Using variation in cattle growth to develop a predictive model of carcass quality

By

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In the Name of Allah,
the Most Beneficent, the Most Merciful.

Read: in the name of your Lord who created. He created man from something which clings. Read and your Lord is the most generous. Who taught with pen. Taught man what he knew not..."
(The Holy Qur'an 96:1-5)

Dedication

First of all, most importantly, I am very much grateful to my **Lord *(Allah)***, who granted me so many things. He provided me the good genes and environment so I can make better use of life in this universe.

I dedicate this study to the memory of *all the people in my home country* that so generously allowed me to continue my study abroad.

Also, this thesis is dedicated to *my parents* who have supported me all the way since the beginning of my studies.

and with all my love to

……………………………*my wife*
my son, Ali
my son, Reza.

You all keep my spirit alive!

O Lord! Benefit me through knowledge that You have bestowed on me, teach me whatever would benefit me, and increase my knowledge.

My Lord, save me from the useless knowledge.

Table of Contents

List of abbreviations

%	percentage
AAABG	The Association for the Advancement of Animal Breeding and Genetics genetic parameter data base
Age	First order of age (linear)
Age^2	Second order of age (quadratic)
Age^3	Third order of age (cubic)
BW	Birth weight
c^2	Maternal heritability (genetic + maternal permanent environmental)
CV	Coefficient of variation
d	days
df	Degrees of freedom
EMA	eye muscle area
h^2	Additive (direct) heritability
HCWt	Hot carcass weight (kg)
IMF	Intramuscular fat (%)
kg	Kilogram
Ln	Natural logarithm
Log	Logarithm
Mg	Management
P8	Rump (P8) fat depth (mm)
PC1	The first principal component
PC2	The second principal component
PC3	The third principal component
PCA	Principal component analysis
PE	Permanent environmental
PWG	Pre-weaning gain (kg/d)
PWG	Post-weaning gain (kg/d)
r	Correlation coefficient
$r_{EMA,W}$	Correlations between body weight and EMA
REML	Restricted Maximum Liklihood

RGR	Relative growth rate (%/d)
$r_{HCWt,W}$	Correlations between body weight and HCWt
$r_{IMF,W}$	Correlations of body weight and IMF
$r_{P8,W}$	Correlations of body weight and P8
RRM	Random regression model
SD	Standard deviation
Slage	Slaughter age
V.P.	Variance parameters
TE	Temporary environmental
V_A	Additive genetic variance
V_C	Dam genetic variance
V_D	Dominance genetic variance
V_I	Epistatic genetic variance
V_{Mg}	Management variance
V_P	Phenotypic variance
V_S	Sire variance
Wt	Weight (kg)
WW	Weaning weight (kg)
YG	Yearling (365 d) gain (kg/d)
YW	Yearling (365 d) weight (kg)

List of Figures

M1

List of Tables

Declaration

This work contains no material which has been accepted for the award of any other degree or diploma in any university or other tertiary institution and, to the best of my knowledge and belief, contains no material previously published or written by another person, except where due reference has been made in the text.

I give consent to this copy of my thesis, when deposited in the University Libraries, being available for photocopying and loan.

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Abstract

This thesis utilised body weights at various ages, hot carcass weight (HCWt), fat depth (P8), eye muscle area (EMA) and intramuscular fat percentage (IMF) data for heifers and steers from the "Southern Crossbreeding Project" where 581 purebred Hereford cows were mated to semen of sire breeds Angus (11 sires), Belgian Blue (16 sires), Hereford (10 sires), Jersey (12 sires), Limousin (16 sires), South Devon (15 sires) and Wagyu (17 sires). There were generally 12-15 progeny per sire, with an average of 13 calves per sire and 14 sires per breed. The project comprised 1141 of the heifers (female) and steers (castrated male) born in autumn (average birth date 3rd April) at two locations; 'Struan' near Naracoorte and 'Wandilo' near Mount Gambier in the south east of South Australia (S.A.). Calves stayed with their dams on pasture until weaning and calves were grown until 12 to 18 mo of age and then transported to a commercial feedlot. The mixed model for growth traits included fixed effects of sex, sire breed, age (linear, quadratic and cubic), and their interactions between sex and sire breed with age. Random effects were sire, dam, management (location-year-post-weaning groups) and permanent environmental effects. For carcass analysis fixed effects were sex, sire breed, slaughter age nested within sex and random effects were sire, dam, management and environmental effects. The objective of the work described in this thesis was to model relationships between continuous growth traits and carcass quality traits for steers and heifers. The model is being used to predict the effect of growth path on carcass quality. The analyses were based on the following steps:

Step 1. Describing variation in growth using principal component analysis (PCA) and random regression models of growth

Applying PCA indicated that the first two principal components (interpreted as the overall size and feedlot growth) accounted for 85% of total variation. Sire effect was significant for overall size and feedlot growth traits and management had a big impact on both components.

A cubic polynomial with sire as a random effect was the simplest and most stable model. Twenty two (co)variances were able to be estimated, using random regression analysis. Variance components for genetic variation within breeds were generally low. In contrast, management group accounted for the large proportion (79%) of the total variation.

Step 2. Describing variation in carcass quality using principal component analysis (PCA) and multi-trait mixed models

A large proportion (76%) of variation in the carcass traits were explained by two principal components which were interpreted as market suitability and muscling and were similar for both heifer and steers.

A multi-trait mixed sire model was used to estimate 40 (co)variance components of the four carcass traits. Similar to body weights, non-genetic, in particular management group variation contributed to a large proportion of total carcass variations, up to 50% of total variation.

Step 3. Joint modeling of growth and carcass quality

With perseverance, 99 (co)variance components estimated by the joint model to answer the basic questions of how the correlations between growth traits and carcass quality traits change over time. The magnitudes of the coefficient for management correlations were significantly higher than genetic, dam and permanent environmental correlations. Management correlations between live weight and carcass traits during the pre-weaning period were positive except for IMF. The magnitude of those correlations decreased from birth to weaning, then increased dramatically up for the feedlot period, where they plateaud except IMF which decreased from 500-700 days. Genetic correlations between live weight with HCWt and EMA were moderate to high and positive. In contrast, genetic correlations between live weight and fat traits were low. The pattern of phenotypic correlations between live weight and IMF as the animal grew indicated that the intramuscular fat is later developing than subcutaneous fat.

Step 4. Predicting carcass quality

The strength of the model developed lies in its simplicity and the capability to give answers to 'what if' questions. However, due to using random regression with a polynomial, the model was subject to over estimations at the end of the trajectory. In addition, because of large residual between animal variances and very small covariances between carcass fat traits and body weights, predictions were of lower accuracy than would be desirable for commercial application of the model. The model was tested against an independent data set and gave predictions that were reasonable although not great. The model could be improved by including other growth traits and other data sets with greater variation in pre-weaning growth.

Chapter 1

Introduction and review of literature

1.1 Introduction

Production of consistent and high quality carcasses is the goal of the beef industry. This goal must be attainable through a variety of production systems. Today, in the beef industry, it is a challenge to design the "best" management strategy for individual breeder, backgrounder and finisher operations to get optimum (consistent and high quality) end products under different circumstances. In the face of these issues, it is important to develop a flexible and feasible model that predict carcass quality of cattle from growth path under a variety of managements practices, which consequently lead to cattle to be marketed at the optimum time. A successful prediction of the carcass quality following specific growth path depends on the estimates of variation in growth, carcass and association between growth and carcass. Finally, these estimates lead to develop a predictive model for prediction of carcass traits from growth path.

Generally, modelling can be used as a way to explore an uncertain future. Models are essential tools in the understanding of livestock production systems (Spedding, 1988). In recent years, interest in developing growth models for beef cattle has increased amongst both geneticists and segments of the beef cattle industry. One reason for this interest is that growth models summarize information required for an understanding the biological phenomena of growth, an economically important component in beef production systems (Menchaca et al., 1996). Moreover, these models are used to evaluate growth effects on performance traits and economic values (Amer et al., 1997).

Growth in animals is an integrated process and accompanied by concomitant changes with time in the genetic and non-genetic (co)variances components (Mrode and Kennedy, 1993; Atchley et al., 1997; Huisman et al., 2002). The potential for change in performance (carcass quality) traits is thought to be largely dependent on their genetic variation and correlations over the growth path. Producers need to be aware of where these correlations are optimum as well as possible antagonistic relationships among traits over the growth path so that they may account for them in management strategies and breeding programs. Furthermore, these variations are necessary to predict performance and also to examine alternative feeding or management strategies.

Several approaches have been proposed to deal with estimating genetic and non-genetic parameters of growth data. The traditional approach is a multi-trait model, assuming the phenotypic values at distinct ages as different traits. Recently, random regression models has been advocated to fit growth data (Schaeffer and Dekkers, 1994; Jamrozik and Schaeffer, 1997a; Jamrozik et al., 1997b; Jamrozik et al., 1997c; Kettunen et al., 1998; Kettunen et al., 2000; Schenkel et al., 2002; Hassen et al., 2003). In beef cattle, this method was applied by Varona (1997), and was used on the body weights of mature beef cows by Meyer (1999, 2000) and by Arango et al. (2004).

Attempts have been made to develop mathematical models to predict carcass compositions in growing and mature cattle (Sanders and Cartwright, 1979a; Loewer et al., 1983; Oltjen and Owens, 1986, 1987; Oltjen and Garrett, 1988). Keele et al. (1992) and Williams and Benett (1995) devised a general method of estimating total fatness (and proportionately marble score) of cattle grown out under different production conditions and from this, estimated feasible grow-out and finishing pathways for a range of genotypes of cattle under North American production scenarios. Williams and Jenkins (1998) developed a model that was based on a different mathematical formulation from that used by Keele et al. (1992) to predict composition of empty body weight changes in mature cattle. Kilpatrick and Steen (1999) simulated the influence of the feeding regime, based on silage and concentrate, on beef cattle growth and carcass composition. More recently, Archer and Bergh (2000) developed a mechanistic dynamic model of beef cattle growth, which simulates the evolution of body composition through synthesis and degradation equations. However, less information is available to address how continuous growth traits and carcass quality traits were correlated over time and how to predict carcass quality when the growth path is known. Most of the work carried out in the past has investigated such traits in terms of a set of discrete ages and of correlations between them, and have ignored the time dependent continuity that must exist between them i.e. correlations among records at successive ages.

Thus, the objectives of this thesis are to quantify variation in growth and carcass quality traits of crossbred cattle and to predict carcass quality traits from longitudinal live weights over the growth path. The results of this project may be useful for the economic and also the basic biological modelling of crossbreeding systems. In addition, it is expected the results will aid producers manage cattle to closely meet specifications for weight and fatness at slaughter, to minimize time taken to reach a given market specifications and to maximize the number of animals reaching the specification. Moreover, hopefully it will result in higher returns for southern Australia's beef industry through development of management (growth path) systems.

1.2. Review of literature

As stated earlier the first aim of this research project was to investigate variability in the growth and carcass quality traits and association between those traits. This part concerns with the review of literature, which have been published to describe variability in the traits of interest.

1.2.1. Variability in the growth traits

Everything flows, nothing stands still. One thousand five hundred years ago Heraclitus, one of the first few of philosophers in this world, has stated that “no man can cross the same river twice, because neither the man nor the river are the same” and this is the basic concept of the growth i.e. change. However, Heraclitus' view that an explanation of change was foundational to any theory of nature was strongly opposed by Parmenides, who argued that change is an illusion and that everything is fundamentally static (Cohen et al., 1995).

The primary definition of growth is the change in size, volume, weight or other characteristic of interest over a specified time period from zygote formation until mature weight (Parks, 1982). Body size, as a basic indicator of the growth, has often been simply based on “weight for age” which has long been considered a criterion of desirability and a good practical index of efficiency in meat animals. Previous studies indicate that body weight data may contribute to management efficiency, management decision-making and the diagnosis of health problems (Maltz et al., 1991; Maltz et al., 1992; Devir et al., 1997; Halachmi et al., 1997; Maltz, 1997; Maltz et al., 1997; Spahr and Maltz, 1997).

Growth patterns from birth to slaughter

Growth patterns of beef cattle are of primary economic importance to the beef industry. Growth pattern has a direct effect on income and is positively correlated with weight, efficiency of gain and value of retail products. Due to the influence of management and nutrition on the patterns of the growth, the literature will be reviewed in two stages: birth to weaning (pre-weaning growth pattern) and weaning through slaughter (post-weaning growth pattern).

Pre-weaning growth pattern (Birth to weaning)

It would be expected that pre-weaning growth data may be helpful in making decisions for range cow-calf management, especially when feed supplementation is required in case of poor pasture condition which leads to insufficient milk production of the dams. However, there is a dearth of information on pre-weaning growth patterns. In calves, lack of this stems primarily from the fact that such studies require several pre-weaning weight records to be taken on each calf (Ahunu and Makarechian., 1987). Frequently, only one or two weight records are available per animal (birth and weaning weight) (Woodward et al., 1989; Rossi et al., 1992; MacNeil and Snelling, 1996) and growth patterns are estimated using a common covariate for the entire population. In addition, pre-weaning weight in beef cattle is a complex trait since it reflects not only the growth ability of the calf but also the maternal environment provided by its dam. Moreover, this weight is influenced by factors such as sex of the calf, age of dam and date of birth, which are not easily controlled under existing management systems. Furthermore, commonly, an age-adjusted weaning weight is calculated, usually by means of a linear estimation of calf growth from birth to weaning (Gregory et al., 1978; Bolton et al., 1987; Boggess et al., 1991) whereas, the non-linearity of calf growth can lead to bias in age-adjusted weaning weights (Woodward et al., 1989). Consequently, some aspects of the growth pattern in the pre-weaning period may be overlooked as a result of using only a few select measures in evaluating pre-weaning performance.

Sources of variations in pre-weaning growth

Examples of genetic and non-genetic sources of variations in pre-weaning growth data are breed, sex of calf, season (calving date), frame size, age of dam, milk supply and creep feeding.

Genetic

Ahunu et al. (1997), Chase et al. (1998) and Villalba et al. (2000) reported that there are breed differences in pre-weaning growth rate.

Non-genetic

Adjustment for non genetic sources of variation is important to increase the accuracy of ranking animals based on their breeding values and hence the effectiveness of selection. The effect of sex of calf, year of birth and age of dam on birth weight, weaning weight and pre-weaning average daily gain are well documented, and appropriate correction factors to adjust for some of these traits are available to the beef industry (Schaeffer and Wilton, 1974; Tong, 1982).

Sex. Generally, males are heavier at birth and have greater pre-weaning average daily gain (ADG) than females (Menchaca et al., 1996; Varona et al., 1997; Villalba et al., 2000). Numerous cases of an association between sex differences and level of environment have been reported, for instance, when calves grow faster (creep feed or from high milk producing dam), differences between male and female calves tend to be greater (Hopkins, 1977a, b; Barlow and O'Neill, 1978).

Season. The direct effect of season on growth curves could have important implications for production management decisions (McCarter et al., 1991; Menchaca et al., 1996; Ahunu et al., 1997; Villalba et al., 2000). Furthermore, growth is related to the feeding resources available for the cattle through the year and the normal transformations in digestive physiology of the pre weaned calf and seasonal dynamics of range forages (Fredeen et al., 1972; Baker, 1982; Menchaca et al., 1996). In other words, time of calving affects weaning weights by changing the plane of nutrition for the cow and her calf. Therefore, examination of intermittent rates of live weight gain of calves may identify periods of inconsistent production and infer alternative management opportunities to maximize growth rates. However, it is not appropriate to accept the results of one year only as indicative of what might happen every year as seasonal conditions often alter enormously between different years.

It is asserted that the effect of calving date is highly confounded with the range condition. Low et al. (1981) reported that early-born calves generally grow faster, are more efficient and achieve a steadier gain than calves born later during the calving season. Also McCarter et al. (1991) have shown that birth weights of spring-born calves were significantly heavier than those of fall-born calves. This argument is similar to that of Ahunu and Makarechian (1987) who found that the rate of growth in early-born and mid-season-born calves was higher than that of the late-born calves.

Frame size. Growth curves were characterized by stage of life cycle for small, medium, and large frame Brahman cattle (Laster et al., 1976; Gilbert et al., 1993; Menchaca et al., 1996). Menchaca et al. (1996) have established a growth model for each frame size from birth to weaning and indicated that their growth curves differed in shape from birth to weaning; however, frame curves did not differ from weaning to 32 month of age. In these models, points of inflection showed that maximum instantaneous daily gains were attained approximately 2.6 month before weaning. The decrease in rate of growth after this time was possibly due to decreasing milk production of the dams and decreasing quality of pasture as the season progressed.

Age of dam. Many investigators have drawn attention to the importance of age of dam effect on pre-weaning traits, especially the view that age of dam, in terms of parity, has an effect on birth weight (Ahunu and Makarechain, 1987; Hearnshaw et al., 1995a; Villalba et al., 2000). Fitzhugh (1978) has emphasized that age is more important in the first 4-years, while Cundiff et al. (1966) considered that adjustment factors over this period should be made for each 3-5 month of age difference of dam, rather than on the normal yearly basis.

Interactions. The concept of matching animal genetic resources with production environment, considered by Lush and Shorde (1950), has been of interest. Falconer and Mackay (1996) suggested that the environment in which selection is practiced could be either the conditions in which the breed will be expected to live or conditions more favourable for expression of the desired character. Existence of a genotype by environment interaction (GxE) would reduce the effectiveness of selection (i.e. when the superior genotype in one environment is not superior in another environment (Eisen and Saxton, 1983).

However, if GxE was not important, response would be greatest when selection is practiced in the environment in which the highest heritability is expressed (Falconer and Mackay, 1996).

Heterosis, maternal effects, and direct genetic effects are genetic effects that have been used in improving the efficiency of commercial cattle production (Brown et al., 1993). However, there is evidence that these genetic effects may not be stable across production environments (Koger et al., 1975; Barlow and O' Neill, 1980; Long, 1981). Therefore, it has been suggested that there be more studies to investigate the interaction of these genetic resources with environment (Barlow and O' Neill, 1980).

Post-weaning growth pattern (weaning to slaughter)

Post-weaning growth encompasses the period from weaning to slaughter in steers and surplus heifers, and from weaning to maturity in heifers and bulls used for breeding.

Sources of variations in post-weaning growth

There are some genetic and non-genetic factors that determine growth potential in the post-weaning period such as breed, sex, weaning weight, age, the plane of nutrition and the management system.

Genetic

Nadarajah et al. (1984) investigated breed type effects on growth pattern. They have found that breed type significantly affected body weight at all ages. Differences in weight among breed types increased from birth to 44 months and stabilized thereafter. These workers also reported that environmental effects influenced weights at early ages more than weight at later ages and adjustment for condition significantly reduced phenotypic variation in weight at all ages. Breed type by year interactions significantly affected weights. They suggested that the changing environment affected different types somewhat differently.

