montpellier, France **33**: 467-470.

Conference Abstract

1. **Afolayan, R.A., Pitchford, W.S. and Bottema, C.D.K. (2001)**. Mapping quantitative trait loci for growth and development in cattle. 1. Preliminary results for genetic effects. Poster (P707), Plant & Animal Genome IX Conference, Town & Country Hotel, San Diego, USA, 13th – 17th January, 2001.

Appendix 1. Estimates of correlations (phenotypic, genetic and environmental) for body composition traits between specific ages

Correlations	Weight	Height	Length	Girth	Muscle	Fat depth
r_P						
Birth-Wean	0.39±0.02	0.16±0.01	0.06±0.01	0.08±0.01	.	.
" – 400d	0.39±0.02	0.17±0.01	0.07±0.01	0.08±0.01	.	.
" – 600d	0.32±0.02	0.19±0.02	0.02±0.01	0.04±0.02	.	.
Wean-400d	0.73±0.01	0.46±0.02	0.21±0.01	0.23±0.01	0.12±0.05	0.51±0.02
" – 600d	0.42±0.02	0.44±0.03	0.10±0.02	0.11±0.02	0.23±0.08	0.48±0.03
400d – 600d	0.53±0.02	0.52±0.03	0.11±0.02	0.18±0.02	0.32±0.05	0.69±0.02
r_G						
Birth-Wean	0.44±0.15	0.21±0.07	0.19±0.07	0.20±0.06	.	.
" – 400d	0.46±0.12	0.25±0.07	0.18±0.06	0.17±0.06	.	.
" – 600d	0.63±0.16	0.29±0.12	0.00±0.00	-0.01±0.09	.	.
Wean-400d	0.95±0.04	0.82±0.10	0.62±0.09	0.41±0.07	0.50±0.31	0.66±0.11
" – 600d	0.67±0.14	0.73±0.15	0.22±0.09	0.20±0.09	0.44±0.68	0.45±0.16
400d – 600d	0.80±0.13	1.02±0.17	0.20±0.10	0.36±0.10	0.49±0.36	0.75±0.10
r_E						
Birth-Wean	0.38±0.05	0.13±0.04	-0.02±0.03	0.00±0.03	.	.
" – 400d	0.37±0.05	0.10±0.05	0.00±0.03	0.01±0.03	.	.
" – 600d	0.20±0.06	0.10±0.09	0.03±0.02	0.08±0.06	.	.
Wean-400d	0.60±0.03	0.23±0.05	-0.01±0.03	0.10±0.03	-0.04±0.14	0.43±0.07
" – 600d	0.29±0.06	0.22±0.10	0.00±0.06	0.04±0.05	0.19±0.17	0.50±0.08
400d – 600d	0.35±0.06	0.14±0.08	0.05±0.06	0.03±0.06	0.28±0.13	0.64±0.07

Wean = Weaning

Appendix 2. Estimates of correlations (phenotypic, genetic and environmental) between pre-weaning weight gains and body composition at different ages

Trait(s)	r_P	r_G	r_E
Adgwt1+Bwt	0.24±0.03	0.26±0.21	0.23±0.07
+Wwt	0.66±0.01	0.83±0.07	0.58±0.04
+400-d wt	0.51±0.02	0.81±0.08	0.35±0.05
+600-d wt	0.30±0.02	0.60±0.14	0.16±0.06
Adgwt1+Bht	0.17±0.02	0.12±0.10	0.21±0.05
+Wht	0.33±0.02	0.36±0.11	0.32±0.05
+400-d ht	0.30±0.02	0.33±0.11	0.30±0.06
+600-d ht	0.22±0.04	0.37±0.18	0.14±0.11
Adgwt1+Blh	0.14±0.02	0.12±0.11	0.15±0.05
+Wlh	0.31±0.02	0.44±0.09	0.25±0.04
+400-d lh	0.24±0.02	0.40±0.10	0.16±0.04
+600-d lh	0.16±0.02	0.34±0.14	0.07±0.07
Adgwt1+Bgh	0.16±0.02	0.24±0.11	0.12±0.05
+Wgh	0.36±0.01	0.57±0.09	0.24±0.04
+400-d gh	0.29±0.02	0.57±0.11	0.16±0.04
+600-d gh	0.17±0.02	0.36±0.13	0.07±0.07
Adgwt1+Wmus	0.10±0.04	-0.24±0.33	0.21±0.10
+400-d mus	0.06±0.04	0.18±0.21	-0.01±0.01
+600-d mus	-0.01±0.06	-0.39±0.39	0.12±0.13
Adgwt1+Wfd	0.24±0.03	0.08±0.20	0.30±0.07
+400-d fd	0.12±0.03	-0.06±0.19	0.21±0.09
+600-d fd	0.12±0.04	0.49±0.20	-0.06±0.10

Appendix 3. Estimates of correlations (phenotypic, genetic and environmental) between post-weaning dry season weight gains and body composition at different ages

Trait(s)	r_P	r_G	r_E
Adgwt2+Bwt	0.08±0.03	0.51±0.28	-0.00±0.06
+Wwt	-0.14±0.02	0.70±0.30	-0.36.±0.06
+400-d wt	0.38±0.02	0.92±0.20	0.27±0.04
+600-d wt	0.20±0.02	0.76±0.27	0.06±0.06
Adgwt2+Bht	0.04±0.02	0.20±0.15	-0.01±0.04
+Wht	0.00±0.02	0.41±0.18	-0.13±0.05
+400-d ht	0.10±0.02	0.39±0.17	0.01±0.05
+600-d ht	0.14±0.04	0.52±0.27	0.02±0.10
Adgwt2+Blh	0.03±0.02	-0.02±0.16	0.04±0.04
+Wlh	0.02±0.02	0.65±0.24	-0.16±0.04
+400-d lh	0.09±0.02	0.64±0.22	-0.05±0.04
+600-d lh	0.08±0.02	0.07±0.19	0.10±0.06
Adgwt2+Bgh	0.04±0.02	0.24±0.16	-0.03±0.04
+Wgh	-0.05±0.01	0.04±0.12	-0.09±0.04
+400-d gh	0.15±0.01	0.59±0.23	0.05±0.03
+600-d gh	0.12±0.02	0.56±0.24	-0.00±0.06
Adgwt2+Wmus	-0.03±0.04	-0.14±0.42	-0.00±0.08
+400-d mus	0.05±0.04	0.20±0.27	0.01±0.09
+600-d mus	-0.01±0.06	-0.58±0.47	0.11±0.11
Adgwt2+Wfd	-0.20±0.03	-0.30±0.25	-0.18±0.06
+400-d fd	0.13±0.03	-0.14±0.26	0.21±0.07
+600-d fd	-0.00±0.04	-0.27±0.29	0.07±0.08

Appendix 4. Estimates of correlations (phenotypic, genetic and environmental) between post-weaning wet season weight gains and body composition at different ages

Trait(s)	r_P	r_G	r_E
Adgwt3+Bwt	0.18±0.04	0.58±0.23	-0.11±0.08
+Wwt	0.08±0.03	-0.05±0.19	0.17±0.11
+400-d wt	0.03±0.03	0.27±0.17	-0.14±0.10
+600-d wt	0.48±0.02	0.54±0.11	0.43±0.07
Adgwt3+Bht	0.14±0.02	0.49±0.13	-0.11±0.08
+Wht	0.10±0.03	0.23±0.13	0.00±0.08
+400-d ht	0.17±0.03	0.47±0.13	-0.09±0.09
+600-d ht	0.29±0.04	0.61±0.17	0.00±0.15
Adgwt3+Blh	0.13±0.02	0.48±0.13	-0.12±0.08
+Wlh	0.01±0.02	0.14±0.12	-0.09±0.07
+400-d lh	0.11±0.02	0.45±0.13	-0.12±0.07
+600-d lh	0.10±0.03	0.27±0.14	-0.02±0.09
Adgwt3+Bgh	0.08±0.02	0.45±0.15	-0.17±0.08
+Wgh	0.01±0.02	-0.15±0.11	0.13±0.07
+400-d gh	0.05±0.02	0.07±0.11	0.03±0.07
+600-d gh	0.19±0.03	0.06±0.13	0.29±0.09
Adgwt3+Wmus	0.01±0.10	-0.86±0.42	0.40±0.23
+400-d mus	0.16±0.06	-0.26±0.31	0.45±0.19
+ 600-d mus	0.09±0.07	0.47±0.44	-0.09±0.21
Adgwt3+Wfd	-0.08±0.04	0.08±0.25	-0.17±0.12
+400-d fd	-0.07±0.05	0.27±0.23	-0.31±0.15
+400-d fd	0.12±0.04	0.38±0.23	-0.03±0.13

Appendix 5a. QTL effects on growth and development for individual main and gain traits

Chr.	(M)	Trait	QTL effect±S.E (σ) F_1 Sire per family 1(361)	2(368)	3(398)	F	Pos-ition (cM)	P
1	**(9)**	BWT	-0.36±0.21	-0.53±0.20***	0.43±0.24	4.3	64	0.05
		ADGWT2	0.63±0.20***	-0.31±0.21	0.36±0.26	4.6	92	0.05
		ADGGH2	0.40±0.20	-0.57±0.19***	-0.11±0.21	4.4	20	0.05
2	**(10)**	WMUS	0.12±0.23	-0.34±0.22	0.75±0.21***	5.1	80	0.01
		400D MUS	-0.41±0.24	-0.38±0.24	0.76±0.23***	5.4	16	0.01
		600D HT	-0.69±0.18***	-0.06±0.17	0.16±0.20	5.4	92	0.01
		600D MUS	-0.51±0.20**	-0.10±0.22	0.72±0.20***	6.6	28	0.01
		ADGWT3	-0.56±0.23**	0.04±0.21	-0.74±0.22***	5.7	72	0.01
		ADGLH3	0.10±0.21	-0.69±0.20***	-0.41±0.24	5.1	52	0.01
		ADGFD3	0.09±0.20	0.32±0.22	-0.71±0.20***	4.9	28	0.05
4	**(13)**	600D LH	0.14±0.19	0.31±0.19	0.79±0.21***	5.9	16	0.01
		ADGLH3	-0.34±0.20	0.52±0.21**	0.38±0.21	4.3	32	0.05
5	**(9)**	BWT	-0.07±0.18	-0.25±0.28	0.73±0.21***	4.5	36	0.05
		BHT	0.27±0.19	-0.57±0.23**	0.83±0.22***	6.8	28	0.01
6	**(8)**	WWT	0.53±0.20***	0.39±0.20	0.79±0.39*	5.0	112	0.01
		ADGWT1	0.59±0.22***	0.47±0.21*	0.63±0.36	5.2	108	0.05
7	**(11)**	ADGGH2	0.04±0.21	-0.38±0.20	0.83±0.24***	5.3	48	0.01
8	**(10)**	400D FD	0.36±0.27	-0.62±0.19***	-0.20±0.22	4.3	28	0.05
9	**(10)**	WGH	0.71±0.20***	0.22±0.19	-0.06±0.20	4.7	56	0.05
		400D LH	0.50±0.21**	0.21±0.19	-0.49±0.21***	4.4	56	0.05
		ADGGH3	-0.61±0.18***	-0.05±0.18	0.37±0.18*	5.1	84	0.05
13	**(9)**	600D MUS	0.35±0.19	0.29±0.19	0.64±0.23***	4.6	60	0.05
		ADGHT2	-0.00±0.20	-0.31±0.19	0.64±0.20***	4.4	36	0.05

(M) = Number of markers per chromosome. Test of significant @ 4cM interval

Appendix 5b. QTL effects on growth and development for individual main and gain traits