An attempt was made by Williams et al. (1995) to develop a simulated model for prediction the response of 17 biological types of steers grown under different production systems and slaughtered at different marketing end points. The results suggested that sire breeds used to produce these steers could be used over a wide range of nutritional and management environments, and that a mixed group of steers can be fed and managed similarly from weaning to slaughter to produce a carcass with a specified composition, retail product, or quality.

Non-genetic

Sex. It has clearly been shown that bulls are superior in post-weaning growth to steers and that steers are superior to heifers (DeNise and Torabi, 1989; Hennessy et al., 2001). It is noted that most of the studies have been carried out under intensive feeding conditions and have shown that bulls usually grow 10 to 20 percent faster than steers.

Weaning weight. Weaning weight is likely to influence post-weaning gain in a positive direction, but birth weight is of lesser importance, and the indications are that pre-weaning gain is negatively related to birth weight (Ahunu and Makarechian., 1987).

Plane of nutrition. The plane of nutrition controls the rate of growth in the post-weaning growth period (DeNise and Ray, 1987; Dicker et al., 2001; Robinson et al., 2001). DeNise and Ray (1987) investigated post-weaning weights and gains of cattle raised under range condition and gain test environments. They reported that age and also year and sire by environment interaction were significant sources of variation for all post-weaning traits. The growth of cattle grazing on pasture throughout the year has been studied extensively in Australia (Robinson et al., 2001). In general it was found that when pasture dried off in summer, cattle stopped growing and often did not commence to grow again until the end of the winter about six months later. The actual growth curves varied according to the pattern of rainfall and pasture availability. Dicker et al. (2001) concluded that the most effective growth pattern was based on autumn weaned calves from Bos taurous breeds with supplementary feeding in winter-spring to compensate for the winter feed gap.

Age of calf. Short et al. (1999) showed that age of calf affected average daily gain and efficiency of live weight gain. This is in general agreement with the earlier findings of DeNise and Ray (1987) who reported that age when tested was a significant source of variation for initial and final weights.

Growth parameters

Growth curves are considered infinite-dimensional traits (Kirkpatrick and Heckman, 1989) or function-valued traits (Pletcher and Geyer, 1999) because the trait can be described by an infinite set of measurements. Genetic analysis of growth curves has been applied to body weight-age curves in beef cattle (DeNise and Brinks, 1985; Rekaya et al., 1999), body length-age curves in fish (Rocchetta et al., 1995) and lactation curves of dairy cows (Rekaya et al., 1999). Determining the genetic control of growth curves is important because they correct for irregularities in the data caused by human error or random environmental effects and allow for prediction of growth at ages where measurements are missing.

Mohiuddin (1993) and AAABG (2004) summarised available estimates of heritabilities (h^2) for growth traits. The estimates were derived from various procedure: paternal half-sib correlation, paternal half-sib correlation with threshold model, offspring-parent regression, REML with sire or animal model. These methods make different assumptions about additive, non-additive and environmental effects and consequently, estimates of heritability for the same trait obtained by different methods are not necessarily the same. The majority of the estimates of heritability for various growth traits (Table 1.1) were computed using paternal half-sib correlation.

The accuracy of estimation of h^2 using paternal half-sib correlation depends on having a large number of degrees of freedom for sires, the absence of selection between sires, the absence of environmental correlations between half-sibs and having a large number of progeny per sire (Carter and Kincade, 1959). Since the average relationship among half-sibs is one-fourth, so the interclass correlation is multiplied by four. The advantage of this method is in considering only the additive variance but its limitation is that it ignores three fourths of the genetic variance rather than getting a combined estimate based on all the genetic relationships. Now, for some traits, restricted maximum likelihood (Patterson and Thompson, 1971) and sire and/or animal model have become the method of choice for the estimations of h^2 (Muhiuddin, 1993).

The average estimate of h^2 for birth weight was 0.35 summarising 172 estimations reported in AAABG (2004). The average estimates summarised by Muhiuddin (1993) for male and female were 0.46 and 0.39, respectively and 0.24 being across sexes.

The estimates of h^2 for weaning weight reported 0.26 on average, 0.27 in steers and 0.23 in females (Table 1.1). Muhiuddin (1993) reported wide range of h^2 estimates from –0.13-0.84 in steers and 0.00-0.64 in females. Small and negative estimates of sire components (Messey and Benyshek, 1981) may be due to sampling error or genotype-environmental interactions. They suggested that more than 800 observations are needed if information per sire is limited to fewer than 30-40 progeny.

The average estimates of h^2 for yearling weight are 0.35 (Table 1.1) and range between 0.04-0.73 in males, 0.16-0.71 in females and 0.14-0.48 across sexes (Muhiuddin, 1993). The average estimates of h^2 for pre-weaning gain, weaning gain and yearling gain are 0.39, 0.27 and 0.28, respectively. Also the average estimate of h^2 for relative growth rate is 0.15. Most of these estimates are moderated to high, therefore, it seems that growth traits will respond to selection.

Maternal effects significantly influence variation in beef weight therefore they are an important consideration when evaluating beef cattle performance. Extensive studies have been conducted to quantify maternal effects for a variety of traits, especially those measured during the pre-weaning period (Trus, 1988; Meyer, 1992; Meyer and Hill, 1997; Meyer, 2000). In beef cattle, the dam makes at least two contributions to the offspring phenotypic value. These contributions are the sample half of her genes passed directly to the offspring and the maternal effect she provides her calf. The dam effects are partially genetic and partially environmental. A maternal effect is defined as any environmental influence that the dam contributes to the phenotype of her offspring. The contribution of the dam is environmental with respect to the calf (mothering ability, milk production, environment, maternal instinct). The genetics of the dam contribute to the environment she creates for her calf. Maternal effects are important during the nursing period with diminishing effects post -weaning. Optimum improvement programs for early growth traits require knowledge of parameters involving the joint influence of genetic and environmental effects on direct growth potential and maternal ability (Robinson, 1981).

The heritability estimates due to additive genetic and maternal effects on birth weight in order range between 0.14-0.61 and 0.03-0.82 in different breeds, 0.3 and 0.1 being the average, respectively (Muhiuddin, 1993). The average of direct heritability and maternal heritability on weaning weight are 0.22 and 0.13 respectively.

Baker (1980) reported the average estimates of genetic parameters due to maternal effects on growth traits higher than those reviewed by Muhiuddin (1993). For example, the average of direct heritability and maternal heritability reported by Baker (1980) are 0.40 and 0.19, respectively for birth weight and 0.30 and 0.52 for weaning weight In general, maternal heritabilities were lower than direct heritabilities, indicating that growth traits were determined more by the genetic characteristics of the calf than by those of the dam (Muhiuddin, 1993). As expected, estimates of maternal heritability are highest for weaning weight, followed by yearling and birth weight in turn, implying importance of maternal effects for weaning weight rather than others. Genetic relationships between direct and maternal genetic effects were generally antagonistic (Meyer, 2000; Eriksson et al., 2003, 2004).

Phenotypic and genetic correlations between growth traits are given in Table 1.1. In general, the correlations were positive and moderate to high and genetic correlations were higher than phenotypic correlations.

The average phenotypic correlation between birth weight and weaning weight was 0.3 in males, 0.39 in females (Muhiuddin, 1993). In combined data set it was reported 0.65 and 0.36 by AAABG (2004) and Muhiuddin (1993), respectively. A negative genetic correlation between birth weight and weaning weight was reported by (Pabst, 1977) who observed positive correlations between birth weight and weight at 90 days of age with pure breed cattle but negative estimates with crosses. The average environmental correlations between birth weight and weaning weight are low to moderate, 0.16 (ranged 0.08-0.23) in males, 0.22 (ranged 0.19-0.33) in females and 0.25 (ranged 0.25-0.34) (Muhiuddin, 1993). It could be concluded that higher birth weight will be associated with higher yearling weight. The average environmental correlations between birth weight and yearling weight are also low to moderate positive. The phenotypic correlation between weaning weight and yearling weight is 0.26 (AAABG, 2004) and vary from 0.57 to 0.85 in different breeds (Muhiuddin, 1993). Wide range of estimates (0.16-0.92) reported for the genetic correlation between weaning weight and yearling weight in different breeds, clustering around 0.8 (Muhiuddin, 1993) and 0.46 (AAABG, 2004). High and positive correlations between theses two traits indicated that increased weaning weight will improve yearling weight and will result in desirable economical important carcass traits. The average environmental correlation of 0.66 (range 0.48-0.83) between weaning weight and yearling weight is moderate to high in magnitude, suggesting that environmental affects on yearling weight are not independent of those on weaning weight (Muhiuddin, 1993).

Table 1.1. Estimates of heritability (on diagonal) phenotypic correlations (above diagonal) and genetic correlation (below diagonal) and number of estimation for growth traits from literature sources, number of studies has shown in the brackets (AAABG, 2004)

	BW[a]	PWG[b]	RGR[c]	WG[d]	WW[e]	YG[f]	YW[g]
BW (832)	**0.35(172)**	0.20 (42)	-0.03 (3)	0.18 (27)	0.36 (66)	0.31 (5)	0.37 (36)
PWG (976)	0.34 (43)	**0.39(183)**	0.80 (6)	0.14 (36)	0.11 (60)	0.71 (6)	0.67 (54)
RGR (84)	-0.12 (3)	0.87 (6)	**0.15 (12)**	-0.51 (1)	-0.30 (4)	0.22 (1)	0.36 (4)
WG (464)	0.35 (31)	0.38 (36)	0.28 (1)	**0.27(108)**	0.94 (33)	0.73 (2)	0.68 (22)
WW (1148)	0.46 (77)	0.38 (66)	-0.09 (4)	0.97 (37)	**0.26(239)**	0.72 (77)	0.26(239)
YG (111)	0.46 (6)	0.73 (7)	0.22 (1)	0.87 (2)	0.71 (6)	**0.28 (24)**	0.98 (5)
YW (843)	0.48 (37)	0.80 (58)	0.34 (4)	0.75 (23)	0.78 (66)	0.99 (5)	**0.35(154)**

[a]BW=Birth weight, [b]PWG= Pre-weaning gain, [c]RGR=relative growth rate, [d]WG=weaning gain, [e]WW=weaning weight, [f]YG=yearling gain, [g]YW=yearling weight

1.2.2. Variability in the carcass quality traits

Carcass attributes of commercial interest include the size of carcass and proportions of meat, fat and bone which affect processing efficiency. Therefore, the main predictor traits are carcass weight and fat depth as well as eye muscle area. Meat quality is also important and carcass quality is usually determined by meat colour (indication of tenderness) and marbling score (or intramuscular fat content).

Sources of variations in the carcass quality traits

The primary sources of variation in carcass traits are genetic and environmental. Cundiff (1988) stated that the range for differences between breeds is comparable in magnitude to the range for individuals within breeds for most traits, implying that the between breed variation is of similar magnitude to the within breed variation. Examples of genetic and non-genetic factors affecting carcass traits are breed (growth type), sex, age and live weight, conformation, hormones, days on feed, age and weight at slaughter, plane of nutrition compensatory growth, growth path.

Genetic

Genetic differences in partitioning of fat among the major carcass depots have been documented in cattle by several investigators (Callow, 1961; Fortin et al., 1981; Truscott et al., 1983; Kempster et al., 1986; Newman et al., 1993; Short et al., 1999).

Callow (1961) has found characteristic differences in the relative development of the major carcass fat depots (intramuscular, subcutaneous and internal fat) among Hereford, Shorthorn (a dual purpose breed) and Friesian (a dairy breed) steers. In that study, Herefords (a beef breed) had a high ratio of subcutaneous to intramuscular and a low proportion of internal fat, whereas, Friesians had a low ratio of subcutaneous to intramuscular fat and a high proportion of internal fat. Shorthorns were intermediate in their relative development of subcutaneous and internal fat. Using these findings as a basis, Callow (1961) theorized that distribution of fat in the bovine carcass is closely related to selection history. Namely, cattle selected intensely for traditional beef characteristics tend to deposit a comparatively high proportion of subcutaneous fat, in contrast to cattle selected for milk production, which tend to deposit a high proportion of internal fat.

Interesting findings in support of Callow's theory were those of Fortin et al. (1981) and Kempster et al. (1986) which suggest that the most extreme differences in fat distribution exist between breeds selected most intensely for beef production (Angus and Hereford) and those selected most intensely for milk production (Jersey, Friesian). The available evidence concerning fat distribution in the continental breeds shows that they tend to have an intermediate position relative to the British and dairy breeds (Charles and Johnson, 1976). But it is interesting to note that late-fattening genotypes (such as continental breeds and certain dairy breeds) tend to have a lower proportion of subcutaneous relative to intramuscular and internal fat than genotypes (such as the british beef breeds) that fatten earlier. Moreover, they proposed that genetic tendencies toward early fattening result in an increased proportion of subcutaneous relative to intramuscular and internal fat, while late fattening produces the opposite effect.

Contrary evidence can be found in the results of LeVan et al. (1979) who suggested neither breed nor slaughter weight had marked effects on the relative distribution of retail lean, fat or bone throughout the animal's body. Berg et al. (1978) also found no significant sire-breed differences in the regression of muscle, fat or bone on various body dimensions. In regressions involving fat, however, the fattest (Herefords) had higher regressions, and the leanest Blonde Aquitaine fattened more slowly relative to muscle and bone growth (Berg et al., 1978). Breeds differed significantly in amount of muscle, fat and bone when compared at standard weights. In an experiment, Bertrand et al. (1983) observed that the dairy breeds (Holstein and Brown Swiss) had heavier slaughter and carcass weights and less external fat than the beef breeds (Aberdin Angus and Hereford). In another study, Gregory et al. (1994) showed that heterosis was generally significant for weights of retail product, trimmed fat, and percentages of carcass lean, fat.

A number of experiments have shown a genetic variation in marbling in beef cattle (Marshall, 1994; Franke, 1997). Malau Aduli et al. (2000) observed that the relationships between breed means for marbling and intramuscular fat are high (0.97). In several studies, researchers have found significant heterosis above the direct effects of breed for marbling (Thompson and Barlow, 1981; Bertrand et al., 1983; Wilson et al., 1983; Newman et al., 1993; Gregory et al., 1994). Bertrand et al. (1983) reported that the cross of beef and dairy steers were similar to beef steers in marbling score, they were intermediate between beef and dairy steers in external fat deposition, and were similar to dairy steers in amount of lean produced.

Non-genetic

Slaughter age. In experimental studies, cattle have been slaughtered at (or the data adjusted to) several end points, yet age has been the most common criterion (Koots, 1994a; Marshall, 1994; Shanks, 2001). Slaughter end point can alter the expression of genetic and environmental differences (Koch et al., 1995). When animals, slaughtered at the same age, have been assigned to different levels of nutrition, their carcass usually differs in fatness. Since nutritional effects are confounded with fatness it is more suitable to consider changes due to fattening. Owens et al. (1997) found that longer feeding times and advanced slaughter age were related to greater subcutaneous fat thickness. In contrast, heavier initial weights were associated with less external fat. Considering this finding, they suggested that steers with greater initial weight fed for a short time should have the least fat cover and highest yield grades. Furthermore, their results implied that increased slaughter age, decreased the marbling/subcutaneous fat thickness ratio. They also observed that heavier initial weights and an older age at slaughter tended to decrease (improve) that ratio. Owens et al. (1995) also reported that marbling score increased obviously with slaughter age and slightly with days fed, but it decreased as initial weight increased.

Cianzio et al. (1982) reported that small cattle tended to fatten at younger ages and lighter weights than their large contemporaries. Furthermore, smaller cattle had a greater amount of subcutaneous fat when the two groups were compared at a constant weight of total body fat. The above results stress that in addition to cattle growth type, the end point of production is critical in order for producers to successfully target carcass characteristics (Wheeler et al., 1996).

Maturity. Existing knowledge implied that physiological maturity has effects on carcass weight, fat depth, muscling and intramuscular fat content (Aass, 1996a, 1996b; Tatum et al., 1986; Wulf et al., 1996). In all literature cited, differences observed among the cattle frame-size groups contrasted early-, intermediate- and late fattening genotypes.

Plane of nutrition. Among the many factors, which contribute to variation in growth performance and carcass composition in cattle, plane of nutrition plays the major role. Effects of finishing based on grain or pasture on carcass composition and carcass quality traits have been described broadly in the literature [Keele, 1992 #32;Williams, 1995 #33;Dicker, 2001 #193;Wolter, 2003a #230;Wolter, 2003a #231] and is reviewed (Muir et al., 1998). However, this literature has reported mixed results on carcass quality traits. Some researchers have reported that composition of carcasses is similar whether cattle are fed a grain-based diet immediately after weaning or after a period of slower growth. Other investigators have indicated, however, that nutrition impacts carcass composition (Dikeman et al., 1985) and stated that nutritional environment has a profound effect on growth and fatness of beef cattle (Keele *et al.* 1992; Williams and Bennett 1995). Previously, Mandell (1998) noted that many studies that compared forage vs grain finishing have been confounded regarding back fat finish and days on feed between forage- and grain-fed beef. In those studies, forage-fed cattle often had minimal amounts of finish or were slaughtered at ages older than those of grain-fed cattle.

Smith et al. (1989) discouraged forage finishing because of deleterious effects on carcass and beef quality, but others (Crouse and Glimp, 1973; Bidner et al., 1981; Fortin et al., 1985) found no differences in those attributes between forage- and grain finished beef. Beckett et al. (1992) found that the rib eye area, marbling score, back fat thickness were not affected by the levels of roughage. Carcasses of forage fed beef are lighter and have less marbling and lower quality grades but have higher cutability (meat yield) than carcasses of grain-fed steers (Dinius and Cross, 1978; Harrison et al., 1978). Greater lean yield in forage-fed beef relative to grain-fed beef has been reported previously Bowling et al. (1977), Bidner et al. (1981) have found smaller longissmous muscle area in forage-fed cattle vs grain-fed cattle. However, the lack of significant differences for longissmous muscle area with other contrasts agrees with past studies (Bidner et al., 1981; Fortin et al., 1985) in which forage finishing did not decrease longissmous muscle area relative to grain finishing when times on feed differed between diets.

Carcass parameters

Literature reports on heritability estimates, genetic and phenotypic relationships among carcass measurements in beef cattle have been summarised (Mohiuddin, 1993; Koots, 1994a; Marshall, 1994; Bertrand et al., 2001; AAABG, 2004). Heritability estimates for considered carcass quality traits are given in Table 1.2. These estimates were adjusted to an age constant, time-on-feed (finish) constant, weight constant or unadjusted basis. In general, the average heritability estimates for all the traits were in the moderate to high range (Bertrand et al., 2001, AAABG, 2004). Heritability estimates for carcass weight, P8 fat, ribeye area, marbling score, and cutability averaged across studies evaluating carcasses at a fat constant endpoint were also moderate to high (Johnston et al., 1992; Wulf et al., 1996; Elzo et al., 1998; AAABG, 2004). Benyshek (1981) and Arnold and Bennett (1991) reported that heritabilities for fat thickness, ribeye area, and marbling score were all above 0.23 when carcass data were adjusted to a weight constant basis. Estimates of genetic parameters of marbling are dependent upon the method used to measure the trait, the method of finishing cattle, and age and weight at the time of measurement. In a data set where different measures of marbling were made on the same carcasses, the estimate of heritability of marbling assessed by the Australian AusMeat system was 0.15, compared to 0.32 for the Meat Standards Australia and USDA (2000) system and 0.43 for measure of intramuscular fat by chemical extraction from the visually assessed site (Johnston, 1999). Splan et al. (2002) also observed the heritabilities for carcass traits of steers were moderate to high (0.34 to 0.60).