Chr.	(M)	Trait	QTL effect±S.E (σ) F_1 Sire per family 1(361)	2(368)	3(398)	F	Position (cM)	P
14	**(9)**	BWT	-0.63±0.18***	-0.28±0.19	-0.13±0.19	5.1	28	0.01
		BLH	-0.55±0.17***	-0.08±0.18	-0.25±0.18	4.1	28	0.05
		BGH	-0.61±0.17***	-0.04±0.18	0.03±0.18	4.3	28	0.05
		WWT	-0.72±0.20***	-0.19±0.19	-0.10±0.20	4.9	24	0.01
		WHT	-0.71±0.20***	-0.15±0.21	-0.51±0.20**	6.4	12	0.01
		WGH	-0.76±0.20***	-0.04±0.19	-0.25±0.20	5.4	24	0.01
		400D HT	-0.74±0.20***	-0.12±0.20	-0.39±0.20	5.9	16	0.01
		600D WT	-0.66±0.19***	-0.13±0.20	-0.27±0.19	5.0	32	0.01
		600D HT	-0.70±0.20***	-0.30±0.19	-0.39±0.20	6.3	16	0.01
		ADGWT3	-0.47±0.21**	-0.03±0.22	-0.59±0.21***	4.4	8	0.05
16	**(9)**	WWT	-0.37±0.19	-0.35±0.18	-0.47±0.19**	4.5	72	0.05
		400D WT	-0.26±0.19	-0.28±0.18	-0.59±0.19***	4.6	72	0.05
		ADGWT2	-0.49±0.20**	-0.35±0.19	-0.41±0.21	4.4	68	0.05
17	**(9)**	ADGLH2	-0.06±0.21	0.70±0.20***	-0.12±0.25	4.2	92	0.05
		ADGFD1	-0.39±0.19*	-0.49±0.18***	0.16±0.24	4.1	84	0.05
19	**(8)**	WHT	0.43±0.22*	-0.21±0.20	0.50±0.19***	4.1	44	0.05
		ADGGH2	-0.54±0.24*	0.14±0.22	-0.63±0.21***	5.0	40	0.01
21	**(9)**	400D FD	-0.57±0.20***	-0.49±0.19***	-0.15±0.21	5.0	44	0.01
22	**(9)**	BHT	-0.19±0.20	0.64±0.19***	-0.03±0.21	4.3	16	0.05
23	**(6)**	WGH	0.73±0.24***	-0.48±0.31	-0.10±0.31	4.0	12	0.05
25	**(4)**	WWT	-0.10±0.29	-0.31±0.18	0.65±0.21***	4.3	32	0.05
		ADGWT1	-0.16±0.29	-0.32±0.18	0.61±0.21***	4.0	32	0.05

(M) = Number of markers per chromosome. Test of significant @ 4cM interval

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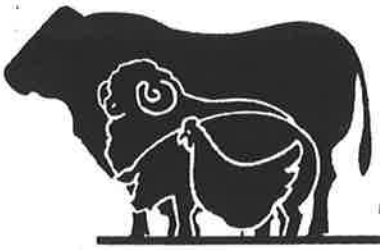

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GENETIC EFFECTS ON SHAPE AND FATNESS OF CALVES FROM DIVERSE CROSSES

R.A. Afolayan, W.S. Pitchford and C.D.K. Bottema

Livestock Systems Alliance, Adelaide University, Roseworthy, SA 5371

SUMMARY

The importance of direct genetic, maternal, heterosis and epistatic effects were examined on pre- and post-weaning dry and wet season average daily gains in weight, height, fat depth and a measure of muscle (ratio of stifle to hip width). The genotype used were two pure breeds (Jersey, JJ and Limousin, LL), the Limousin x Jersey LJ, and two backcrosses (LJ x Jersey dams and LJ x Limousin dams). Direct genetic effects were large ($P<0.01$) in all the traits. Jersey maternal effects were large for weight ($P<0.01$), fat depth ($P<0.001$) and muscle ($P<0.001$) in the post-weaning wet season performance. This is an indication of the impact of Jersey genes beyond weaning. There were large heterosis effects relative to direct effects on fat depth at pre- and post-weaning ages. Epistatic effects were observed only in post-weaning gain in weight and fat depth which is an indication that this effect is more expressed in advanced age.

Key words: Genetic effects, weight, height, fat depth, muscle.

INTRODUCTION

Body weight of beef cattle is influenced by both direct and maternal effects (Pitchford *et al.* 1993). Many reports limit the assessment of these effects to weight and changes in weight expressed in early life of the calf. Body composition measurements (bone, fat and muscle) are also required to sufficiently describe variation in saleable yield performance of beef cattle. Therefore, the objective of this study was to evaluate four genetic effects on growth and development of Jersey and Limousin cross cattle in different seasons and stages of growth.

MATERIALS AND METHODS

General procedures. In 1993, 280 purebred Jersey and Limousin dams were procured as part of the Davies Mapping herd. These dams were mated to purebred Jersey (2) and Limousin (2) sires to produce purebred Jersey (JJ), purebred Limousin (LL) or LJ calves born in 1994 and 1995. Mating LJ (3) bulls to parental breed cows (Jersey and Limousin) began in 1995 and backcross progeny [3/4 Jersey (XJ), 3/4 Limousin (XL)] were produced from 1996 until 1998. In the design, which involved two phases, year and genotype were partially confounded. However, some purebred JJ calves were produced in 1996 to link the two phases. Sires and dams were commonly used across years.

Calving took place each year in autumn from early March through mid-May. Calves stayed with their dams on pasture until weaning (average age of 250 days). After weaning, calves grazed grass pasture for 430 – 500 days. The animals' post-weaning weight (Wt), height (Ht), fat depth scanned at P8 site (Fat) and muscularity (Mus) (McKiernan 1990) (measured, using calipers, by stifle width as a proportion of hip width expressed as percent) were obtained at approximately 400- and 600-days after birth, corresponding to the winter after the dry season (dry season) and summer after the wet season (wet season) respectively. So, season was confounded with age. The degree of muscularity was not

taken at weaning for calves born in 1994 and at 400 days of age for the 1996 drop. Also, there was no 600-day measurement of height, for heifers born in 1994. The growth rate (for Wt, Ht, Fat, Mus) was calculated from birth to weaning (1), between weaning and 400-days (2), and between 400 and 600-days (3). Fat was assumed to be 0mm at birth. Mus was also not measured at birth.

Statistical Analysis. Eleven traits (Table 1) were analysed with a model containing fixed effects of year of birth (1994-1998), day of birth (5 classes with each comprising 20% of calves born in succession to allow for non-linearity), sex of calf (heifer or steer), genotype of calf (JJ, XJ, LJ, XL, LL) and year x sex interaction with sire and dam fitted as random effects (SAS 1992). Since there were no values for weaning muscle in 1994 and 400-day muscle in 1996, the model for Mus2 included the fixed effect of genotype nested within phase.

Genetic effects were defined in terms of direct additive, maternal additive, direct heterosis and direct epistatic effects. These effects were estimated as originally proposed by Dickerson (1969) but modified because of the genotype combinations used. Effects were estimated in a similar manner to Pitchford *et al.* (1993). The four genetic effects were estimated from the five genotype combinations (as shown below) as deviations from the purebred mean. Because there were only 5 genotype combinations, the epistatic effect was completely confounded with paternal heterosis. The effects were calculated as linear contrasts between genotype least square means with T- tests for significant deviation from zero. Significance was defined as $P<0.05$.

$$\text{Jersey direct} = JJ - LL - XJ + XL = \text{- Limousin direct}$$
$$\text{Jersey maternal} = (LL - JJ)/2 + XJ - XL = \text{- Limousin maternal}$$
$$\text{Heterosis} = LJ - LL - XJ + XL$$
$$\text{Epistasis} = 2(XJ) - LJ - JJ$$

RESULTS

Genotype and genetic effects. Genotype effects were highly significant ($P<0.01$) for all the traits. For pre-weaning traits, the purebred Limousin were the heaviest (Wt) and highest (Ht) with the purebred Jersey at the other extreme. These traits showed a gradual trend in genotypes from purebred Jersey to purebred Limousin. The LJ calves were the fattest with the two purebreds having the least back fat. The significant Jersey direct genetic effects resulted in calves with far lower Wt and Ht (Table 1). There was also a small Jersey maternal effect on Wt. Heterosis was large ($P<0.001$) and positive for Fat only. Epistatic effects were not significant for any of the pre-weaning traits.

In the dry season (weaning to 400d), XL calves had the highest Wt gain, followed by XJ = LL, LJ and JJ. The ranking order for Ht was similar to pre-weaning. Mus also followed the same trend (Figure 1a). However, there was a significant Fat loss in LJ and the XJ and XL gained less than the purebred mean. The direct Jersey effects resulted in increased Mus gain but reduced Wt and Fat gain. There was a positive but low Jersey maternal effect on Ht and Fat, and a negative and low maternal effect on Mus. Heterosis and epistasis were the same as for pre-weaning (Table 1).

In the wet season (400d to 600d), the gains in all traits were faster than the dry season for all the genotypes. The ranking was similar to the dry season performance. However, the amount of Fat and Mus lost in the dry season by genotypes affected the level of the wet season gain (Figure 1b). The

direct Jersey effects in the wet- and dry- season were similar for gain in Wt, Fat and Mus. However, the wet season as compared to the dry season led to greater expression of the direct effect on Wt, Fat and Mus gain (Table 1). Also, the significant direct effect on dry season Ht was no longer apparent in the wet season. The Jersey maternal effect on Wt was significant and was higher in significance for Fat and Mus in wet compared to dry season. The maternal effect resulted in calves with increased Wt, additional Fat and less Mus gain. The heterosis effect was significant and positive for Mus with calves gaining more muscle. However, the significant heterosis on Fat gain in the dry was not evident in the wet season. Although no epistatic effect was observed for any dry season trait, there was a positive epistatic effect for Wt and negative epistatic effect for Fat during the following wet season.

Table 1. Genetic effects and tests of significance (diff. from zero) for pre and post-weaning traits

Trait	Purebred mean	Jersey direct	Jersey maternal	Heterosis	Epistasis
Wt1(g/d)	713±22	-135±28***	36±16*	-51±16**	74±53
Wt2(g/d)	168±18	-45±22*	16±15	-20±22	89±52
Wt3(g/d)	957±37	-282±49***	86±29**	-39±34	231±96*
Ht1(mm/d)	142±4	-13±5**	6±3*	-2±3	1±9
Ht2(mm/d)	48±5	-15±6**	8±4*	-2±5	6±13
Ht3(mm/d)	53±5	-5±7	-1±4	-7±6	22±14
Fat1(µm/d)	3±1	-2±1	-1±1	5±1***	-1±2
Fat2(µm/d)	2±1	-4±2*	3±1*	-9±2***	8±4
Fat3(µm/d)	20±3	-18±4***	9±2***	3±3	-16±8*
Mus2(%/d x 10^{-3})	-5±1	43±14**	-21±9*	25±13	-
Mus3(%/d x 10^{-3})	4±1	16±2***	-8±1***	10±2***	-

*P<0.05, **P<0.01, ***P<0.001

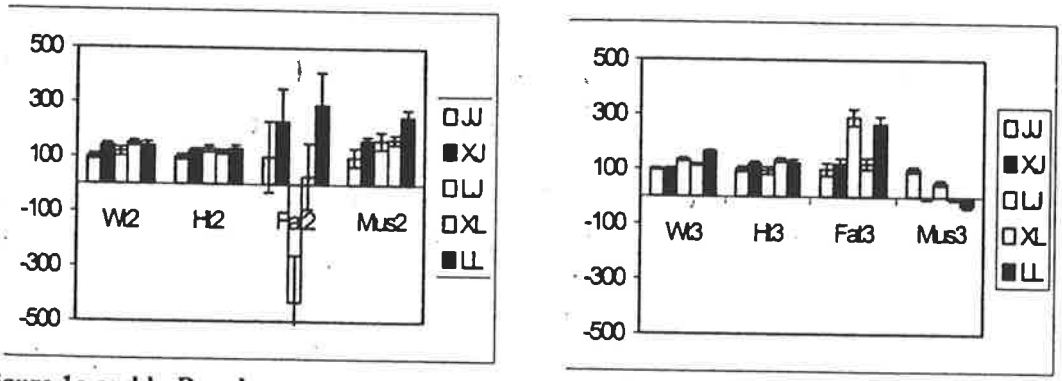

Figure 1a and b. Breed means as a percentage of JJ for post-weaning dry and wet season gains. Bars- indicates standard errors. Wt2,Wt3; Ht2,Ht3; Fat2,Fat3; Mus2,Mus3 = Dry and wet season gains in weight, height, fat depth and muscle. JJ= Jersey, XJ= Jersey backcross, LJ= JJ x LL, XL= Limousin backcross, LL= Limousin.

DISCUSSION

The genetic effects on growth were smaller in the dry compared to the wet season due to improved nutrition. Arthur *et al.* (1994) acknowledged the significance of the influence of post-weaning environment on the magnitude and direction of the genetic effect on a trait. The direct genetic effects were larger than the other genetic effects. Jersey direct effects were consistent across the ages for Wt, Ht and Fat but not for muscle. For example, it led to low Wt, Ht and Fat gain but high post-weaning muscle gain. Koch *et al.* (1994) also reported that the post-weaning muscle is primarily influenced by direct effect. The unexpected positive direct effect on muscle gain at older ages, since the effect was negative at weaning (-21%, unpublished), may be due to faster maturation of Jersey relative to Limousin at these ages.

The Jersey is a dairy breed and has high milk supply. Thus, the positive pre- and post-weaning Jersey maternal effects on most traits were due to large milk supply from the Jersey dam. However, there was a negative effect on post-weaning muscle gain. This may be due to the expression of compensatory growth in calves with Limousin dam relative to Jersey dam when exposed to a good post-weaning environment. This is further demonstrated in the genotype by seasonal re-ranking in Wt (Dry: JJ<LJ<XJ=LL<XL Vs Wet: JJ<XJ<XL<LJ<LL) and Ht (Dry: JJ<XL<XJ<LJ<LL Vs Wet: LJ<JJ<XJ<LL<XL).