Table 1.3 presents average phenotypic and genetic correlations from several studies for carcass quality. Almost, all measures of efficiency whether biological or economical are related to live weight especially slaughter weight and beef carcass value is mainly based on the amount of saleable meat contained in the carcass. Therefore, the relationship between live weight and carcass weight and meat yield is highly important.

The phenotypic correlations averaged across all the studies between carcass weight-P8 fat, carcass weight-EMA and carcass weight-marbling score were 0.32, 0.41 and 0.09, respectively and their corresponding genetic correlations were 0.26, 0.52 and –0.20, respectively (Bertrand et al., 2001, AAABG, 2004). Pitchford et al. (2002) observed that the phenotypic correlation between carcass weight and fat thickness was 0.31, but the genetic correlation was not significant. Of interest were the moderately large average phenotypic and genetic correlations between carcass weight and EMA. Owens and Gardner (1999) observed that longissimus muscle area increased as carcass weight increased; however, the increase in longissimus muscle area was only 10% with a 19% (from 293 to 351 kg) increase in carcass weight. They concluded that longissimus muscle area as a percentage of carcass weight decreased by about 7% as carcass weight increased across this range. They explained that the decrease in longissimus muscle area in relation to carcass weight might stem from several factors. *"First, longissimus muscle area is a surface measurement, whereas carcass weight is volumetric, and longissimus muscle length may increase without a change in surface area. Second, muscle size may reach a plateau (maturity) before body weight, reflecting the natural progression from lean to fat deposition with maturity"*. They also reported that fat thickness and marbling scores increased slightly with carcass weight. A survey was conducted by Laville et al. (1996) to investigate the relationships among carcass weight and carcass composition (i.e. muscle weight, bone weight and fat weight). They indicated that the percentage of muscle was best predicted by only three carcass measurements with a relatively low value of fit (R^2 = 0.70), whereas, when carcass weight was added the fit was (R^2 = 0.98). Ewers et al. (1999) also found similar results.

Gregory et al. (1994) reported a correlation of –0.94 between marbling score and cutability among breed group means. The results from these two reports suggested that it may be possible to select sires within a breed that can both increase marbling score and percentage retail product relative to the breed mean.

Koots et al. (1994b) reported correlation of 0.15 between carcass weight and marbling score. Pitchford et al. (2002) found no correlation between intramuscular fat content and carcass weight, analysing "Australian Southern Crossbreeding project" data set.

The phenotypic correlations averaged across all the studies between marbling score-backfat thickness, marbling score-ribeye area and marbling score-cutability were -0.14, -0.03, and -0.18, respectively. However, the average genetic correlations of those were 0.35, -0.22 and –0.54, respectively (Bertrand et al., 2001; AAABG, 2004).

In the study with Hereford, Angus and Simmental cattle, genetic correlations of marbling with fat thickness ranged from strongly positive to slightly negative and with cutability or retail yield ranged from moderately negative to slightly positive (Koch, 1978; Koch et al., 1982; Lamb et al., 1990; Woodward et al., 1992). However, phenotypic correlations of marbling with fat thickness and cutability were reported consistently in the direction of an antagonism and were small to moderate in magnitude (Gilbert et al., 1993; Marshall, 1994; Pitchford et al., 2002). In a similar connection, Arnold and Bennett (1991) observed that reduced fat thickness was associated with larger longissimous muscle area and reduced marbling in weight constant analyses. Betrand et al. (2001) stated that intense selection could increase marbling without increasing fat thickness. Pitchford et al. (2002), in a study on 1215 calves over four years concluded that it seems to be possible to select animals within breeds for improvement in both subcutaneous (low) and intramascular (high) fat.

Table 1.2. Estimates of heritability for carcass traits from literature sources (Koots et al., 1994a and Bertrand et al., 2001)

Source	HCWt	Fat depth	EMA	Marbling	Cutability
1. Benyshek (1981)	0.48	0.52	0.4	0.47	0.49
2. Koch et al. (1982)	0.43	0.41	0.28	0.34	0.38
3. Van Vleck (1992)	-	-	0.6	0.45	-
4. Woodward et al. (1992)	-	-	-	0.23	0.18
5. Veseth (1993)	0.38	-	0.51	0.31	-
6. Wilson et al. (1993)	0.31	0.26	0.32	0.26	-
7. Shackelford (1994)	-	-	-	0.93	0.45
8. Gregory (1995)	0.23	0.25	0.22	0.48	0.47
9. Barkhouse (1996)	-	-	-	0.4	-
10. Hirooka (1996)	0.37	0.35	0.38	0.4	-
11. Wheeler et al. (1996)	0.15	0.56	0.65	0.73	-
12. ASA (1997)	0.34	-	-	0.35	0.26
13. Kim (1998)	-	0.34	0.51	0.79	-
14. Moser (1998)	0.59	0.27	0.39	-	-
15. Pariacote (1998)	0.6	0.46	0.97	0.88	-
16. Robinson et al. (1998)	-	0.18	-	0.3	0.52
17. Robinson (1998)	-	0.29	-	0.15	0.49
18. AAA (2000)	0.3	0.23	0.27	0.36	0.23
19. Pitchford et al (2002)	0.36	0.26	-	0.18_a(IMF)	-
20. AAABG	0.44_b(19)	0.42_b(25)	0.43_b (16)	0.36_b(12)	0.40_b(12)
Average	0.34	0.47	0.34	0.46	0.41

$_a$. intramuscular fat, $_b$. average of several studies, number of studies in brackets

Table 1.3. Phenotypic and genetic correlations (Koots et al., 1994b and Bertrand et al., 2001)

		Phenotypic correlations	Source	Genetic correlations	Source
Carcass wt	Fat depth	0.42, 0.36, 0.32	2, 6, 19	0.47, 0.12, 0.80, 0.26	2, 5, 6, 19
	EMA	0.37, 0.43,0.580.41	2, 5, 6, 19	0.13,−0.22, 0.39,0.52	2, 6, 8, 19
	Marbling	0.18, 0.13,0.28,	2, 5, 6, 19	0.09,−0.10, 0.38, -0.20	2, 5, 6, 19
	Cutability	0.84	2	−0.09,−0.13, 0.00	2, 8, 18
Fat depth	Rib-eye	-0.08, 0.04, 0.01	2, 6, 19	−0.21,−0.43, −0.05, -0.26	2, 6, 8, 19
	Marbling	0.25, 0.24, 0.14	2, 6, 19	−0.01,−0.37, 0.51,0.25	2, 3, 5, 19
	Cutability	0.07, -0.05	2	0.48, 0.32, 0.58	2,8,18
EMA	Marbling	-0.03,0.03, -0.03	2, 3, 5, 19	0.10,−0.13, 0.44, -0.29	2, 6, 8, 19
	Cutability	0.55, 0.60	2	−0.78, −0.84, −0.74	2, 8, 18
Marbling	Cutability	-0.04, -0.07	2	−0.28,−0.63, 0.15	2, 4, 18

1.2.3. Relationships between growth and carcass quality traits

It has shown that growth affects subsequent performance. Under- nutrition disturbs the normal relationship between chronological and physiological ages such that for animals on a low plane of nutrition, physiological ageing proceeds at a slower rate. When such retarded animals are fed ad-libitum, they tend to grow at a rate appropriate to their physiological age rather than their chronological age. Harris (1997) has reported that slow growth in early life can lead to a reduction in carcass quality due to increased carcass fatness. Often, feed restriction at a young age and consequently slow early growth may be followed by compensatory gain later in life resulting in a similar body weight and body composition at slaughter as in unrestricted animals (Berge, 1991). This gain is valuable for enhanced efficiency when attempting to grow animals to particular slaughter weights but the combination of slow early growth and compensatory growth can affect carcass components differently from that in animals growing continuously, depending on the severity and duration of restricted growth and when it occurs (Ryan, 1993). Also, animals undergoing compensation take longer to reach their required weight. For example, calves weaned at 148 kg compared to 214 kg were 42 kg lighter when slaughtered at 33 months of age (Hearnshaw, 1995a, 1995b). Morgan (1972) imposed live weight losses on calves from 112 days until weaning (8 months) and found that they had gains at pasture 35% higher than their well-fed cohort, although their slaughter date was 6 weeks later when killed at a similar live weight to the well-fed group. In a study, low-growth rates pre-weaning were increased above 600 g/day (Hennessy et al., 2001), consequently, the carcasses were heavier for those animals that had higher pre-weaning growths although they also tended to be fatter than carcasses from animals that had low pre-weaning growth rates. Because of their small pre-weaning growth rates, calves from the 'low' group were estimated to take 34 days longer than those animals from the high group to have reached a target live weight of 530 kg in the feedlot. These studies imply that calves with low weaning weights have greater difficulty in reaching slaughter weights within the same time period than those calves that are heavier at weaning and they further suggest that the deposition of subcutaneous fat is greater for these lighter calves. Therefore, reasonable growth rates pre-weaning are important for cattle entering feedlots. Fell et al. (1999), for example, reported on the lack of suitability of light-weight animals for intensive production.

Polkinghorne et al. (1999) suggested that growth rates for cattle should exceed 600 g/day for each of their major growth phases to ensure tender meat. Hennessy et al. (2001) found that steers and heifers were inconsistent in their growth path following the pre-weaning restriction. During the post-weaning phase, steers grew faster than heifers from either of the previously 'low' or 'high' growth rate groups. However, steers were affected more by the pre-weaning restriction than were heifers and had reduced compensatory growth during the post-weaning pasture phase so that they only matched heifer live weight at the end of this phase.

Some workers reported that differences in growth before feedlot entry may be associated with degrees of compensatory growth in feedlot (Drouillard et al., 1991) and fat deposition hence yield of saleable meat (Carstens et al., 1991). Accordingly, the relationships between growth rate before finishing and finishing performance is more or less managed by ensuring animals entering grain finishing are within a comparatively narrow range of live weight and fat thickness. Interesting findings in support of the concept of growth history effect were those of Robinson (2001) who reported that systems of finishing (feedlot or pasture) had significant influence on fat thickness and on intramuscular fat content. This probably occurred because the high growth rate of feedlot-finished cattle predisposes them to increased fatness (Keele et al., 1992) and even at the same growth rate, feedlot finished cattle deposit more fat that range finished cattle (Tudor and O'Rourke, 1980; Sainz et al., 1995). This is likely due to reduced maintenance needs in grain fed cattle because of lower visceral mass and improved efficiency of nutrient use in grain fed cattle because of increased supply of glucose precursor molecules (Oddy et al., 1997).

Muir et al. (2001) found no difference in carcass fatness (adjusted for hot carcass weight) between restricted and non-restricted steers slaughtered at the end of winter, nor at targeted slaughter weights. Morgan et al. (1972) also did not find differences in carcass fat between steers restricted, between 100 and 210 days of age, and those not restricted when slaughtered at 17 months.

Correlations between growth and carcass traits

Marshall (1995), Bertrand et al. (2001) and AAABG (2004) have reviewed genetic and phenotypic correlations between growth and carcass traits. Genetic and phenotypic correlations between growth traits and carcass quality traits from age-, weight- or finish-constant analyses are presented in Tables 1.4 and 1.5. The average phenotypic correlations between birth weight and carcass traits were lower than the average genetic correlations. The phenotypic correlations of birth weight with fat depth (-0.07) and marbling (-0.02) were negative and very low (Koch et al., 1982). The genetic correlation between birth weight and fat depth are generally low and negative, implying that there are very few genes that affect both traits and that there will be little correlated change in one trait as a result of selection for the other trait (AAABG, 2004). However, the genetic correlation between birth weight and marbling are positive and low to moderate, on average 0.3 (Koch et al., 1982). The genetic correlation between birth weight and carcass weight is the highest but between birth weight and cutability is the least.

In general, the literature cited herein reported positive and moderate to high phenotypic and genetic correlations for pre-weaning growth rate and weaning weight with carcass weight, longissimous muscle area and cutability (Koch, 1978; Koch et al., 1982; Lamb et al., 1990; Reynolds et al., 1991; Veseth et al., 1993). These publications indicated positive and low phenotypic and genetic correlations between pre-weaning gain- and weaning weight-fat depth (Koch, 1978; Koch et al., 1982; Lamb et al., 1990, AAABG, 2004). However, Arnold and Bennett (1991) and Dinkel and Busch (1973) reported that weaning fat thickness was negatively genetically associated with weaning weight. Arnold and Bennett (1991) found that carcass marbling was uncorrelated with weaning weight. Likewise, the phenotypic and genetic correlations averaged across studies were positive and low between pre-weaning gain and marbling but the genetic correlation were negative and low between weaning weight and marbling (AAABG, 2004). However, others observed positive and moderate genetic correlation between pre-weaning growth and marbling score, indicating a favourable relationship between selection for increased weaning weight and increased marbling (Koch, 1978; Koch et al., 1982; Lamb et al., 1990; Reynold et al., 1991; Woodward et al., 1992; Veseth et al., 1993). Gregory et al. (1995) reported a genetic correlation of 0.15 between weaning weight and fat thickness, 0.12 between weaning weight and marbling score, and -0.09 between weaning weight cutability. Koots et al. (1994b) and Marshall (1994) provided average literature genetic correlation estimates, respectively, of 0.07 and 0.22 for weaning weight and fat thickness, -0.17. Even though the literature is clear that selection for weaning weight increases both age adjusted rib-eye area and carcass weight (Koots et al., 1994b, Marshall, 1994), the result of selection for growth upon external fat thickness, marbling, and percentage retail product adjusted to an age constant or days-on-feed endpoint is not as clear (Bertrand et al., 2001). Splan et al. (2002) reported estimates of genetic correlations between direct genetic effects for weaning weight and hot carcass weight (0.70), rib-eye area (0.29), and adjusted fat thickness (0.26). The largest estimates of genetic correlations between maternal genetic effects for weaning weight and direct genetic effects for carcass traits were found for hot carcass weight (0.61), retail product percentage (-0.33), rib-eye area (0.29), marbling score (0.28) and adjusted fat thickness (0.25), indicating that maternal effects for weaning weight may be correlated with genotype for propensity to fatten in steers (Splan et al., 2002).

Positive genetic and phenotypic correlations were found for post-weaning growth rate with carcass weight, rib-eye area, and cutability. The phenotypic and genetic correlations of post-weaning growth rate with carcass weight averaged across studies are 0.8 and 0.9, respectively (AAABG, 2004). Shackelford et al. (1994) and Reynolds et al. (1991) observed the values of 1.1 and 1.16 for genetic correlations between post-weaning growth rate with carcass weight.

The genetic correlation between post-weaning growth rate and eye-rib area vary widely, from –0.7 (Benyshek, 1981) to 0.82 (Shackelford et al., 1994). Koch (1978) found that rib-eye area was uncorrelated with post-weaning growth rate but Arnold and Bennett (1991) observed positive and high genetic correlation between them. The phenotypic correlations between post-weaning growth rate and carcass fat thickness is positive (averaged 0.31) (Marshall, 1994; AAABG, 2004). However, the genetic correlations between those traits is quite variable (ranged from -0.20 to 0.62, averaging .13 (Marshall, 1994). Arnold and Bennett (1991) reported that fat thickness was positively associated with post-weaning gain (0.17). Marbling score was positively phenotypically but negatively genetically associated with yearling weight, 0.14 and -0.36, respectively (AAABG, 2004).

The average genetic correlation between post-weaning gain and marbling was 0.05, although estimates varied widely across studies (ranged from -0.62 to 0.48). Arnold and Bennett (1991) asserted that marbling was positively correlated with post-weaning gain (0.54) on a weight-constant basis. Relative growth rate indicated phenotypically low but genetically high positive correlation with considered carcass traits.

Table 1.4. Phenotypic and genetic correlations between carcass traits and growth traits

Trait	Phenotypic correlations		Genetic correlations	
	Wean wt or preweaning gain	Postweaning gain	Wean wt or preweaning gain	Postweaning gain
Carcass wt	0.59 (1)	0.74 (1)	0.48 (1)	0.78 (1)
	0.61 (1)	0.72 (1)	0.73 (1)	0.89 (1)
	0.68 (7)	0.64 (2)	0.94 (4)	0.94 (2)
	-	0.79 (7)	1.11 (7)	1.11 (7)
Rib-eye area	0.23 (1)	0.27 (1)	0.16 (1)	-0.7(1)
	0.25 (1)	0.32 (1)	0.49 (1)	0.34 (1)
	0.38 (1)	0.34 (2)	0.43 (2)	0.48 (2)
	0.35 (2)	0.44 (7)	0.72 (7)	0.82 (7)
Fat depth	0.12 (7)	0.32 (1)	0.59 (1)	0.62 (1)
	0.31 (1)	0.17 (1)	0.04 (1)	0.05 (1)
	0.20 (2)	0.29 (2)	0.49 (2)	0.05 (2)
	-	0.24 (7)	-	-0.20 (3)
Marbling score	-0.05 (1)	0.20 (1)	-0.02 (1)	-0.62 (1)
	0.10 (1)	0.07 (1)	0.31 (1)	0.15 (1)
	0.15 (2)	0.24 (2)	0.71 (2)	0.48 (2)
	0.02 (6)	0.24 (7)	0.16 (6)	0.19 (7)
	0.16 (7)	-	0.81 (7)	-
Cutability wt	0.59 (1)	0.62 (1)	0.37 (1)	0.73 (1)
	0.47 (1)	0.66 (1)	0.62 (1)	0.73 (1)
	-	0.74 (5)	-	0.92 (5)

1) Koch, 1978, 1982, 2) Lamb et al., 1990, 3) MacNeil et al., 1991 , 4) Reynolds et al., 1991 , 5) Shackelford et al., 1992 , 6) Woodward et at., 1992 , 7) Veseth et al., 1993

Table 1.5. Phenotypic and genetic correlations between carcass traits and growth traits, number of studies has shown in the brackets (AAABG, 2004)

	Fat depth	Cutability	Carcass wt	Marbling	Meat wt	Rib-eye
			Phenotypic correlation			
BW (832)	-0.07 (1)	0.05 (1)	0.40 (1)	-0.02 (1)	0.37 (12)	0.17 (1)
PWG (976)	0.18 (10)	0.25 (4)	0.60 (4)	0.15 (6)	0.72 (14)	0.24 (5)
RGR (84)	0.05 (2)	-0.10 (1)	0.28 (1)	0.08 (1)	0.29 (1)	0.17 (1)
WG (464)	0.30 (1)	-0.28 (1)	0.60 (1)	0.10 (1)	0.64 (7)	0.25 (1)
WW (1148)	0.15 (8)	0.33 (3)	0.56 (2)	-0.04 (5)	0.64 (17)	0.21 (3)
YG (111)	-	-	0.89 (1)	-	0.95 (1)	-
YW (843)	0.31 (5)	0.84 (2)	0.80 (2)	0.14 (2)	0.70 (11)	0.34 (1)
			Genetic correlation			
BW (832)	-0.27 (1)	0.05 (1)	0.59 (1)	0.30 (1)	0.53 (12)	0.30 (1)
PWG (976)	0.21 (11)	0.25 (4)	0.76 (5)	0.07 (6)	0.75 (18)	0.23 (6)
RGR (84)	0.84 (1)	-0.54 (1)	0.71 (1)	1.04 (1)	0.54 (1)	0.46 (1)
WG (464)	0.04 (1)	-0.02 (1)	0.83 (2)	0.30 (1)	0.71 (7)	0.48 (1)
WW (1148)	0.07 (8)	0.42 (3)	0.84 (3)	-0.17 (5)	0.71 (19)	0.39 (4)
YG (111)	-	-	0.94 (1)	-	0.89 (2)	-
YW (843)	0.31 (6)	0.86 (2)	0.90 (3)	-0.36 (2)	0.63 (12)	0.28 (2)

1.2.4. Techniques for describing variability in growth and carcass quality

Many phenotypes, such as body weight and body composition of an individual calf change with age. Berg et al. (1978) stated that because of the differential growth rates of specific body organs, the size and shape of animals change during development. Practically, it is not possible to continuously measure many of these growth processes. Therefore, it is preferable to model measurements using mathematical and statistical functions. This allows interpolation of unmeasured points. Thus, the aims of growth models are to integrate existing knowledge for the prediction of growth rate and the indication of possible areas of research where knowledge is limited (Oltjen and Owens, 1986). Development of growth models for animals began with traditional static approaches, and these were not computerized until the early 1970s. Growth models have been developed by a number of workers (Menchaca et al., 1996; Milgen, 1999a; Milgen and Noblet, 1999b; MacNeil and Mott, 2000; Villalba et al., 2000). Strategies for altering the shape of the growth curve were discussed by Fitzhugh (1978). Much consideration in these models has been given to general patterns of life-cycle growth (Brown et al., 1976; DeNise and Brinks, 1985; Beltran et al., 1992). These fitted non-linear models have been evaluated with regard to their goodness of fit, biological interpretation of the parameters, computational ease, and evaluation of genetic and environmental effects on the growth patterns parameters (Dodenhoff et al., 1999; Oliveira et al., 2000; Ramirez Valverde et al., 2001). In animal breeding, selected growth curves, such as Gompertz or Richards functions, have commonly been fitted to growth records. Pitchford et al. (1993) reported that von Bertalanffy, Gompertz and logistic curves overestimated weights at early ages. He suggested the use of a modified Gompertz curve to predict W_t, the weight of an animal at time t, with intercept equal to its birth weight (W_0) which has two biological meaningful parameters, namely the average mature size maintained, A, and the rate of maturation, K.:

$$W_t = Ae^{(\ln W_0 - \ln A)e^{-Kt}}$$

To date, however, this has generally been done independently to the estimation of fixed and random effects, i.e. not within a linear mixed model framework. The use of mixed models for the analysis of longitudinal data should provide a more accurate characterization of growth patterns because this methodology allows some parameters to be fixed and others to vary with animal, through random effects (Villalba et al., 2000; Wang and Goonewardene, 2004). Mixed models compromises between population models that do take into account within-animal correlation and animal-specific models that could be overparameterised and are inadequate when data are unbalanced. Also, separation of variation within individuals from variation between individuals for each of the parameters the curve (Andersen and Pedersen, 1996a; Littell, 1996; Littell et al., 1998) could be useful for stochastic models of growth. Simulations can be carried out using animals with different growth patterns instead of an average animal with the average parameters of the population (Werth et al., 1991; Davis et al., 1994).

There are two possible approaches to develop a beef growth model, the empirical and the mechanistic approach. The empirical model consists of a function that fits the data. The mechanistic approach attempts to simulate the biological processes and give a real understanding of the system under study. Many attempts have been made in developing empirical and mechanistic models to estimate beef cattle growth and body composition. Empirical models allow an animal's weight gain to be expressed as a relatively simple function, allowing experimental comparison of different genetics and/or feeding regimes (Thompson, 1985; Thompson and Barlow, 1986). Sanders and

Cartwright (1979a, 1979b), Oltjen and Owens (1986, 1987), Oltjen and Garrett (1988) and Loewer et al. (1983) made attemts to develop mathematical models to predict carcass compositions in growing and mature cattle. Robelin et al. (1990) fitted a Gompertz curve on body weight data for different continental breeds. Arnold and Bennett (1991) evaluated four growth models, by comparing simulation results and experimental data. They showed that these models simulated animal body weight quite successfully, but failed to predict body composition. Keele et al. (1992) and Williams et al. (1995) devised a general method of estimating total fatness (and proportionately marble score) of cattle grown out under different production conditions and from this, estimated feasible grow-out and finishing pathways for a range of genotypes of cattle under North American production scenarios. Keele et al. (1992) developed a dynamic computer model to predict composition of empty body weight gain (empty-body ether-extractable lipid and fat-free mass in cattle, as a function of rate of empty body weight gain. Williams and Jenkins (1997) developed a model that was based on a different mathematical formulation from that used by Keele et al. (1992) to predict composition of empty body weights changes in mature cattle. Kilpatrick and Steen (1999) simulated the influence of the feeding regime, based on silage and sometimes concentrate, on beef cattle growth and carcass composition. More recently, Hoch and Agabriel (2004a) developed a mechanistic dynamic model of beef cattle growth, which simulates the change of body composition through synthesis and degradation equations.

As mentioned, the current work seeks to estimate (co)variance components of growth and carcass quality traits to build the prediction model. This part of review deals with the methods, as random regression analysis and principal component analysis, which have been employed to study growth and carcass variations.

Random regression model (RRM)

Kirkpatrick et al. (1990) showed that phenotypic changes with age could be represented as a function of time. The traditional genetic evaluation of growth for beef cattle is based on a multiple-trait model (MTM), defining the actual weights in different age intervals as different traits (BIF, 2000; Meyer, 2000). For example, genetic evaluation of beef cattle often considers four different growth traits, namely birth, weaning, yearling and final weights. Because the actual weights are recorded at different ages, actual records made within specific age intervals are pre-adjusted to fixed ages, whereas records outside the age intervals are not used. Both pre-adjustment and removing out of age range records lowers the accuracy of the evaluation. The application of longitudinal models for growth (Varona et al., 1997; Meyer, 1999; Villalba et al., 2000) allows use of all available records; therefore, pre-adjustment constant ages are not needed (Huisman et al., 2002).

RRM have recently been recognised as ideally suited to the analysis of longitudinal data in animal breeding (Meyer and Hill, 1997; Meyer, 1998; Schaeffer, 2004). RRM allow for the use of all available records without pre-adjustment or censoring, and would provide estimates of breeding values at any age. In particular, RRM accommodate 'repeated' records for traits, which change smoothly over time, and they do not require stringent assumptions about constancy of variances and correlations (Meyer, 2000). RRM allow quantification of genetic merit at an infinite number of specific ages, which is of great interest to industry. This also allows more informed selection decisions, as it will potentially provide the industry with the information required to utilise variation in growth curves. (Kirkpatrick et al., 1990; Meyer, 2004a; Meyer et al., 2004b). Therefore, genetic and environmental parameters for growth can be estimated including all body weight records in the analysis through random regression models. In the random regression approach the growth curve is split into two parts: a fixed part (average growth curve) and a random animal specific part (deviations from the average curve). The variance components of the random regression coefficients determine the covariance function of each pair of weight-age values. Kirkpatrick et al. (1990) indicated that variance components for longitudinal data could be modelled through covariance functions. Meyer (1998) demonstrated that RRM could be applied to estimate covariance functions directly from data.

Compared to multivariate models (Hassen et al., 2003), RRM are able to predict covariance structures at any point along a continuous scale e.g. age or weight (van der Werf et al., 1998), estimate variances and covariances more smoothly and with less bias (Kirkpatrick et al., 1990) and require fewer parameters to describe the same data. Applying RRM is expected to result in an increase in accuracy of selection compared to a multiple trait selection program. This is illustrated using parameters for live weight of growing pigs estimated by (Huisman et al., 2002). Moreover, Meyer et al. (2004b) showed that accuracy of genetic evaluation for growth in a field data set of beef cattle was improved by around 5% by replacing a multi-trait model with a RR model. She concluded that this arose largely from a more appropriate modelling of the genetic parameters. Because the use of RRM will lead to more accurate prediction of breeding values, a higher genetic progress should be possible Huisman et al. (2002). However, Schenkel (2002) found no proof that RRM would bring higher genetic progress.

It is asserted that estimates derived from RRM seem to contain artifacts due to the tendency of polynomials to provide poor fit at the extremes when there is uneven distribution of data points (Misztal et al., 2000). Therefore, the main disadvantage of the random regression model is that it fails to reliably extrapolate outside the trajectory in which parameters are estimated (Huisman et al., 2002). In parameter estimation with RRM, parameters corresponding to the extremes of trajectories or where data are sparse may be poor (Meyer, 1999). Meyer (1998) observed that data points at the beginning and end of the lactation trajectory for which an animal has records have a relatively large impact on the regression coefficient estimates, when polynomials are used as the covariance function. Fischer et al. (2004) observed that the direct heritability increased sharply towards the end of the trajectory, where the least records were considered, in particular beyond 450 days in lambs. Similar behaviour of covariance function estimates for ages where the least data is present has been shown, i.e. at the edge of the trajectory (Meyer, 2002; van der Werf et al., 1998) and even when data are evenly spread across the trajectory (Fischer et al., 2004). Jamrozik and Schaeffer (1997a) and Kettunen et al. (1998) showed unexpected high estimates of heritabilities for daily yields as well as negative genetic correlations between the most distant test days when using the Ali and Schaeffer (1987) curve. Kettunen et al. (1998) concluded that the overestimation of the genetic variances at the edges of the defined lactation curve trajectory was likely due to the mathematical characteristics of the sub-model, i.e. the function chosen within the test day model.

Incomplete lactation records might affect the weighting of data points because the model has to extrapolate the lactation record. Further most models assume that the residuals are distributed normally and independent with zero mean and equal variance, but in practice a systematic pattern was observed in the residuals over the lactation trajectory (Jamrozik and Schaeffer, 1997a; Liu, 1998).

As a result of incomplete lactation records, Nobre (2003a) and Nobre et al. (2003b) found that evaluations from RRM with parameters estimated from the data were worse than from multiple-trait models. He proposed that one methodology for assessing the quality of parameters in RRM is to compare estimates obtained by RRM with estimates from MTM. Although the MTM estimates may be biased or less accurate compared to the underlying model due to pre-adjustments, these estimates are less likely to be affected by extremes of trajectories. Misztal et al. (2000) described the so-called "constructive approach" to form artifact-free estimates of parameters of RRM. The basic idea was to assemble functions of variances along the trajectory and of correlations across two trajectories, construct multiple-trait model parameters for a large number of traits, and then fit random regression model parameters, as in Kirkpatrick et al. (1990). Other studies have successfully applied parametric covariance structures, such as structured ante-dependence models, to longitudinal data to eliminate this problem (Albuquerque and Meyer, 2001; Albuerque and Meyer, 2004b). They looked at estimates of covariances using RRM in Nellore beef cattle. Computations were simplified by assuming that the direct-maternal correlation was zero. Artifacts of RRM were visible especially for later ages, and parameters varied strongly among samples. Parameters by RRM were compared with univariate but not MTM analyses. The purpose of those studies was to obtain genetic parameters for sequential growth of beef cattle using RRM with data sets with different structures and to compare these estimates with those obtained by MTM.

This remains an unresolved problem for modelling that utilises polynomials, hence departure from the use of polynomials may solve this problem. Two curve-fitting methods use patterned covariance matrices in the analysis of longitudinal data (i.e. random regressions and spline fitting). The mixed model representation of the smoothing spline (Verbyla et al., 1999) may suggest these models could be useful extensions of random regression models. The flexibility of splines allows more "general" shapes for growth. To put it simply, the advantage of spline functions is that those functions do not exhibit the end-effects of a polynomial, which tends to bend more sharply at the extremities. The difficulty however, is the structure of the underlying covariance model; the form is σ^2_S G_S, where G_S is a known matrix determined by the observation ages. Thus only σ^2_S is a free parameter and introduced correlations between growth and carcass traits is difficult and in reality not very natural (Verbyla et al., 1999).

Applications of RRM in beef cattle so far have concentrated on genetic parameter estimates (Varona et al., 1997; Koenen and Veerkamp, 1998; Albuquerque and Meyer, 2001; Meyer, 2002; Nobre et al., 2003a; Arango et al., 2004), and on feed intake of individually tested beef steers (Schenkel et al., 2004b). Meyer (1999) presented an application to mature cow weight records in beef cattle, contrasting analyses fitting RRM coefficients for phenotypic animal effects only to those attempting to partition growth curves into their genetic and environmental components. Data for the latter study (Meyer, 1999) originated from a selection experiment, which involved monthly weighing of animals.

Andersen (1996b) showed how RRM can be employed in modelling growth curves of pigs on a phenotypic level. RRM also was applied for description of lamb growth (Lewis and Brotherstone, 2002; Fischer et al., 2004). RRM have been used for some time in the analysis of growth curve in rainbow trout (McKay and McMillan, 1995; Quinton et al., 2004) and analysis of human growth curve data (Lesaffre et al., 1999). RRM are also used for traits such as feed intake of lactating heifers (Veerkamp and Thompson, 1999), feed intake of beef steer (Archer and Bergh, 2000; Arthur et al., 2001; Schenkel et al., 2004a), feed intake of pig (Schnyder et al., 2001) and longevity (Veerkamp et al., 2002), test-day records in dairy cattle (Olori et al., 1999; Rekaya et al., 1999; Jamrozik et al., 2000; Kettunen et al., 2000; Pool and Meuwissen, 2000; Lidauer et al., 2003; Lopez-Romero and Carabano, 2003).

As a conclusion, body growth is determined by genetic and non-genetic factors. The genetic make up of the individual includes additive and non-additive genetic combinations that determine growth. These combinations interact with environmental conditions such as climate, nutrition, and management and intrinsic factors such as sex, age, physiological status, as well as other extrinsic factors such as maternal effects and random environmental factors to determine the ultimate phenotypic expression of growth (Arango et al., 2002). Growth generally follows a sigmoid or S-shaped curve through which the rate of growth varies with age until the rate slowly declines to zero reaching a plateau when the animal achieves mature weight.

Several approaches have been proposed to deal with growth data. The most simplistic model assumes that different weights of the same animal represent the same trait with constant variance during the animal's life. The so-called 'repeatability model' considers sequential weights of an animal as repeated measurements of a single trait. Another approach is to consider measurements at different ages as separate traits that are genetically correlated, with heterogeneous variances, and treat them with a 'multivariate model'. One problem with this approach is that it requires arbitrary subdivision of age segments to represent different traits (Arango et al., 2002).

Most of the growth models have been fitted by ordinary least squares, which seems to be inefficient because of the strong dependence structure within the growth process (Sandland and McGilchrist, 1979). Improved versions of the traditional growth functions have allowed data for each animal to be fitted individually and for estimation of parameters within the context of the mixed model approach using restricted maximum likelihood techniques as described by Meyer (1995) and (Kaps et al., 1999). At extremes of the age range, usual approaches for genetic analysis of longitudinal measurements of growth do not seem adequate either because they do not account for the intrinsic variability of the process (repeatability models) or they lead to overparameterized models with a large number of parameters, which are difficult to interpret and which do not account for ordering and spacing of the records over time (Meyer and Hill, 1997; Meyer, 1998c). The growth curves impose artificial mathematical constraints on the biological variation inherent to growth (Johnson et al., 1990) and restrict the relationship of size and age to a deterministic equation in which all animals share the same growth pattern (same curve shape), and do not always account for the complexity of the process (Arango et al., 2002).

Principal component analysis (PCA)

Principal component analysis is a multivariate procedure that is particularly suited to deal with situations in which a large number of correlated variables are measured in highly variable individual groups (Manly et al., 1995). Variables (traits) concerning growth and carcass quality have different economic and genetic rates and values. Likewise, different kinds of analyses, chemical, physical and probably sensory, are needed for approaching those variables. Two approaches that have been taken to manage large data sets are principal component analysis and cluster analysis. PCA reduces the number of variables by finding two or three new variables that are combinations of old characters that describe the majority of the variations, and cluster analysis, which reduces the number of objects by placing them into groups. Multivariate analysis of statistical data can provide useful information about the shape and form of growth curves (Fitzhugh and Tylor, 1971; Fitzhugh, 1978).

Live traits

There have been many attempts to develop the application of principal component analysis (PCA) in animal science. The first time, PCA was introduced to animal breeders was by Wright (1932). Kirkpatrick and Meyer (2004) and Meyer (2004a,c) have shown that it is possible to estimate genetic principal components directly through a simple reparameterisation of the usual linear, mixed model. PCA has proved useful in studies on the relationship between measures of size and shape of living animals (Wright, 1932; Brown et al., 1973; McCurley and McLaren, 1981; Arnason and Thorsteinsson, 1982; Hammack and Shrode, 1986) and construction of genetic selection indices (Arnason and Thorsteinsson, 1982; Van Steenbergen, 1989; Karlsson, 1992; Flhacekak, 1997; Janssens and Vandepitte, 2004).

In his first report, Brown et al. (1973) conducted PCA on 267 Hereford and Angus bulls at 4, 8 and 12 mo of age. The first principal component (PC1) for each age group accounted for 56-68% of the variation in nine skeletal measurements and body weight. PC1 provided a linear function of size with nearly equal emphasis on all 10 standardized traits. In the same project, Brown et al. (1974) considered the same 10 measures of body measures or combinations pre-weaning. The skeletal measures and principal components were used separately in step down regression models to predict post-weaning gains, feed conversion rate and weight at the end of a 140-day test period (about yearling age). The coefficients of multiple determination indicated that about 25% of the variation in gain could be explained by a combination of skeletal measurements, but only 16% by combinations of principal components (size and shape). Nearly 65% of the variation in final weight and 45% of the variation in feed consumption were accounted for by variation in pre-weaning body measures. More recently, some researchers have argued that a problem associated with the use of principal component analysis in animal production is the desire to give each component a name, and to attach causal significance to it (Frausto da Silva et al., 1998; Ramirez Valverde et al., 2001).