The Fat differences of the LJ calves, as compared to other genotypes at all ages, was mainly due to heterosis but also partly due to the maternal effect. The significant negative heterotic effect on Wt is contrary to earlier reports. Pitchford *et al.* (1993) found that heterotic effects were 1-21% for mature weight and 0-4% for mature height depending on the pre-weaning environment. Also, in male and female lines of three composite populations (MARC I, II and III), heterosis was positive for gain from weaning to 368-day, 368-day weight, and 368-day condition score (Gregory *et al.* 1991). Rarely has heterosis been estimated to have a negative effect on growth as in this study. The limitation of small number of sires per breed (2-3) may partly explained the reason for the deviation. However, there were large numbers of dams from a wide range of sources. Also, the difference between breeds (Limousin and Jersey) especially for carcass traits, is larger than for most other studies. The study has also shown that the epistatic effects on Wt and Fat may be larger at older than younger ages. The breed re-ranking referred to above was also a function of non-additive genetic effects.

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PREDICTION OF CARCASS MEAT, FAT AND BONE YIELD ACROSS DIVERSE CATTLE GENOTYPES USING LIVE-ANIMAL MEASUREMENTS

R.A. AFOLAYAN [A], M.P.B. DELAND [B], D.L RUTLEY [A], C.D.K. BOTTEMA [A], A.L. EWERS [C], R.W. PONZONI [D] and W.S. PITCHFORD [A]

[A] Livestock Systems Alliance, Adelaide University, Roseworthy, SA 5371, Australia
[B] South Australian Research and Development Institute (SARDI), Struan Naracoorte, SA 5271, Australia
[C] Primary Industries and Resources, Pt Augusta, SA 5700, Australia
[D] Livestock Systems Alliance, SARDI, Roseworthy, SA 5371, Australia

SUMMARY

Live measurements of weight, height, length, girth, fat depth, stifle- and hip-width were obtained prior to slaughter to develop prediction equations for carcass traits. The animals were boned out after slaughter and comprised 182 steers from the Southern Crossbreeding Program (progeny from Hereford cows crossed with seven sire breeds: Angus, Belgian Blue, Hereford, Jersey, Limousin, South Devon and Wagyu) and 59 steers from the Davies Gene Mapping Project (pure Limousin, pure Jersey and Limousin x Jersey). Stepwise regression was used to indicate the relative importance of variables in each model designed to estimate the percentage of meat, bone and fat from the carcass weight. The meat, bone and fat yields correspond to 70, 19 and 11% of the carcass on weight basis. The prediction equations developed accounted for 93, 87, 74 and 65% of the variation in carcass, meat, bone and fat weight respectively without breed in the model. This study has shown that some carcass traits may be determined accurately from measurements on live animal.

Keywords: live-measurements, prediction, cattle, carcass traits

INTRODUCTION

The accuracy of functions used to predict carcass composition from live animal measurements is of immense potential contribution to livestock production enterprises. The value of beef cattle lies in their ability to efficiently produce a carcass composed of optimal proportions of muscle, bone, and fat at market weight (Tatum *et al.* 1986) or market specifications. The ability of the producer and buyers of livestock to relate objective live animal characteristics to carcass characteristics is essential for optimum production and value based trading systems. This ability will also enable processors to more accurately determine returns from meat processing and it may increase the rate of genetic gains in meat quantity traits in breeding herds.

In the past, many subjective live animal assessments (e.g. conformation score and butt shape profile) have been found to be poor indicators of carcass composition (Kempster *et al.* 1982). The problem has been the associated confounding of the relationship of muscle and yield with that of fat and yield. Other live measurements studies include the use of ultrasound technology (Hearing *et al.* 1994) that may not be cost-effective and/or may be of less application. In view of these challenges, this study examines the effectiveness of predicting carcass yield from objective live animal measurements.

MATERIALS AND METHODS

Animals

The animals used in the study were 241 steers born in March and April 1995 from two projects. 182 of the steers by 26 sires were the second calf drop of the Southern Crossbreeding Project, which comprised of progeny from seven sire breeds (Angus, Belgian Blue, Hereford, Jersey, Limousin, South Devon and Wagyu) mated to Hereford cows (Rutley *et al.* 1995). There were also 59 steers (14 Jersey, 28 Limousin, 17 Limousin x Jersey) born to 4 sires (2 Jersey and 2 Limousin) from the second drop in the first phase of the Davies Gene Mapping Project. Steers management and feeding from birth to slaughter have been described (Ewers *et al.* 1999; Afolayan *et al.* 2001).

Live measurement

Prior to slaughtering, empty weight (24h off feed) of all the steers were taken. The body measurements taken, apart from live weight, using a tape included the following traits; height (measured as the distance from the top of midline between the hips to the ground), the length (measured as the distance between the first sacral bone on the shoulder and the butt of the tail), and the girth (measured as the

body circumference immediately posterior to the front leg). Other measurements along those mentioned earlier before slaughter were fat depth scanned at the P8 site on the rump plus hip width (bone) and stifle width (muscle) measured using calipers. Stifle width as a proportion (%) of hip width has been used previously (Afolayan *et al.* 2001) based on an indication of muscularity by McKiernan (1990) when developing visual techniques for assessing meat yield.

Slaughter and bone out procedure

The site and sequence of slaughtering of animals was as reported by Ewers *et al.* (1999). Each carcass was subjected to the standard minimal Ausmeat trim on the slaughter floor. Fat on the topside and brisket was not removed in order to increase the accuracy of information gained from the carcass measurements. Prior to boning out, the left sides of each carcass were quartered between the 10^{th} and 11^{th} rib and were assessed by an Ausmeat accredited assessor. The processing was carried out by a group of one boner, one slicer and one packer supplied by the abattoir. Individual animal weights for all the primal cuts before and after slicing were recorded. The trimmings from the primal cuts and each of the bones were also weighed.

Statistical analysis

The traits analyzed included carcass, meat, fat and bone weights and percentages (Table 1). Live animal measurements were as indicated above. Equations were formulated on a whole-carcass basis. The REG procedure in SAS (1992) was used to determine the relative importance of variables in a model designed to estimate the seven carcass traits. The stepwise method was used. The variables included by the stepwise regression method were then used to develop an equation for each of the traits. The amount of variation due to breed differences in traits was determined using the PROC GLM statement in SAS (1992).