In two similar trials, PCA were performed on the variables recorded pre-weaning and at weaning (McCurley and McLaren, 1981; Hammack and Shrode, 1986). Hammack and Shrode (1986) showed that the first principal component (PC1) provided a means of ranking animals according to overall size and had positive coefficients for all variables. Other components provided indices, which elucidated differences in shape. Results demonstrated that the most valuable components were PC1 and PC2 (a contrast of condition against length and width). Weaning variables generally resulted in larger R^2 values than did pre-weaning variables. Relationships were such that animals with high rates of gain tended to be heavy, long-bodied and thin before weaning and at weaning, with positive values for PC1 and negative values for PC2. Those with high yearling condition tended to be heavy, short-bodied and high in condition, with positive values for both PC1 and PC2. They concluded that measures of skeletal size and body fatness were of value in predicting performance, by making a more accurate appraisal of stage of maturity.

Some results concerning live animal measurements using principal component analysis are summarized in Table 1.6. This table shows kinds of traits, the number and variance percentages explained by principal components (PC) and the interpretation as well as variance percentages explained by any one of the principal components.

Carcass traits

PCA have been performed to characterise breeds (Mitsumoto, 1972; Thiele, 1986; Butler Hogg and Whelehan, 1987; Eisen, 1987; Zembayashi and Emoto, 1990; Karlsson, 1992; Flhacekak, 1997; Hernandez, et al., 1997; Frausto da Silva et al., 1998; Destefanis et al., 2000; Cozzolino and Murray, 2004; Liu et al., 2003), to predict market specification (Hodgson et al., 1992; Silva et al., 1998) and to examine relationships among morphometric variables taken from carcasses for allometry studies (Laville et al., 1996; Zembayashi, 1999).

Table 1.6. Application of principal component analysis for live traits from literature sources published since 1970

Author	Traits	V%^{a}	NO^b	PC1^c
Eller (1972)	BM, fatness	*	*	
Ibe and Ezekwe (1994	BW^d, BM^e	98	2	
Aman et al. (1978)	BW, BM	60	3	
McCurley and McLaren (1981)	BW, BM, fatness (cow)	72.5	2	General size (56.2%)
Colleau et al. (1982)	BM	91	2	General size (76%)
Mukai et al. (1982)	BW, BM	*	3	General size (64.8%)
Oksuka et al. (1984)	BW, BM	70	3	General size
Togashi et al. (1984)	BW, BM	*	3	
Arthur and Ahunu (1989)	BW, BM	73	2	General size (60%)
Xu and Chen (1990)	BW, BM	90.1	3	
Kuchida et al. (1994)	BW, BM, con^f (cows)	*	*	
Guo et al. (1997)	BW, 8 BM	84.59	6	Growth, Development
Buxadera et al. (1998)	BM, reproduction traits	76.6	5	

^{a} V%, variance percentage explained by principal components
^{b}NO, means a number of components representing much more variance of variables
^{c} PC1, interpretation of first principal component and it's variance
*, data is unavailable ^{d}BW= Body weight, ^{e}BM= Body measurements, ^{f}Con= conformation

These works (Table 1.6) have demonstrated that principal component analysis is an effective procedure for obtaining a synthetic judgment of meat quality. Frausto da Silva et al. (1998) reported the distribution of muscular and adipose tissues of young bulls in four Portuguese breeds. The results showed that in the analysis of weight of both muscle and fat, the first principal component explained most of the variance. Therefore, the first principal component is an index of the size or mass. For the distribution of fat tissue, it was found that the main source of variation between the breeds, accounting for 33% of the variance, is a different partition among the subcutaneous and intermuscular depots and the kidney knob and channel fat. They concluded that the PCA identified the most important indicators in each beef unit and those variables to be considered in the future for planning efficient production of meat according to the available resources.

In two experiments, PCA was conducted to examine the relationship among morphological traits and bovine carcass traits. Laville et al. (1996) selected carcass measurements to derive equations for predicting muscle weight, percentage of muscle and muscle to bone ratio. Carcasses were weighed and a sub-group of carcass measurements was selected from the results of a principal component analysis, performed on 76 measurements taken from carcass photographs. The first ten components explained 80% of the total variability. Only the first four components (47% of total variation) could be interpreted biologically. PC1 achieved the dorso-ventral recorded on the medial aspects of carcass. PC2 explained 10% of the variation and was determined by measurements from the dorsi aspects of carcass, which show lateral broadening. PC3 was determined by measurements reflecting thickening of muscular planes, which are strongly related to carcass weight. Lastly, PC4 was determined by the lengthening of the carcass, principally the vertebral axis. In a similar experiment performed by Zambayashi (1999) principal component analysis was undertaken by using a correlation matrix of 24 carcass morphometric measurements, in order to investigate the effect of morphological differences on prediction accuracy. It was suggested that the PC1 was the "size" component; because all of the eigenvectors obtained were positive and their absolute values were similar. The proportion of the PC1 to the total eigenvalues was 60%. PC2 was interpreted as a factor related to the "shape" of the carcass, indicating the thinness of the carcass relative to its length. PC3 was interpreted as a factor indicating a large carcass in width relative to its thickness and a carcass with short thighs relative to its thickness. PC4 was also interpreted as a factor indicating small forequarter size relative to thick loin and belly and long sacrum. In this experiment, the difference in the eigenvectors of PC2 among breeds was significant. Similarly, findings using principal components analysis to derive the multivariate analogue of the quadratic part of quadratic allometry were reported by Butler Hogg (1987). They published results from an experiment involving 28 Clun and 28 Southdown sheep, in which 5 of each breed were slaughtered at birth and at 50, 100, 150 and 200 days of age and 3 of each breed at 415 days of age. They also pointed out that muscle weight distribution appears to be almost fixed within the first few weeks after birth. Despite their differences in conformation and mature size, Clun and Southdown lambs had similar distributions of muscle weight at the same age.

1.3. Research questions

The Southern Crossbreeding Project data set is well placed to answer major points of interest within this study:

- To describe and characterise variation in body weights from birth to slaughter for seven crossbred cattle crosses under different managements
- To describe variaion in four economically important carcass quality traits
- To address how different models affect estimates of (co)variance components and subsequent genetic parameter estimates?
- To determine the estimate size of genetic and non-genetic (co)variance components and their phenotypic and genetic relationships
- To describe how body weights and carcass quality traits were correlated over time?
- To identify how to predict carcass quality from longitudinal body weights.
- To investigate whether an alternative model (piecewise linear regression procedure) fits body weights better than the cubic model at the end of growth or not?

1.4. Thesis overview

This thesis has 11 chapters. Chapter 1 introduces the motivation for and objectives of the thesis as well as giving an overview of beef growth and carcass quality traits. Chapter 2 includes a general description of "The Southern Crossbreeding Project" and the data which is analysed. Chapter 3 attempts to explore the variation in growth traits using principal component analysis. Chapter 4 describes the main sources of shared variability in carcass quality traits considered in this analysis applying principal component analysis. Chapter 5 employs cubic mixed models with random regression to estimate genetic and non-genetic components of live weights. Chapter 6 compares estimations of the genetic and non-genetic variance components among four carcass quality traits obtained from sire and animal mixed multi-trait models and then relates these findings to results from chapter 4. Chapter 7 provides estimations of the genetic and non-genetic correlations between longitudinal live weights and carcass quality traits using the joint growth-carcass sire models with random regression. Chapter 8 deals with correlations between growth and carcass quality traits over growth path. Chapter 9 seeks to develop an empirical model to predict carcass quality traits of crossbred steers and heifers from live weights over time. Chapter 10 is concerned with investigating the ability of a piecewise linear regression procedure to estimate genetic and non-genetic components of live weights. Finally, chapter 11 integrates concluding remarks resulting from this thesis.

Chapter 2

Materials and methods

2.1. The Southern Crossbreeding Project

The data from the "Southern Crossbreeding Project" have been used for this research. The Southern Crossbreeding Project was designed to characterise between and within breed variations with the aim of improving utilisation of existing breeds for meeting a range of market specifications in southern Australia. It used a topcross design and has been described by Rutley et al. (1995). Purebred Hereford cows (581) were artificially inciminated with semen of sire breeds Angus (11 sires), Belgian Blue (16 sires), Hereford (10 sires), Jersey (12 sires), Limousin (16 sires), South Devon (15 sires) and Wagyu (17 sires) over four years. There were generally 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 a few exceptions, whereas dams were commonly used for more than one year. The number of sires per breed used in this project was lower but there were approximately twice the number of progeny per sire than in the United States Department of Agriculture Germ Plasm Evaluation in Cattle Project (Cundiff et al., 1988). All cows were 3 years or older when calving, so no maiden heifers were used. The average number of calves per dam in this project was under 2, with a range of 1-4 calves. The number of subgroups of animals used in this thesis are given in Table 2.1. They were artificially inseminated in June and July and if they did not conceive after two insemination attempts they were removed from the experiment until the next mating. The cows calved in March-April 1994, 1995, 1996 and 1997.

The research used data from 1141 of the heifers and steers born in autumn (average birth date 3rd April) at two locations; 'Struan' near Naracoorte and 'Wandilo' near Mount Gambier in the south east of South Australia (S.A.). Calves were weaned in summer (mid December-early January) at 250 to 300 days of age, each year, i.e. in most years the last weight represented a weaning weight. Some variation in weaning dates was necessitated by seasonal conditions. At weaning, all calves born at Wandilo were transferred to Struan. Calves stayed with their dams on pasture until weaning, were pasture fed until 12 to 18 months of age and then transported to a commercial feedlot for finishing except the 1997 steers which, after a good pasture season in 1998, reached marketable weight without requiring grain finishing (Pitchford et al., 2002). All cattle were slaughtered commercially at abattoirs and they were processed depending on which market they were to be sent.

Table 2.1. Breakdown of animals into subgroups used in the analyses

Number of animal	1141
Number of steers	572
Number of heifers	569
Number of dam	581
Sire breeds:	
Angus	11
Belgian Blue	16
Hereford	10
Jersey	12
Limousin	16
South Devon	15
Wagyu	17
Average of progeny per sire	13
Average of sires per breed	14

Location

The "Southern Crossbreeding Project" was conducted at Struan (37° 7' 0S, 140° 46' 60E; altitude 70 m) and Wandilo (36° 17' 60S, 149° 50' 60E; altitude 195 m) located in the South Australia. The Climate is classified typical "Mediterranean" with hot dry summers and cool wet winters. Average annual rainfall of 641.3 mm with winter dominance (12.6% incidence between December and February), a wide temperature range, and precipitation exceeding evaporation only in winter months (Table 2.2). Seasonal conditions during the study comprised below average rainfall 523.7 mm and

541.6 in 1994 and 1997, respectively to above average rainfall in 1995 and 1996, respectively (Table 2.2). The significance of the rainfall events for herbage mass production is described graphically in Figure 2.1 The annual temperature range is 11.7°C, the mean maximum and minimum temperature in the warmest month (February) are 26.7 and 11.9°C, respectively; the mean maximum and minimum temperature in the coldest month (July) are 13.6 and 4.9°C, respectively.

Table 2.2. Rainfall and temperature at Struan (1994–1996) (GrassGro version 2.4.1, 2002)

	Jan	Feb	Mar	Apr	May	June	July	Aug	Sept	Oct	Nov	Dec	
Rainfall (mm)													Annual
LTM*	24.4	21	27.2	41.7	58.6	66.6	80.8	75.6	64.4	54.2	38.1	31.2	48.7
1994	39.2	16.2	1.2	5.6	58.6	71.6	83.6	27.8	28.2	61.6	23.2	6	35.2
1995	74.8	20.6	14.2	85.8	35.8	110	129	33.6	25.6	31	14.4	32.6	50.6
1996	26.2	15.4	18.8	25.2	8.2	99.2	102.4	90	108.2	24.8	8.2	13	45.0
1997	29.8	9.8	8.8	9.8	92.4	39.2	30.4	56.6	90.2	87.2	24	2.2	40.0
Temperature (°C)													
LTM													Ave.
Max.	27.9	27.9	25.1	20.9	17.1	14.6	14	15.1	17.2	19.7	22.4	25.2	20.6
Min.	11.7	12.1	10.6	8.2	6.7	5	4.6	5.1	6.2	7.3	8.7	10.4	8.1
1994													
Max.	25.9	27.6	26.5	22.1	17.6	15.2	15.2	14.7	16.1	20.7	21.3	28.7	21.0
Min.	11	13.3	10.2	9.2	6.1	6.1	5.1	3.9	5.8	7.8	8.5	11.9	8.2
1995													
Max.	28.5	29.1	23.6	18.7	16.4	14.4	13.2	17	17.6	19.7	23	24.2	20.5
Min.	13.5	13.1	11.3	7.8	7.5	6.4	5.7	5.8	6.3	7.5	9.3	9.1	8.6
1996													
Max.	27.3	27.6	26.4	18.8	18.6	15.5	14.1	15.1	16.8	20.3	21.7	24.1	20.5
Min.	11.9	12.2	10.9	8.4	7.7	5.7	5.7	6.5	7	8	8.8	9.5	8.5
1997													
Max.	30.1	32	23.2	21.8	16.5	15.1	14.1	14.8	17.7	21.2	24	26.1	21.4
Min.	13.7	15.5	10.2	9.1	8.2	5.7	3.2	5.4	6.6	8.4	10.3	11.3	9.0

*Long-term means (LTM) are based on 58 years (1943–2001) of records at Struan

Pasture growth. As outlined earlier, nutrition, especially during the pre-weaning period in the current study was based on the pasture. It is obvious that calves performance and management of calves on pasture is directly related to issues of pasture quantity and quality. So, knowledge of the seasonal pasture growth and identifying periods of high and low pasture quantity and quality is extremely important for understanding the interaction between calves and pasture. Generally, pasture quantity is determined by the amount of herbage mass available, i.e. the height and density of the pasture (Figure 2.1). Quantity is assessed in Kilograms of Dry Matter per Hectare (KgDM/ha). Pasture quantity influences the length of time animals spend grazing and pasture growth rates. Roughly speaking, pasture quality is identified by the digestibility of the pasture. Digestibility is a measure of the percentage of the pasture eaten that an animal can utilise. Digestibility influences the speed of digestion and movement of feed through the calves, and reflects the energy and protein content of the pasture.

The dry season occurred after weaning (~250 days) to approximately 470 days (December up to June) and the wet season, between approximately 470 days and 600 days (July to December) every year. It was evident that the limitations of the feed year include a feed gap in summer–early autumn due to low herbage mass associated with the dry season, and a feed gap in summer–autumn associated with only moderate pasture quality (digestibility) of secondary re-growth pasture. In the feedlot, the animals 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).

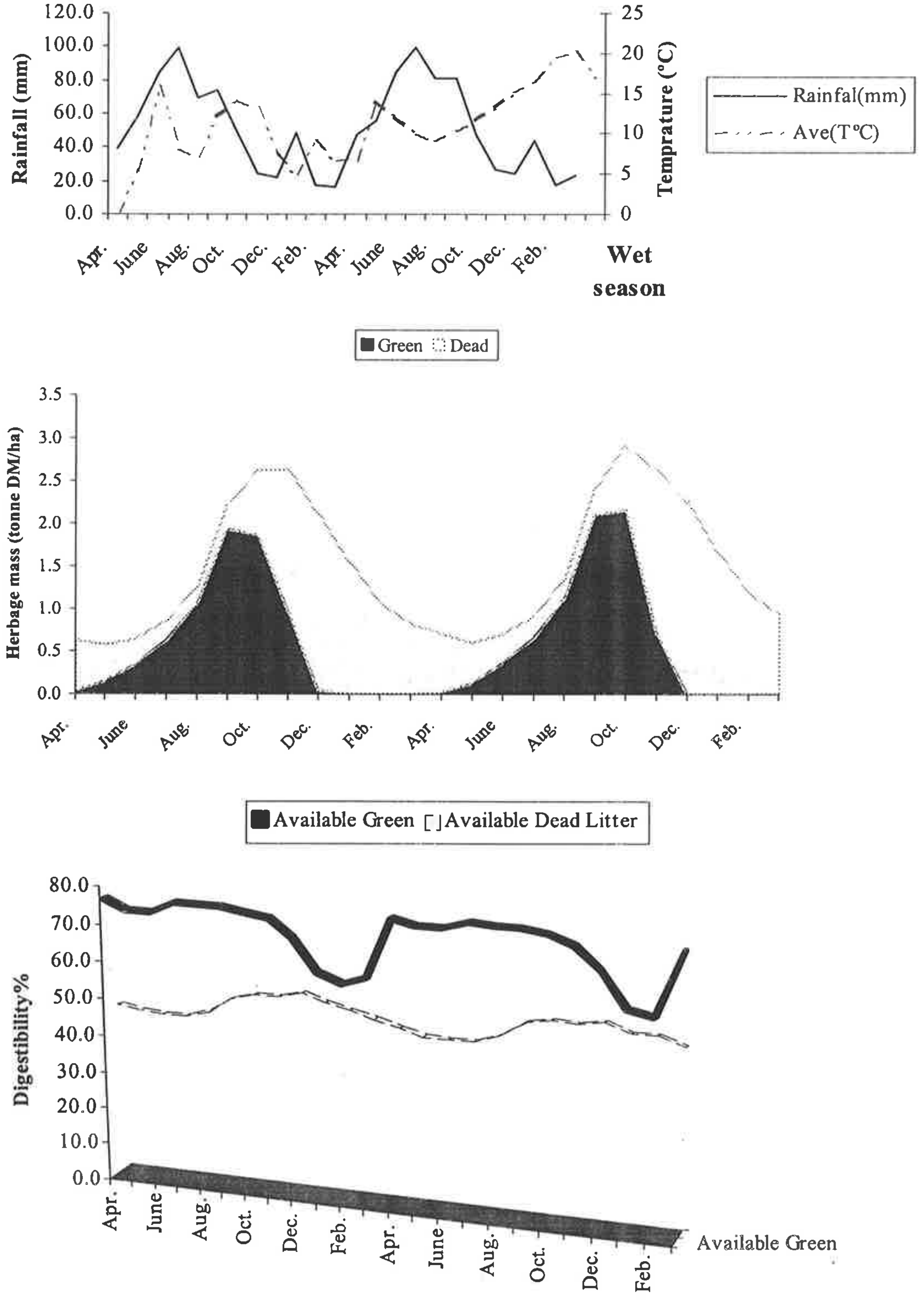


Figure 2.1. The relationship between climate (rainfall and temperature), herbage mass and digestibility of nutrition (pasture growth) at Struan (1994–1996) (GrassGro, version 2.4.1)

2.2. Exploratory data analysis

This section presents some basic facts about the data before analysis, focusing on the exploration of the data. Data in this study consist of live measurements (traits): body weight, and carcass measurements (traits): hot carcass weight, P8 fat depth, eye muscle area and intramuscular fat. As stated earlier, this study deals with the variation in body weight over time, carcass traits and association between growth and carcass traits.