RESULTS

Means and ranges for the body measurements and carcass traits were determined (Table 1). In general, the range of values for the predicted carcass traits indicated a slight over- and under-estimation for the smaller and larger animal respectively (Table 1).

Table 1. Summary of live-measurements and carcass traits

Item	Mean	CV	Minimum Actual value	Maximum Actual value	Minimum Predicted value	Maximum Predicted value
Weight (kg)	555.3	9	391.0	736.0		
Height (cm)	134.5	24	119.0	156.0		
Length (cm)	146.8	26	102.0	159.0		
Girth (cm)	202.4	22	169.0	221.0		
Hip (cm)	48.5	18	38.0	63.0		
Stifle (cm)	44.9	10	33.0	55.0		
P8 Fat (mm)	11.9	3	1.0	22.0		
Carcass (kg)	322.8	7	203.2	436.0	208.0	417.0
Meat (kg)	225.6	25	133.2	325.2	132.9	290.3
(%)	69.8	8	59.9	77.1	63.6	76.4
Bone (kg)	60.9	7	41.8	78.0	43.3	75.4
(%)	19.0	12	14.8	26.1	13.5	20.4
Fat (kg)	36.2	4	114.8	77.9	15.0	74.2
(%)	11.3	5	5.7	21.7	10.4	24.8

Live-weight was the most accurate predictor of carcass quantity components [meat (R^2=0.70) and bone (R^2=0.62) weight]. Of the live measurements apart from live-weight, stifle (R^2=0.13) was next most accurate in estimating meat weight and the correlation between these two traits was 0.80. Variables like height, length, girth, stifle, hip and measure of muscularity (defined as stifle/hip x 100, Afolayan *et al.* 2001), which are directly related to size and weight, displayed moderately to high positive correlations with quantity carcass components (0.27 – 0.94). For the percentage of carcass components, the highest correlation of 0.64 was found between muscularity and percent meat. However, a negative correlation (-0.26) was obtained between percent meat and P8 fat depth but a positive correlation (0.53) existed between the latter and percent carcass fat.

A minimum of three and a maximum of seven live measurement variables were significant ($P<0.01$) for the prediction of the carcass traits in the stepwise procedure (Table 2). Carcass weight was predicted at the 1% level of significance by using 3 live measurements. These variables (live weight,

stifle width and height) accounted for 93% of the breed differences in the prediction equation (Table 2). The live-weight (R^2=0.88) was the best variable but the addition of the other two variables (stifle width and height) increased the R^2 value and decreased the residual standard deviation. Eighty seven percent of predicted meat weight was accounted for by the same variables in carcass weight with one additional variable (hip width). The inclusion of hip width alone improved the model for meat weight up to 86%.

Table 2. Regression equations using live-measurements to predict carcass traits

Dependent variable		Constant	Weight kg	Height cm	Length cm	Girth cm	Hip cm	Stifle Cm	P8 Fat mm	R^2 %	Res. SD
Carcass	kg	-183.23	.48	1.01				2.45			
			(88)	(1)				(5)		93	11.8
Meat	kg	-178.81	.31	1.23			-1.38	3.15	-.85		
			(70)	(2)			(1)	(13)	(1)	87	13.2
	*kg	-194.22	.28	1.42			-1.49	3.20			
			(70)	(2)			(1)	(13)		86	13.4
	%	53.24		.12			-.37	.44	-.30		
				(3)			(6)	(31)	(17)	56	2.3
	*%	61.89		.20		-.14	-.33	.51			
				(6)		(4)	(11)	(30)		52	2.3
Bone	kg	- 82.24	.03	.25	.17	.28	.32		-.35		
			(62)	(4)	(2)	(3)	(1)		(3)	74	3.7
	*kg	-83.37	.03	.32	.21	.21	.29				
			(62)	(4)	(2)	(3)	(1)			72	3.9
	%	8.31	-.02		.05	.06	.12	-.09	-.13		
			(18)		(5)	(3)	(4)	(3)	(4)	39	1.2
	*%	13.28	-.01		.07		.12	-.07			
			(20)		(5)		(4)	(2)		31	1.3
Fat	kg	33.24	.10	-.41			.66	-.89	1.39		
			(8)	(2)			(7)	(2)	(45)	65	6.9
	*kg	-1.70	.10	-.70		.49	.68	-1.09			
			(4)	(6)		(28)	(2)	(13)		52	8.0
	%	30.99	.02	-.17			.20	-.37	.39		
			(2)	(2)			(3)	(23)	(27)	56	2.1
	*%	11.66		-.21		.18	.25	-.40			
				(7)		(16)	(3)	(15)		42	2.4

() Percentage contribution of each measurement to each prediction equation
* Prediction values without P8 fat depth information included

The percentage variation of each variable in the bone (R^2=0.74) and fat (R^2=0.65) weight models were calculated (Table 2). The major variable fitted to each trait differs. Live-weight explained 62% of the variation and was recognized as the best in order of predictive significance for bone weight but P8 fat depth (45%) was the best for fat weight. However, adding other important variables to each of the model accounted for an additional 19 and 23% of variation in predicting bone and fat weights, respectively. Live measurements traits accounted for 56, 56 and 39 % prediction for differences in meat, fat and bone percent of the carcass yield. The single measurement that accounted for the highest prediction was live-weight (18%) for bone, stifle (31%) for meat and P8 fat depth (27%) for fat percent. Weight was insignificant for the prediction of meat % (Table 2).

Prediction equation was also calculated for all the seven traits under consideration by excluding P8 fat depth in the list of variables (Table 2). Basically, carcass (R^2=0.93) and meat weight (R^2=0.86) were predicted with the same level of accuracy but the R^2 values dropped for all other traits. Also, breed differences were highly significant ($P<0.01$) for all traits. However, when breed was fitted after the live measurement traits in Table 2, it was no longer significant for carcass weight but was for the other traits (result not presented).

DISCUSSION

Use of practical methods of estimation of carcass components would assist development of breeding objectives and meat marketing. Estimation of carcass components (meat, fat and bone) by dissection in commercial boning rooms is difficult, expensive and becoming almost impossible as regulations related to export licenses become tightened. The results presented here show that carcass weight and meat weight can be predicted accurately from measurements taken on live animals, thus avoiding the high cost and difficulties of dissection.