2.2.1. Live body weights

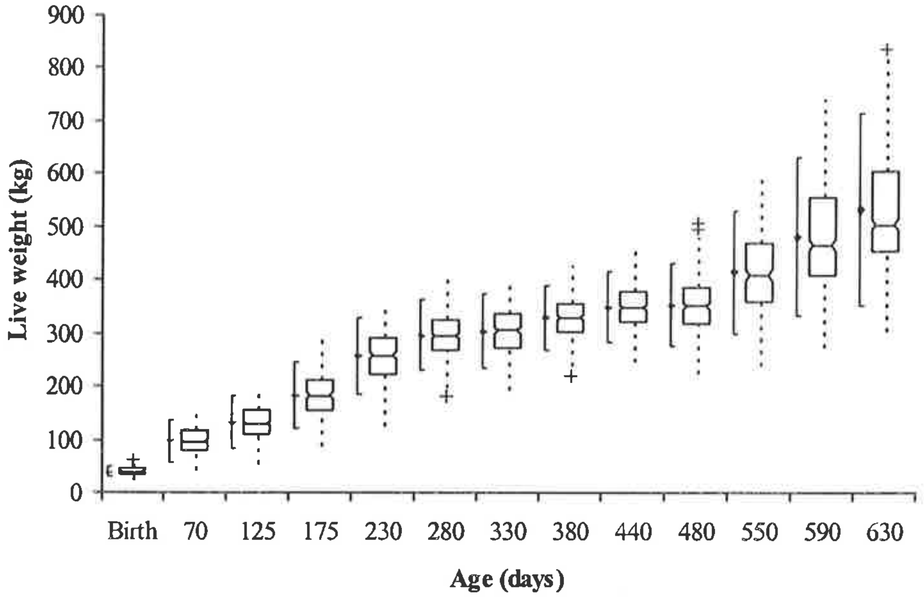
Thirteen live body weights (unfasted) were taken for steers and eight measurements for heifers at approximately every 50 days from birth until slaughter. In the first instance, the location (center), variation and the nature of the distribution of traits were presented. These characteristics are investigated by calculating the values of the mean and standard deviation (SD). Table 2.3 shows summary statistics of the weight-age array from birth to slaughter for steers and heifers. The means were averaged over all four years. Mean body weight ranged from 37 and 39 kg at the first weighing to a maximum of 334 and 533 kg at the last weighing for heifers and steers, respectively. From Table 2.3, it is clear that the SD for live weight of both heifers and steers increased from the first weighing to the last weighing. In other words, the SD is larger for the larger values of age. In both heifers and steers, the coefficients of variation (CV) after weaning were lower than pre-weaning body weights (Table 2.3).

Table 2.3 Mean, standard deviation (SD) and coefficient of variation (CV) of age-weight of steers and heifers from birth to slaughter

Heifers						Steers					
Mean (day)	S.D [a]	C.V [b]	Mean (kg)	S.D	C.V	Mean (day)	S.D	C.V	Mean (kg)	S.D	C.V
0	0		37	6	17	0	0		39	6	16
75	22	29	93	23	25	75	22	31	98	24	25
125	21	17	124	29	23	125	22	18	131	30	23
175	19	11	173	36	21	175	20	12	183	38	21
230	26	11	240	43	18	230	27	12	256	44	17
280	28	10	278	40	15	280	29	10	296	40	14
330	32	10	296	50	17	330	33	10	303	42	14
415	20	5	334	48	14	387	32	8	329	37	11
-	-	-	-	-	-	438	36	8	349	40	12
-	-	-	-	-	-	482	27	6	353	48	14
-	-	-	-	-	-	545	36	7	414	70	17
-	-	-	-	-	-	593	44	8	482	92	19
-	-	-	-	-	-	630	65	10	533	110	21

[a] Standard deviation, [b] coefficient of variation

To observe changes in the location and variation over time in more detail, a boxplot is presented. (Figure 2.2). This boxplot consisted of a line extending from the minimum value to the maximum value, and a box with lines drawn at the first quartile, *Q*1; the median; and the third quartile, *Q*3. It appears that in both steers and heifers (Figure 2.2) from birth to 450 days of age, the mean body weights were almost close to the median, indicating the nearly normal distribution of the live weights up to this point. The last three time points in steers showed a distribution slightly skewed and with increased variation relative to earlier weights.



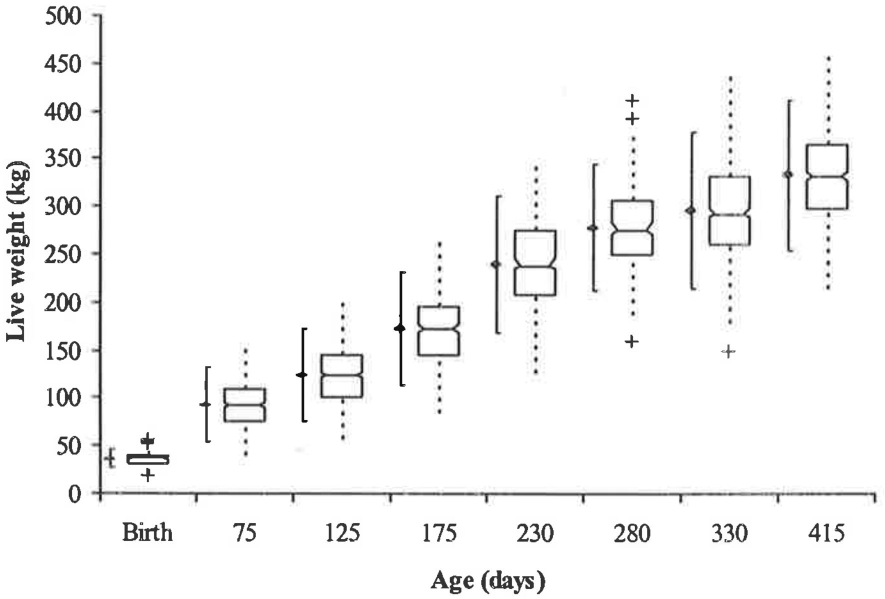


Figure 2.2 Box plot of live body weights of steers (top) and heifers (bottom) at different ages from birth to slaughter

Scatter plots of successive measures are a powerful means of identifying possible outlying observations. Skewness may indicate the need for transformations of the growth data was necessary. To this end, a scatter plot matrix was conducted to assess variation within and between traits (Figure 2.3). Plots were arranged so that adjacent plots share a common axis. All plots in a row share a common live weights (kg) axis, and all plots in a column share a common age (days) axis. The diagonal cells of the matrix contain the corresponded days of age as well as distribution of live weights at that time point.

In Figure 2.3, some points in the graphs represent multiple occurrences of the same values as repeated values were kept in all calculations because they represent different animals. It is clear that all weights are essentially normally distributed and that birth weight was poorly correlated with other weights perhaps due to same age at birth corresponding to different ages for other weights. In addition, adjacent weights generally were highly correlated, however, as expected as time between measurements increased, correlations between weights decreased. Based on the scatter plots of weight as a function of age in Figure 2.4, it could be concluded that the nature of the relationship between weight and age was non-linear. Furthermore, all scatter plots of actual weight-age reveals that body weights were more scattered for larger age (Figure 2.4). To overcome this variance heterogenous, the use of the natural logs of the body weights rather than the original body weights seemed sensible (Figure 2.4). Thus

$$y_t = \ln(\text{Body Weight})_t \sim N(\mu_t, \sigma^2{}_t)$$
$$(\text{Body Weight}) = \exp(y_t)$$

where y is normally distributed with mean μ and standard deviation σ.

Thus, the mean, median and variance of body weight are

1. $E(\text{Body Weight}) = \exp(\mu + \sigma^2 / 2)$
2. The median $(\text{Body Weight}) = \exp(\mu)$
3. $\text{var}(\text{Body Weight}) = \exp[2(\mu + \sigma^2)] - \exp(2\mu + \sigma^2)$

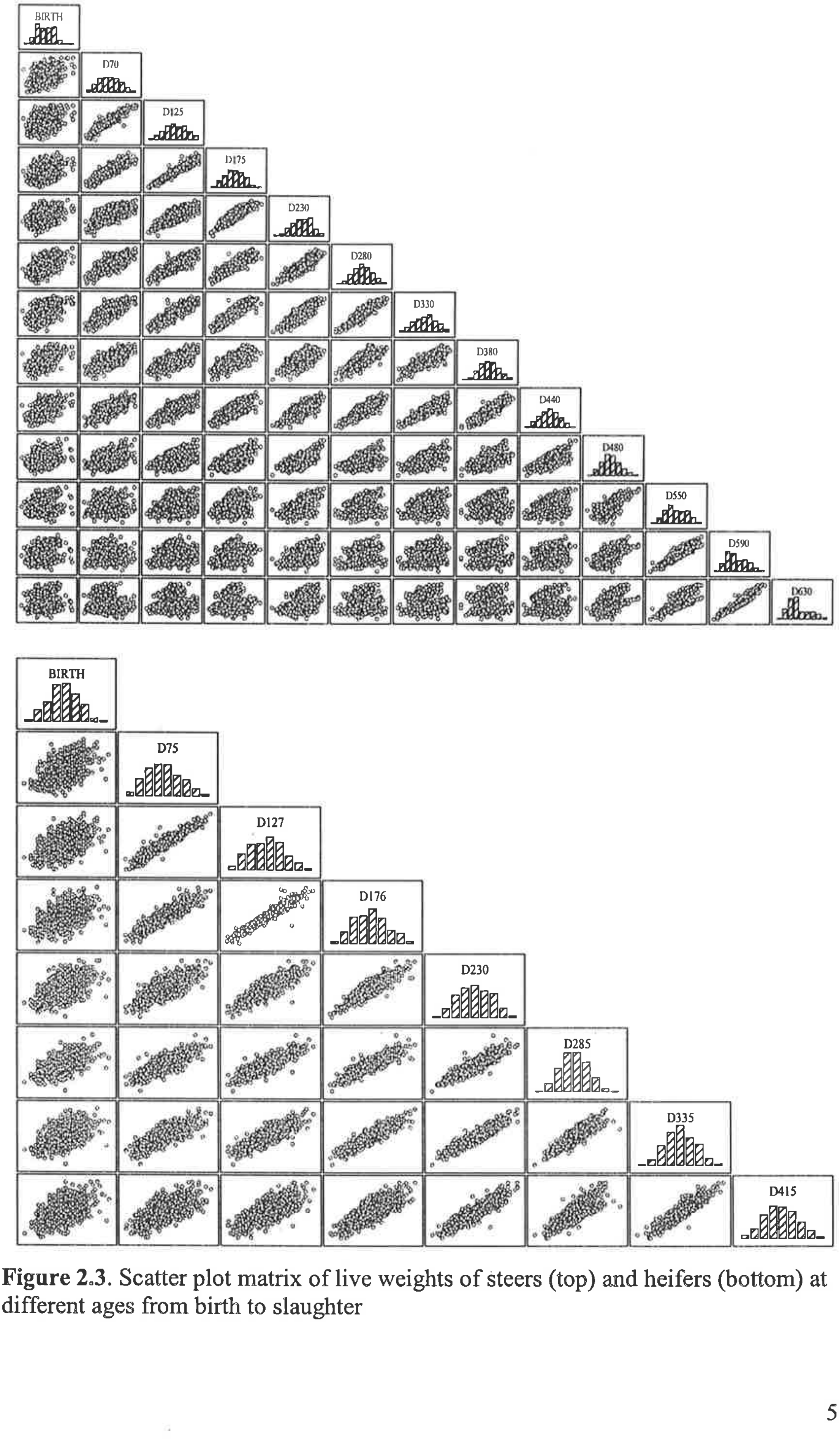
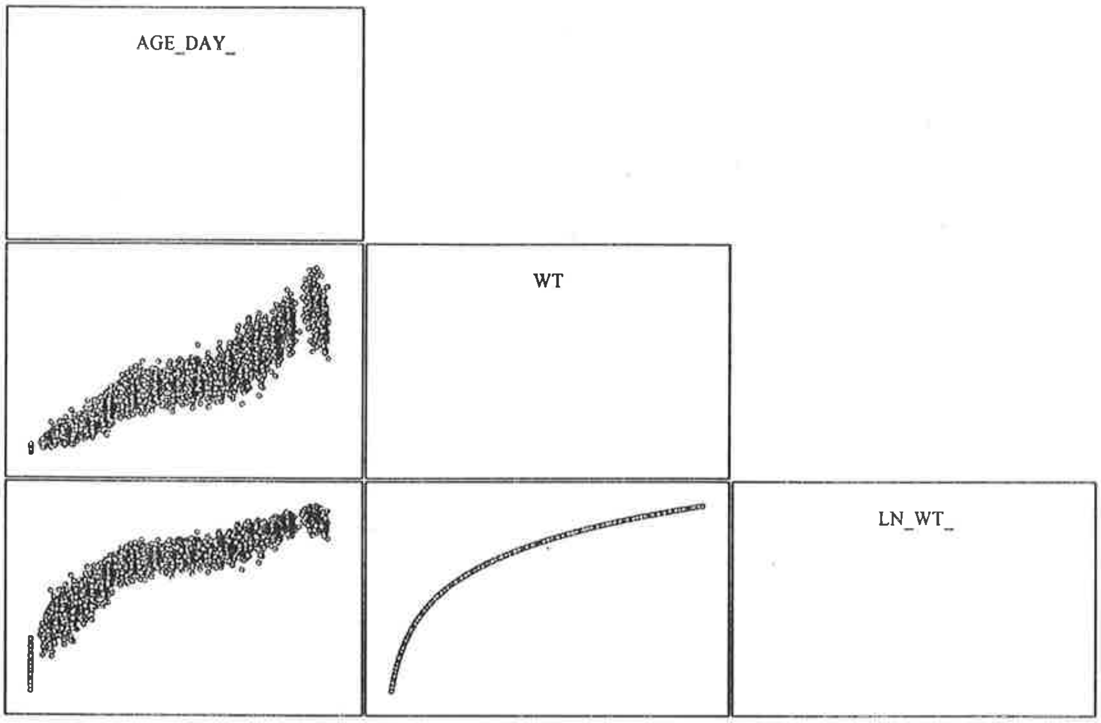


Figure 2.3. Scatter plot matrix of live weights of steers (top) and heifers (bottom) at different ages from birth to slaughter

Steer



Heifer

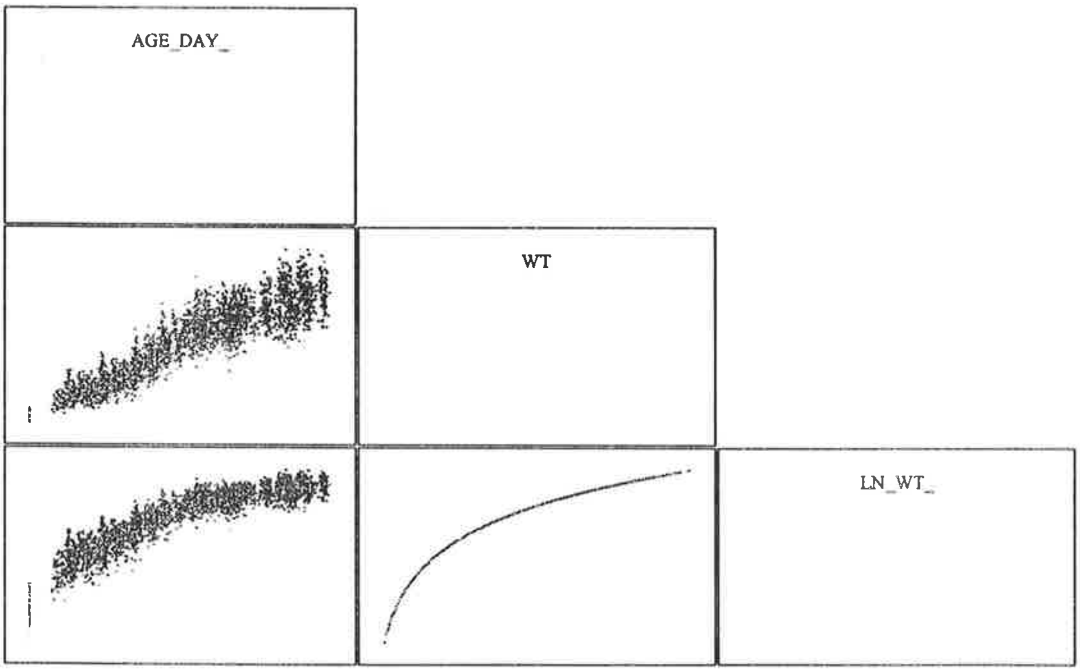


Figure 2.4. Scatter plot matrix of age, actual body weights and log body weights of steers (top) and heifers (bottom)

2.2.2. Carcass traits

The carcass data that will be used thought the thesis (chapters 4, 6, 7, 8 and 9) were collected at various commercial abattoirs throughout southern Australia. Steers and heifers were slaughtered at average 700 and 500 days of age, respectively. The structure of the carcass data set is presented in Table 2.4. Carcass quality traits included quantity traits (HCWt and EMA) and fat traits (P8 and IMF). Hot carcass weight was assessed based on a standard trim (AUSMEAT, 1995). Eye Muscle Area was measured at the 12th rib by using a grid in cm^2 (Figure 2.5). P8 fat depth was measured over the rump at the P8 position (Figure 2.7). IMF (%) was the chemical extraction of fat from a meat sample taken as a slice (approximately 100g) off the longissimus dorsi between the 12th and 13th ribs.