The R^2 values of 93% (Table 2) for predicting carcass weight and 86% for meat weight using weight, height, stifle and hip measurement indicated a reasonable prediction based on these traits with or without P8 fat depth. There were indications herein that the body dimensional traits, as measured in this study, are directly related to size and weight. The good relationship between stifle (greater than other live measurements apart from live-weight) and meat weight explained the higher ranking compared to others in percentage contribution to the prediction equation. For the percent meat, the R^2 value of a 56% in this study was in the range of 60% and 51% obtained by Wallace *et al.* (1977) for predicting percentage primal and retail yield, respectively, using ultrasound rib fat measurement between 5th and 6th ribs but higher compared to that reported by Herring *et al.* (1994) for the prediction of various retail cuts from visual score and ultrasound live animal measurements (24 – 48%). Perry *et al.* (1993a;b) indicated R^2 values of 46% and 62% for saleable meat yield of commercial stock based on live-weight, P8 fat depth and muscle score. This study has demonstrated an alternative estimation of percent carcass meat based on some objective live-body measurements plus P8 fat depth with a similar level of accuracy.

As expected (Perry *et al.* 1993a), an animal with higher P8 fat depth had lower meat percentage because of the negative correlation (-0.26) between these two traits. Consequently, the compromise for the producers will then be to use antagonizing relationship of P8 fat depth and McKiernans' (1990) muscularity measurement to saleable meat yield in selecting live animals for targeted markets. Moreover, this result has supported earlier study (Perry *et al.* 1993b) that some carcass traits may be predicted without P8 fat depth (which may require trained, skilled assessor) measurements while the precision of prediction for others significantly decreased without this information. For meat and bone, P8 fat depth added very little accuracy to their estimation but was very important for fat traits. There were no systematic departures from expectation when the plots of actual against predicted values (graphs not shown) were examined for the carcass traits. Thus, even at extremely low and high values, the predictions were reasonable.

Based on the results of this study, carcass weight may be reasonably predicted based on live animal measurement regardless of the breed type. However, for precision in other carcass traits (including meat weight and percent meat in the carcass) the breed difference is still required to develop their equations. Effective and reliable prediction of carcass yields from the low-cost objective rather than high-cost objective (e.g. ultrasound) and/or subjective (muscle score) live animal measurements would reduce production costs and enjoy wider application by producers.

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Email: raphael.afolayan@adelaide.edu.au

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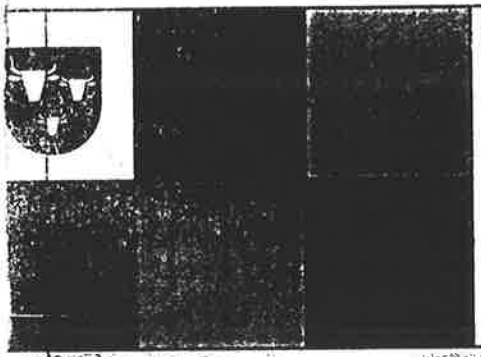

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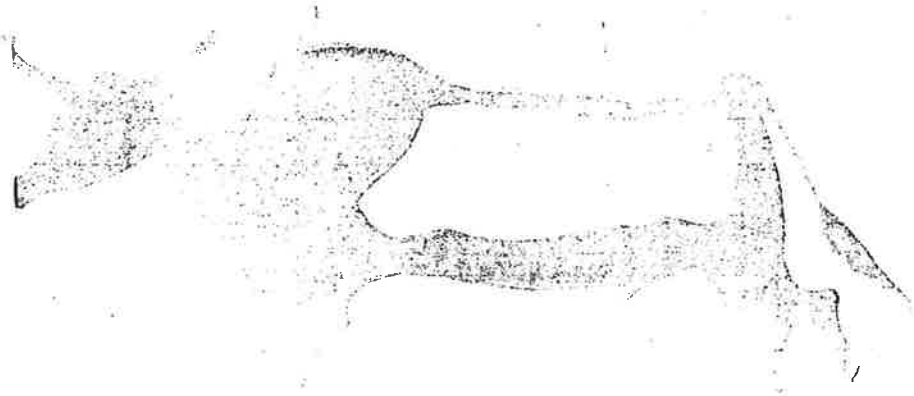

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EVIDENCE OF NON-ADDITIVE GENETIC EFFECTS ON PREDICTED CARCASS COMPOSITION

R.A. Afolayan, C.D.K. Bottema and W.S. Pitchford

Livestock Systems Alliance, Adelaide University, Roseworthy, SA 5371 Australia

INTRODUCTION

Genetic effects on pre- and post-weaning body weight and developmental traits of Jersey and Limousin cross cattle has been reported (Afolayan *et al.*, 2001). As in this earlier study which indicated the importance of epistasis at older ages, maternal effects (Meyer, 1992) and heterotic effects (Pitchford *et al.*, 1993) have also been found on post-weaning growth traits of some breed of beef cattle. Genetic improvement programs in beef cattle could be enhanced through understanding of the genetic effects on live animal traits at various ages. However, the value of beef cattle lies better in their ability to efficiently produce a carcass composed of optimal proportions of muscle, bone and fat at market weight (Tatum *et al.*, 1986). In essence, the knowledge of the genetic effects on different carcass components is of more importance to the breeders/producers of livestock. This study, therefore, examines the estimates of four genetic effects on predicted carcass traits using live-animal measurements.

MATERIALS AND METHODS

Animals. Two hundred and forty steers from two projects [Southern Crossbreeding Project (SXB) and Davies Gene Mapping Project (DGM)] were used to develop the prediction equations for the carcass traits. 182 steers by 26 sires were progeny from SXB and 59 steers (14 Jersey, 28 Limousin, 17 Limousin x Jersey) were part of DGM animals born to 4 sires (2 Jersey and 2 Limousin). The developed prediction equations were then used for the data from all 591 DGM progeny (steers and heifers) which comprised pure Jersey (JJ), pure Limousin (LL), Limousin x Jersey (LJ), Jersey backcross (XJ) and Limousin backcross (XL). Detailed experimental design and management of SXB animals (Pitchford *et al.*, 1998) and DGM animals (Afolayan *et al.*, 2001) have been reported.

Live measurements. Measurements of weight, height, length, girth, fat depth and a measure of muscularity defined as the ratio (%) of stifle width (muscle) to hip width (bone) were taken on the 591 calves at 600-day postpartum. The methods used for the live measurements have been described elsewhere (Afolayan *et al.*, 2001). The same measurements were taken prior to slaughter (at 750 days) on the 241 steers used for developing the prediction equations for carcass traits (carcass kg; meat kg, %; bone kg, %; fat kg, %). The slaughter and bone out procedure for the steers were previously reported (Pitchford *et al.*, 1998).

Statistical Analysis. The REG procedure in SAS (1992) was used for the carcass trait prediction and the detailed stepwise method employed is as described by Afolayan *et al.* (2002). Predicted equations were adapted on live measurements at 600-day postpartum described above and estimates of seven predicted carcass traits were analysed. The model used contain fixed effects of year of birth (1994-1998), day of birth (5 classes with each comprising

20% of calves born in succession to allow for non-linearity), sex of calf (heifer or steer), genotype of calf (JJ, XJ, LJ, XL, LL) and year by sex interaction with sire and dam fitted as random effects (SAS, 1992).

Genetic effects were defined in terms of direct, maternal, heterosis and epistatic effects. These effects were estimated as originally proposed by Dickerson (1969) but modified because of the genotype combinations used. Effects were estimated in a similar manner to Pitchford *et al.* (1993). The four genetic effects were estimated from the five-genotype combinations (as shown below) as deviations from the purebred mean. Because there were only five genotype combinations, epistatic effects were completely confounded with paternal heterosis. The effects were calculated as linear contrasts between genotype least square means with T- tests for significant deviation from zero. Significance was defined as $P< 0.05$.

$$\text{Jersey direct} = JJ - LL - XJ + XL = \text{- Limousin direct}$$
$$\text{Jersey maternal} = (LL - JJ)/2 + XJ - XL = \text{- Limousin maternal}$$
$$\text{Heterosis} = LJ - LL - XJ + XL$$
$$\text{Epistasis} = 2(XJ) - LJ - JJ$$

RESULTS

Means and ranges for the predicted carcass traits based on live-animal measurements at 600-day postpartum were determined (Table 1). The mean predicted carcass composition was 69.0% meat, 21.1% bone and 7.8% fat. These values were approximately ratio of 7:2:1 similar to those obtained for the steers from which the prediction equations were developed (Afolayan *et al.*, 2002).

Table 1. Summary statistics for prediction of carcass traits at 600-day postpartum

Predicted variables	Mean	CV	Minimum value	Maximum value	R^2	Residual SD
Carcass (kg)	209.3	11	93.8	438.3	87	22.7
	141.1	13	48.0	328.1	87	17.8
Meat (kg)	69.0	2	63.9	79.1	69	1.5
(%)	45.2	10	24.3	73.7	77	4.3
Bone (kg)	21.1	3	15.6	23.6	80	0.7
(%)	17.6	24	-5.6	42.2	60	4.3
Fat (kg)	7.8	15	-0.7	11.6	76	1.2
(%)						

Jersey direct effects were highly significant ($P<0.01$) for all the kilogram carcass traits (Table 2). The effects resulted in lower meat, bone and fat weight. However, there was no direct effect ($P>0.05$) on percentage carcass products. The effect due to Jersey dam on progeny was positive for bone and fat weight, but not significant for carcass or meat weight. For the percent meat,

Jersey maternal effect was negative. This effect also resulted in an increase ($P<0.05$) in percent bone.

Heterosis effects were significant for carcass composition. There was a positive effect on meat percent with corresponding negative effects on bone and fat percent. There was also a significant negative effect on bone weight. Epistasis effects were also large for carcass composition with changes in the same direction as heterosis. In addition, there was a corresponding effect on low fat weight (Table 2).

Table 2. Genetic effects and tests of significance (difference from zero) for predicted carcass traits at 600-day postpartum

Traits		Jersey direct	Jersey maternal	Heterosis	Epistasis
Carcass	kg	-58.4±9.3***	9.3±5.1	-5.3±4.7	7.3±16.3
Meat	kg	-41.3±7.5***	3.6±4.1	-1.3±3.8	15.1±13.1
	%	0.6±0.4	-1.4±0.2***	0.7±0.3*	3.9±0.8***
Bone	kg	-10.3±1.7***	2.5±0.9**	-2.0±0.9*	-1.6±3.0
	%	0.3±0.2	0.2±0.1*	-0.5±0.2**	-0.8±0.4*
Fat	kg	-8.2±1.1***	4.4±0.7***	-1.1±0.9	-10.1±2.3***
	%	0.7±0.4	0.4±0.2	-0.9±0.3***	-2.0±0.7***

*P<0.05, **P<0.01, ***P<0.001

DISCUSSION

Reliable prediction of the genetic effects on carcass components from live-animal measurements could be a strong tool towards value based and easy genetic improvement strategies for important economic traits. The strong negative Jersey direct effects on the predicted carcass traits on kilogram weight basis were expected since the Jersey breed is smaller size than the Limousin breed. In a study comprising many different breeds, pure Limousin progeny and those sired by Limousin also ranked higher in carcass, meat and bone weight (Pitchford *et al.*, 1998). However, the positive but not significant Jersey direct for the percentage carcass products may reflect an attribute of Jersey genes on proportion of carcass products. Jersey had greater proportion of bone than Limousin (Pitchford *et al.*, 1998).

The positive Jersey maternal effects on carcass bone and fat weights indicate the importance of the carry-over effects of pre- and post-natal nutrition from Jersey cows relative to Limousin cows. Maternal effect from Jersey dams, being a dairy breed with high milk supply, contributed significantly to the expression of these traits. However, the non-significant maternal effects on carcass and meat weight suggest a limit for the dam influence on progeny performance. Also, the negative but significant Jersey maternal effect on percent meat indicates compensatory growth exhibited by calves born and nursed by Limousin dams, probably due to improved post-weaning nutrition.

Most reported studies have indicated heterosis effects only on growth and corresponding quantitative traits (Koch *et al.*, 1985 ; Pitchford *et al.*, 1993). Koch *et al.* (1985) obtained a greater than expected retained heterosis for post-weaning gain and final weight while Pithford *et al.* (1993) found that heterosis effects were 1-21% for mature weight and 0-4% for mature height depending on the environment. Also, the study by Gregory *et al.* (1991) observed no significant heterotic effects even on post-weaning muscle, an indication of expected carcass products. However, this study has shown reasonable evidence (Table 2) for non-additive genetic effects on carcass composition (% traits). The positive heterosis and epistasis estimates on meat percent and negative effects on bone and fat percent supported this. Thus, non-additive genetic effects (heterosis and epistasis) should be considered when developing a composite population. The large phenotypic differences between the breeds used in this study (Limousin and Jersey) could be the reason for the significant non-additive genetic effects on the percentage carcass products in contrast to other studies.

CONCLUSION

This study has revealed that the genetics of carcass composition may involve complex gene action that could impact on both breeding value estimation and marker or genotype-assisted beef cattle selection programs.

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