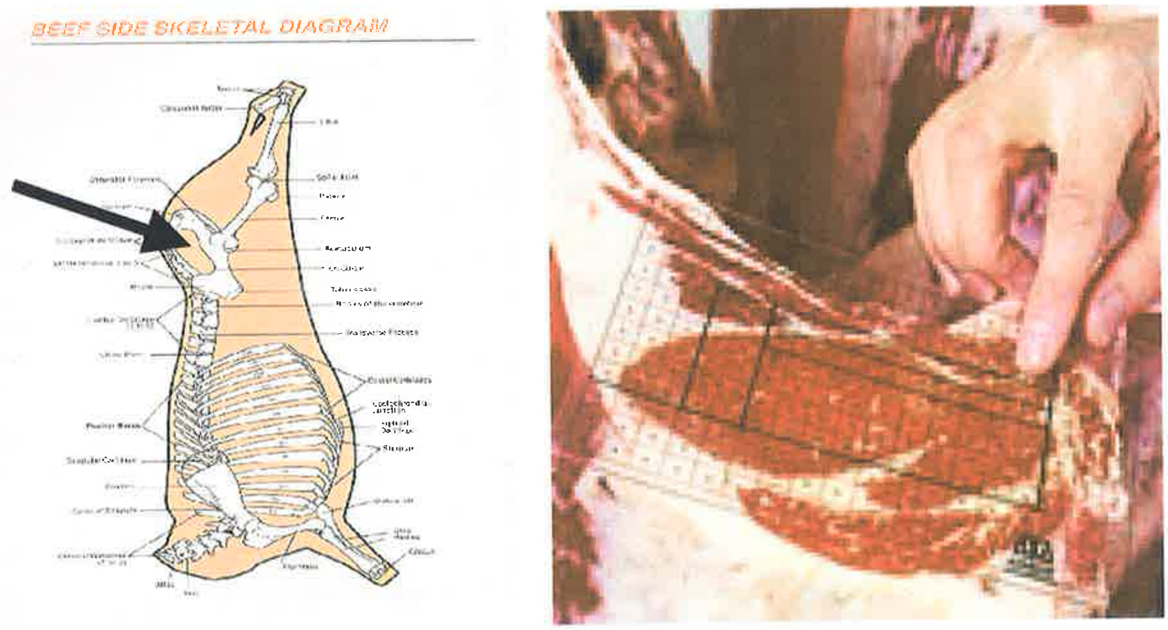


Figure 2.5. Points of P8 (left) and eye muscle area (right) measurements

Table 2.4 lists measures of center (mean and median), measures of variation (standard deviation) of the carcass quality traits considered in this study for heifers and steers.

Table 2.4. Measures of center (mean and median) and variation (SD and CV) for carcass traits

Carcass quality traits	Mean	Median	SD[b]	CV[c]
Heifer				
HCWt	218	216	32	15
P8	10	10	4	38
EMA	62	65	21	33
IMF	4	4	2	46
Slaughter age	495	483	75	15
Steer				
HCWt[a]	324	328	51	16
P8[a]	14	14	5	40
EMA[a]	74	74	15	20
IMF[a]	4	4	3	69
Slaughter age	684	720	103	15

Number of observations 572, 569 and 1141 for steers, heifers and pooled dataset [a] HCWt =carcass weight, [a]P8 =P8 fat depth, [a]EMA = eye muscle area, [a]IMF= intramuscular fat, [b]standard deviation and [c]coefficient of variations (%)

Given the four carcass traits considered in the current study, the scatter plot matrix (Figure 2.7) contains all the pairwise scatter plots of these traits. The reason for presenting the scatter plots is to examine the existence and the nature of any pair wise relationships between the traits, to detect patterns and to examine the possible need for a transformation. The diagonal shows the trait label. Most traits exhibited a skewed distribution and so were transformed. The carcass traits did not appear highly correlated with each other (Figure 2.6). The separation with respect to slaughter age reflects the different management systems for heifers and steers.

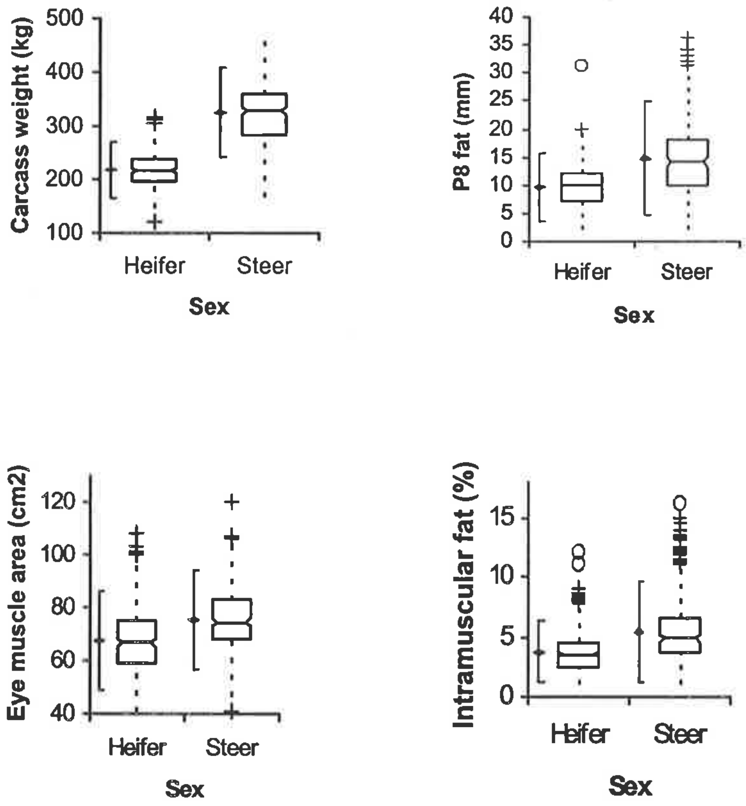
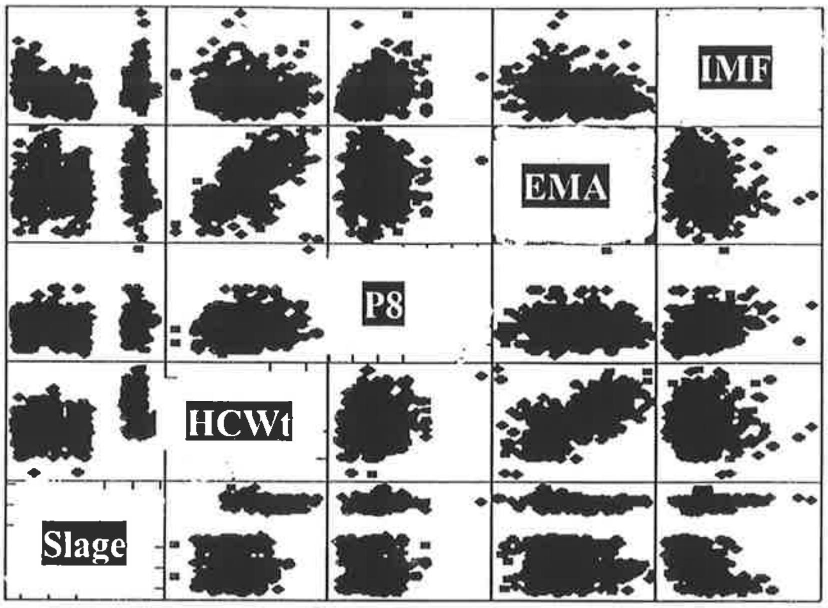
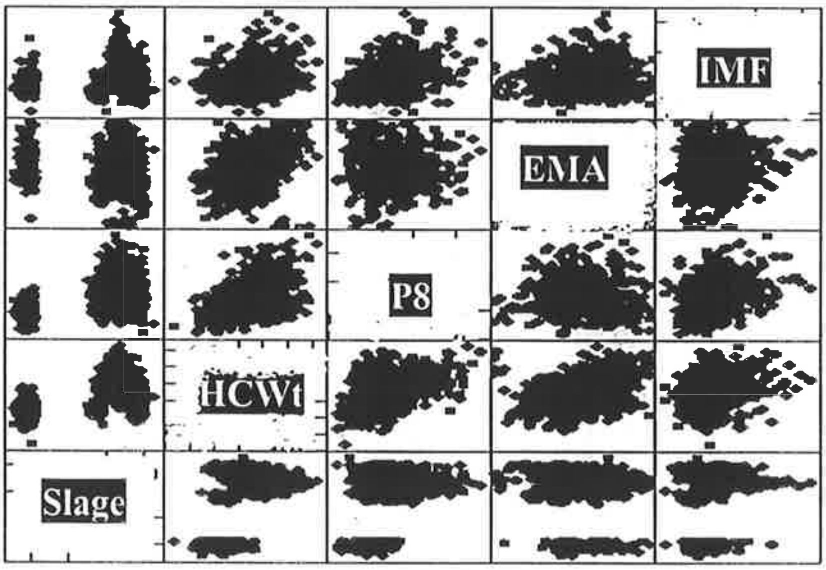


Figure 2.6. Box plot of carcass quality traits for steers and heifers



Scatter Plot Matrix



Scatter Plot Matrix

Figure 2.7. Scatter plot matrix of carcass quality traits for steers (top) and heifers (bottom)

Description of fixed and random effects

In describing variation in data, an effect is some characteristic or trait, which is known - or thought - to have some impact on the measured result. Fixed and random effects used in the current analyses are defined in Table 2.5. It should be noted that sire and dam pedigrees were generally not available and were not utilised in the analysis of this data in the current study.

Table 2. 5. Description of factors fitted as the fixed and random effects

Effects	Definition
Fixed	
Breed	Breed of the animal used as sire Table 2.1
Sex	Steers (castrated male) and heifers (female)
Sex. Slaughter age	Slaughter age nested within sex
Year	Year of birth of offspring (1994 -1997)
Birth month	March and April
Management groups	Combination of location, year of birth and post-weaning groups (Table 2.6)
Age	In cubic model, Centred observed age (age-mean age), In piecewise model, observed age
Age^2	Square of Age
Age^3	Cube of Age
Breed.Age	Interaction of Breed and Age
Breed.Age2	Interaction of Breed and square of Age
Breed.Age3	Interaction of Breed and cube of Age
Sex.Age	Interaction of Sex and Age
Sex.Age2	Interaction of Sex and square of Age
Sex.Age3	Interaction of Sex and cube of Age
Random	
Sire	In sire model, the male parent
Sire.Age	In sire mixed model, interaction of sire of offspring and Age
Sire.Age2	In sire mixed model, interaction of sire of offspring and square of Age
Sire.Age3	In sire mixed model, interaction of sire of offspring and cube of Age
Animal	In animal model, A measure of the variability among animals in their breeding values
Animal.Age	In animal mixed model, interaction of animal and Age
Animal.Age2	In animal mixed model, interaction of animal and square of Age
Animal.Age3	In animal mixed model, interaction of animal and cube of Age
Maternal	The female parent
Maternal.Age	Interaction of dam of offspring and Age
Maternal.Age2	Interaction of dam of offspring and square of Age
Maternal.Age3	Interaction of dam of offspring and cube of Age
Management.Age	Interaction of management groups and Age
Management.Age2	Interaction of management groups and square of Age
Management.Age3	Interaction of management groups and cube of Age
PE.Age	Interaction of permanent environmental and Age
PE.Age2	Interaction of permanent environmental and square of Age
PE.Age3	Interaction of permanent environmental and cube of Age
Environment	In carcass model, assumed the effect of permanent and temporary environmental effects
Residual	Error variance (temporary environmental effects) in growth model

The whole point of this thesis was to fit management groups (Table 2.6) as random effects because they contain significant variation in growth curve that can be used for developing prediction model.

Table 2.6. Description of management groups (Mg) used as a random effect

			Post-weaning groups		
Sex	year	Pre-weaning Location	1	2	3
Heifer	1994	Struan	Mg 1	Mg 2	
		Wandilo		Mg 3	Mg 4
	1995	Struan	Mg 5	Mg 6	Mg 7
		Wandilo	Mg 8		Mg 9
	1996	Struan	Mg 10	Mg11	
		Wandilo	Mg 12	Mg 13	
	1997	Struan	Mg 14		
		Wandilo	Mg 15		
Steer	1994	Struan	Mg 16	Mg 17	
		Wandilo		Mg 18	Mg 19
	1995	Struan	Mg 20	Mg 21	Mg 22
		Wandilo	Mg 23		Mg 24
	1996	Struan			Mg 25
		Wandilo			Mg 26
	1997	Struan		Mg 27	
		Wandilo		Mg 28	

Test of fixed effects

The current approach for testing hypotheses concerning fixed effects in ASREML and GENSTAT is the Wald statistic, which has an asymptotic chi-squared distribution. ASReml produces an approximate *F* test by dividing the Wald test by the numerator degrees of freedom *(r)* to test the significance of fixed effects considered in the model. The asymptotic nature of this test in mixed models is further discussed by (Kenward and Roger, 1997).

Partitioning the phenotypic variance

Phenotypic variation consists of two primary components, namely genotypic and environmental components. Putting that into an equation.

$V_P = V_G + V_E$

where V_P is the *phenotypic variance,* V_G is the *genetic variance,* V_E is the *environmental variance.*

$V_G = V_A + V_D + V_I + V_M$

The genetic variance can be partitioned into *additive genetic variance* (V_A), *dominance genetic variance* (V_D), *epistatic genetic variance* (V_I) and *dam genetic variance* (V_M).

$V_E = V_{PE} + V_{Mg} + V_c + V_{TE}$

The environmental variance could be partitioned into *permanent environmental* (V_{PE}), *systematic management* (V_{Mg}), *common environment* (V_C) and *temporary environment* (V_{TE}).

Permanent environmental effect (PE) is an environmental effect unique to each animal which permanently affects the expression of a repeated trait. Temporary environmental effect (TE) is an environmental effect that influences a single performance record of an animal but does not permanently influence the animal's performance potential for the repeated trait.

In the present study effects fitted include

$$V_P = \text{Sire}\left(\frac{V_A}{4}\right) + \text{Dam}\left(\frac{V_A}{4} + V_M + V_C\right) + \text{Permanent environmental } (V_{PE}) + \text{Systematic management } (V_{Mg}) + \text{Residual within animal } \left(\frac{V_A}{2} + V_{TE}\right) \qquad \textbf{(2.1)}$$

Heritability is that part of the total specific phenotypic variance that is due to genetic variance, assuming exception of systematic management $\left(h^2 = \frac{4V_{sire}}{V_{Sire} + V_{Dam} + V_{PE} + V_{TE}}\right)$.

In the model employed in the present study, systematic management effects were treated as random. In most beef cattle genetic evaluation programs, “herd-year-season” would likely be included as a fixed effect. Thus the residual variance would not include management group effects, just as has been done in this thesis.

Correlations

A correlation is the covariance divided by the standard deviations of the two traits. Correlations between phenotypic measures can be due to genetic effects and environmental effects. These estimates proceed the same way as the analysis of variance components, with the same coefficients for the same class of relatives. Herein, correlations are denoted by r, with subscripts to indicate phenotypic (r_P), genetic (r_G), dam (r_M), management (r_{Mg}), and permanent environmental (r_{PE}) correlations.

Chapter 3

Describing variation in growth using principal component analysis

3.1. Introduction

Growth is characterised both by increase of body mass with age and by changes in form resulting from the differential growth of tissues (Fowler, 1968). The latter is a consequence of changes in functional requirements determined by the normal development of the animal from birth to maturity. Berg et al. (1978) stated that because of the differential growth rates of specific body organs, the size and shape of animals change during development. In addition, visible breed differences in adult size can cause variation in form and rate of tissue distribution. Consequently, growth in animals is an integrated process and accompanied by concomitant changes with time in the phenotypic variances and covariances and their components.

This chapter attempts to explore, the variation in growth traits in some crossbreeds of cattle using principal component analysis. Principal component analysis (PCA) is particularly suited to situations where a large number of correlated variables are measured (Manly, 1994). Moreover, it has been found to be a useful method of characterizing breeds and management systems according to size (Destefanis et al., 2000).

Thus, the objective of this chapter is mainly to describe and characterise changes in size (created multi-trait components) with time for seven crossbred cattle breeds raised under various post-weaning management.

It seems that this rather detailed use of principal components of growth traits of steers and heifers over time serves as an introduction to objectively identify overall size differences in immature growing animals. In addition, the range of various growth traits of diverse genotypes reared under differing management systems in successive years may provide information for attaining desirable market specifications for each crossbreed. Furthermore, new traits obtained from principal components containing information from all of the body measurements can be used as the basis for constructing new indices which have a simpler biological interpretation. Moreover, knowledge of the relationships of immature size and form to growth should aid in understanding developmental processes that may be of economic significance.

3.2. Statistical method

To study the relationships among body weight traits of seven crossbreds, the multivariate technique known PCA was performed using **(PROC PRINCOMP)** (SAS Institute Inc., 1999). The objectives of principal components are to represent points in ρ dimentions in fewer dimentions, which capture the essential variation and to consider whether the new variables have a useful biological interpretations. In other words, the aim is to take ρ variables $\mathbf{X_1}$, $\mathbf{X_2}$,..., **X**ρ and find combinations of these to produce indices (principal components) **PC1**, $\mathbf{PC_2}$,... **PC**ρ those are uncorrelated. The lack of correlation is a useful property because it means that the indices are measuring different dimensions in the data (Manly, 1994). Moreover, the indices are also ordered so that PC_1 displays the largest amount of variation, PC_2 indicates the second largest amount of variation, as so on. Doing PCA it is expected that the variation in the data set can be largely explained by a few PC's variables and the variances of the remaining PC's will be so low as to be negligible. It must be stressed that a principal component analysis does not always work in the sense that a large number of original variables are reduced to a small number of transformed variables. In fact, if the original variables are uncorrelated then the analysis does nothing. The higher the correlations among variables, positive or negative the better the results obtained from PCA (Manly, 1994).

As mentioned earlier, PCA is a data reduction technique used to identify a small set of new variables that account for a large proportion of the total variance in the original variables. Components can be calculated from the correlation matrix or the covariance matrix. The principal component analysis in this study was calculated from a correlation matrix, because the variance of the body weights increase greatly as the animals grow (Figure 2.4). A correlation matrix thereby contains 1's as the diagonal elements and the estimates of the correlation members of the specific pairs of character as the off-diagonal elements. All principal components in this study (PC_j) were of the form:

$$\mathbf{PC_j = C_{1j}Z_1 + C_{2j}\,Z_2 + \ldots + C_{nj}Z_n}$$

where $\mathbf{C_{ij}}$ is the coefficient of i^{th} body measure in the jth component and $\mathbf{Z_i}$ is the i^{th} standardized body measure. The new variable is therefore a weighted sum of the original variables. Standardized measures were calculated as the deviation of the individual's measure from the mean of the character divided by the standard deviation of the character. Therefore, the output consists of the eigenvalues (variances of the principal components), the proportion and cumulative proportion of the total variance explained by each principal component, and eigenvectors coefficients for each principal component.

Since the principal components correspond to progressively smaller fractions of the total variance, one must determine how many components are biologically meaningful (i.e. what is the dimensionality of the reduced space?). There are a few commonly used criteria for deciding on the number of components. Shepard diagrams are one approach, but an empirical rule-of-thumb when using the (co)variance matrix is that one should interpret a principal component if the corresponding eigenvalue (λ) is larger than the mean of the λ's. For a correlation matrix, meaningful components are when eigenvalues are greater than one (PC>1). Another way is the number of components required to account for a meaningful percentage of variance, usually 80-90%. These two criteria concern the amount of variance fitted by the component model. Plotting of the eigenvalues (screeplot) and looking for elbow as well as sorting out how many components are interpretable can aid in choosing a number of components. Hair (1998) stated that though there is no clear rule to determine the importance of a trait coefficient, one rule of thumb is to treat coefficients >0.3 as having large enough effects to be considered significant.

The biplot is a useful approach for studying the relationships among traits resulting from principal components (Gabriel, 1971; Bradu and Gabriel, 1978; Yan and Hunt, 2002). It is a two dimensional projection of observations as well as objects on to the two PCs. In the biplot, points that are near each other are observations that had similar scores. Moreover, on a given axis, negatively correlated traits will generally have opposite signs and positively correlated traits will have the same sign (Manly, 1994). Correlated observations or objects, which are close together, have similar characteristics, while those lying opposite to each other tend to have a negative correlation. An interrelation is implied among traits with high coefficients on the same axis (Brown et al., 1974).

The relative magnitude and direction of the coefficients which define a component are often used to generate an interpretation for each component axis. One approach for studying the relationships among variables consists of scaling the eigenvectors in such a way that the cosines of the angles between the variables axes be proportional to their covariances. The cosine of the angles between vectors is equal to the correlation between those variables. In this approach, the angles between the variable axes are between 0° (maximum positive covariance) and 180° (maximum negative covariance) and the angle of 90° indicates a null covariance (orthogonality) (Mardia et al., 1979; Sharma, 1996; Johnson, 1998). To put it more simply, as explained by Naes et al. (1996), the results concerning both variables (loading plot) and objects (score plot) are presented on an XY plane. Generally, samples to the right in the score plot have high values for variables placed to the right in the loading plot. The same holds for samples to the left, at the top, or at the bottom. The more a variable is away from the axis origin, the better it is represented on the plane under consideration.

In the current study a mixed model analysis (**PROC MIXED,** SAS Institute Inc. 1999) was applied to the data transformed by the coefficients of the principal components (PC scores) for both steers and heifers. Year of birth, management groups nested within years, birth month and breed were considered as fixed effects and the sire nested within breeds were used as random effects. The variance components: additive genetic variance and phenotypic variance and heritability for the components (new indices) were estimated for the overall size and feedlot growth in both steers and heifers using the restricted maximum likelihood (REML) with the following linear mixed model:

$$\mathbf{PC_n} = X\tau + Z\mathbf{u} + \mathbf{e}$$

where:

X is the incidence matrix of fixed effects;

τ is the vector of fixed effects

Z is the incidence matrix of random effects

u is the vector of random effect

e = vector of random residual effect (temporary environmental effect or measurement error), **NID (0, σ^2).**

3.3. Results

Heifers. The first two PCs, accounting for 85% of total variation in the heifer weight data, were chosen for interpretation of the relationships between body weights of heifers over time (Table 3.1). The first principal component described nearly 75% of total variation and clearly was far more important than the others. It was positively related to all body weights, hence it could be interpreted as a measure of general size or an average of the eight postnatal weight (Figure 3.1).

From the coefficients of PC2 it could be seen that it is primarily a contrast between body weights at 330 and 415 days with body weights at 75, 125, 175 and 230 days. In other words, PC2 was highly and positively correlated with feedlot growth on one hand and, on the other hand, pre feedlot growth which was negatively correlated (Table 3.1 and Figure 3.1). However, it seems that the pre feedlot variables did not affect significantly the value of PC2. Therefore, PC2 could be interpreted as a feedlot growth.

Steers. The PCA was performed on body weights at thirteen successive times and yielded PC1 and PC2 eigenvalues that accounted for 61% and 23% of the variability in these data sets, respectively, so that 84% of the total variance in the considered variables can be condensed into two new variables (Table 3.1). As for heifers, the first two PC's were selected for interpretation of variation among calves in the characteristics measured and subsequent use (Table 3.1). These two principal components (PC1 and PC2) used as new traits have a simpler biological interpretation, containing information from all of those traits originally measured. The projection of body weights of steers into ordination space defined by the first two principal components indicated that most of the variation in PC1 is due to the overall size (Figure. 3.1). Since PC1 measured overall size, it seems that stabilising selection may have acted against very large and very small steers. Results showed that all body weights at birth, pre-weaning, post-weaning and feedlot periods were positively correlated with PC1 and also with one another. However, pre-weaning and post-weaning body weights were more correlated with PC1 than feedlot period weights (Table 3.1 and Figure. 3.1). It has also shown in the loading plot (Figure. 3.1) the cosine of angles among these variables placed to the right are very close to each other. That means there is a positive covariance between them.

The second principal component (PC2) accounted for about 23% of variation in the data, showing the importance of feedlot gain that has high and positive coefficients versus pre feedlot gain, which had negative coefficients correlation. However, pre-feedlot variables did not affect the value of PC2 considerably (Table 3.1). Therefore, it could be described as a feedlot growth. These relationships have been observed along the PC2 axis in Figure. 3.1 amongst body weights at 480, 545 and 590 days, which placed on the positive end of the axis, in comparison with pre feedlot body weights, show in the negative end.

Table 3.1. The eigenvectors and eigenvalues of the correlation matrix for the body weights of heifers and steers over time

Heifer					Steer				
Body weights	PC1	PC2	PC3	PC4	Body weights	PC1	PC2	PC3	PC4
Birth	0.29	0.16	0.93	0.07	Birth	0.20	0.05	-0.84	0.39
75 days	0.36	-0.38	-0.01	0.47	75 days	0.30	0.23	0.16	0.29
125 days	0.38	-0.23	-0.12	0.35	125 days	0.32	0.18	0.24	0.27
175 days	0.39	-0.16	-0.16	0.04	175 days	0.33	0.12	0.27	0.16
230 days	0.38	-0.16	-0.11	-0.37	230 days	0.33	-0.10	0.18	0.17
280 days	0.36	-0.21	0.03	-0.69	280 days	0.33	0.11	0.00	0.04
330 days	0.35	0.45	-0.21	0.18	330 days	0.34	0.11	0.00	-0.11
415 days	0.30	0.70	-0.18	-0.04	387 days	0.29	0.18	-0.27	-0.47
-	-	-	-	-	438 days	0.33	0.08	-0.12	-0.33
-	-	-	-	-	480 days	0.26	-0.26	0.02	-0.49
-	-	-	-	-	545 days	0.19	-0.47	0.08	-0.02
-	-	-	-	-	590 days	0.16	-0.51	0.01	0.17
-	-	-	-	-	630 days	0.10	-0.53	-0.10	0.14
Eigenvalues	5.98	0.82	0.53	0.34	-	7.9	2.9	0.82	0.45
% of variance	0.75	0.10	0.07	0.04	-	0.61	0.23	0.06	0.03
Cumulative %	0.75	0.85	0.92	0.96		0.61	0.84	0.90	0.93

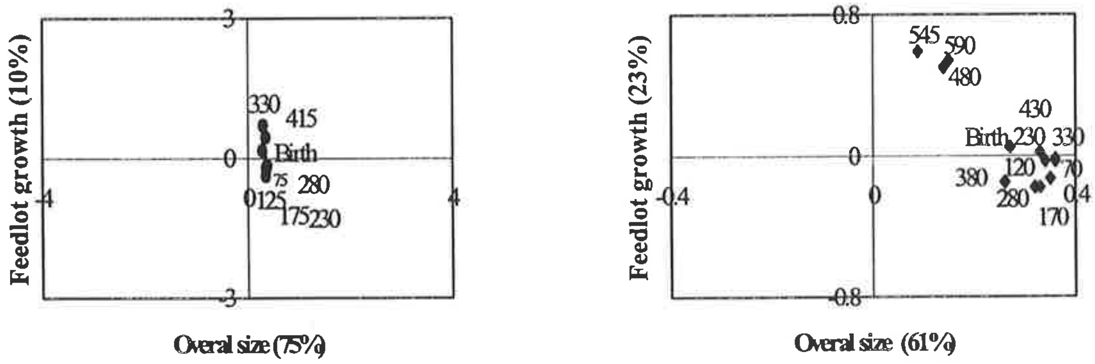


Figure 3.1. The eigenvector plot of PC2 vs PC1 for heifers (left) and steers (right)

Factors affecting principal components of body weights

A mixed model analysis was applied to the data transformed by the coefficients of the principal components (PC scores) in heifers and steers. Table 3.2 presented the analysis of variance of the data on body weights (kg) of heifers and steers transformed by coefficients of the first two principal components. For both heifers and steers, year of birth, management groups nested within years, birth month and breed were considered as fixed effects and the sire nested within breeds was used as a random effect. The year, breed and management groups significantly affect general size. However, birth month did not affect body weights of heifers and steers significantly (Table 3.2). Heritabilities for the first two principal components of heifers and steers presented in Table 3.2. The heritability estimates of general size and feedlot growth of heifers were low (0.10) and medium (0.39), respectively. The estimates for steers were much larger, 0.36 and 0.71, respectively.

Table 3.2. Analysis of variance, phenotypic variance and heritability of principal components of body weights for heifers and steers

Source of variances		Heifers		Steers	
	df[1]	PC1	PC2	PC1	PC2
Year of birth	3	<.0001	<.0001	<.0001	<.0001
Management groups	12	<.0001	<.0003	<.0001	<.0001
Birth months	1	<.0001	<.0832	0.71	0.84
Sire breed	6	<.0001	<.0002	<.0001	<.0001
Phenotypic variance	-	2.80	0.19	3.09	0.64
Heritability	-	0.10	0.39	0.36	0.71

[1] Degrees of freedom

Biplot analysis of management groups

Figure 3.2 indicates a biplot of the predicted mean of management groups resulting from a mixed model analysis of PC1 and PC2. Thirteen management groups: a combination of year (1994 to 1997), location of pre-weaning rearing (Struan and Wandilo), and three post-weaning groups, against their values for overall size (PC1) and feedlot growth (PC2) were characterized (Figure 3.2). The symbol used on the figure refers in order to year, location and postweaning management groups, e.g., 94w1 shows calves born in 1994 at Wandilo under first post-weaning management group. The first feature observed in Figure. 3.2 is that the 1995-drop of heifer at Wandilo located on the bottom right quadrant were characterized by high size and low post-weaning growth. The heifers and steers born in 1997 at Struan and Wandilo located on the top right quadrant were characterized by high size and feedlot growth. On the top left quadrant, the groups consist of all heifers born in 1996 which showed low overall size and pre feedlot growth but high feedlot growth. The steers born in 1996, held in Wandilo under post-weaning 1 condition were the same as 1997-drop. All 1994 groups, 94w2, 94w3, 94s2, were placed in the bottom left quadrant were recognized by lower overall size and feedlot growth but higher pre feedlot growth. All steers born in 1995, located on the bottom right quadrant, demonstrated high general size and pre feedlot growth but low feedlot gain (Figure. 3.2). In contrast, all the 1994-drop progeny, located on the bottom left quadrant, were characterized by both low general size and feedlot growth but high pre feedlot growth. The 1996-drop at Struan under post-weaning 2 practice, placed on the top left quadrant had high feedlot but low general size and pre feedlot growth (Figure. 3.2).

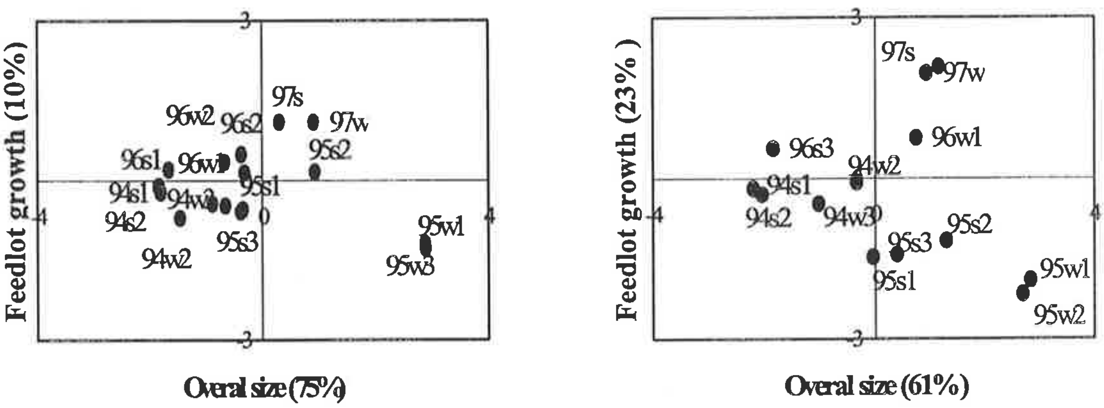


Figure 3.2. Management groups biplot of PC2 vs PC1 for heifers (left) and steers (right), 4 (1994), 5 (1995), 6 (1996), 7 (1997), w (Wandilo), s (Struan), 1 (post weaning group 1), 2 (post weaning group 2), 3 (post weaning group 3)

Biplot-analysis of breeds

Figure 3.3 shows the projection of the body weights across ages into the ordination space, which used to relate the predicted means of breeds resulting from mixed model analysis of principal components to the original body weights. The biplot was conducted to characterise seven sire breeds. The location of the breeds in the multivariate space of the two first principal component score vectors was clearly rather meaningful in terms of what was known about the breeds. Figure. 3.3 showed that in both heifers and steers, breeds were substantially arranged in two groups: the first were Wagyu and Jersey steers, located on the bottom left quadrant which grouped with both low general size and feedlot growth. In contrast, the second group consists of South Devon, Angus, Belgian Blue, Hereford and Limousin steers, located on top right quadrant, and hence high in general size and feedlot growth.

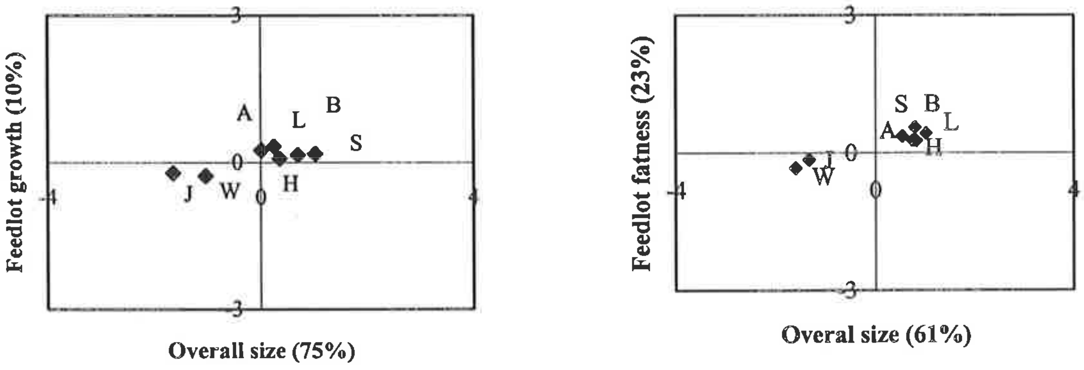


Figure 3.3. Breed biplot of PC2 vs PC1 for heifers (left) and steers (right)

3.4. Discussion

This chapter dealt with application of principal component analysis to investigate variations in body weights of growing crossbred calves. In this analysis, "weight for age" has been a determinant of body size which has long been considered a criterion of desirability and a good practical index of efficiency in meat animals (Holloway and Butts, 1983). Breeders have used body size characteristics to apply strategies for genetic improvement of beef cattle (Jenkins et al., 1991). The variation associated with the first two principal components for body weights of heifers and steers were in consistent with other literature cited (Chapter Table 1.6). PC1 and PC2 were used as a basis for constructing new indices for overall size and feedlot growth of steers and heifers.

As demonstrated in Table 1.6, most other studies have performed PCA on body weights and body measurements. In almost all studies which used PCA on growth (weight) data, the first two principal components accounted for from 60 to 90% of the total variation. PCA were performed on the variables recorded pre-weaning and at weaning (Brown et al., 1973; Brown et al., 1974; McCurley et al., 1981; Hammack and Shrode, 1986; Roso and Fries, 1995). Brown et al. (1973) found that PC1 for each age group accounted for 56-68% of the variation in nine skeletal measurements and body weight. PC1 provided a linear function of size with nearly equal emphasis on all thirteen standardized body weights. Hammack and Shorde (1986) showed that PC1 provided a means of ranking animals according to overall size and had positive coefficients for all variables. Other components provided indices, which elucidated differences in shape.

PCA also provided a valuable method of characterizing breeds and management groups according to overall size and feedlot growth. The present results indicated that sire breed effects were similar for steers and heifers. Considerable differences existed among steers and heifers from Wagyu and Jersey sires on the one hand and Angus, Hereford, South Devon, Limousin and Belgian Blue sires on the other. Although, principal component analysis of body weights did not reveal significant breed differences among steers within each group, there were some differences among heifers the breeds that are large in body size, as in South Devon and Angus, Hereford and Limousin and Belgian Blue and Hereford (Figure 3.3). It was concluded that some differences in growth patterns of diverse breeds using only body weights could not be detected. Hence, it would be worthwhile considering a wider range of traits such as body measurements. No studies report investigations of breed characterisation with respect to growth traits in cattle. Atchley and Rutledge (1980, 1981) examined ontogenetic allometry body traits and skeletal traits in six genetic strains of laboratory rats using PCA.

The direct heritability estimates were moderate and rather high in magnitude for overall size and feedlot growth of steers, respectively. Heritability estimates were low and moderate in magnitude for overall size and feedlot growth of heifers, respectively. Heritabilities of feedlot growth were higher than overall size for both steers and heifers. Although no estimated heritability for principal components is reported across literature cited, these heritability estimates are comparable with those of previous studies for pre-weaning, weaning, post-weaning and yearling gains reported in the literature. However, clearly the number of animals in the current study was not sufficient for more accurate estimation of heritability. Massey and Benyshek (1981) demonstrated that more than 800 observations are needed if information per sire is limited to fewer than 30-40 progeny. This result was consistent with values reported by Togashi and Yokouchi (1981) and Togashi (1982) who found the h^2 for body weight from 4-14 months of age ranged 0.54-0.83, body weight from birth to 3 months, less than 0.20, daily gain in the periods 0-6, 6-12 and 18-24 months, 0.71, 0.59 and 0.54, respectively. Roso and Fries (1995) proposed direct heritability estimates of 0.34 and 0.33 for body weight at 250 and 550 days of age, respectively. Muhiuddin (1993) reviewed the average estimates of h^2 for pre-weaning gain, weaning gain and yearling gain 0.39, 0.27 and 0.28, respectively (Table 1.2). Heritability estimate of body weight was reported to be 0.52 by Atchley (1980).

3.5. Conclusion

The principal component analysis provides a valuable method of characterizing breeds and management systems according to overall size and feedlot growth. Considerable differences existed among Wagyu and Jersey sires on the one hand and Angus, Hereford, South Devon, Limousin and Belgian Blue sires on the other. It also concluded that the sire breed characterisation were similar for steers and heifers. Applying PCA indicated that environment and management has a big impact on breed characterization and body size, especially in heifers.

Chapter 4

Describing variation in carcass quality using principal component analysis

4.1. Introduction

The performance of beef cattle with respect to carcass quality is extremely variable and such variability is a major concern for the beef industry. This variation is a result of two major effects, genetic and environmental differences. So far the principal component analysis has been conducted to examine of variation in live measurements (Chapter 3). In this chapter principal component analysis is used to investigate the main sources of shared variability in four economically important carcass quality traits and to deduce the factors that describe these traits. Principal component analysis has been a useful method for studying variations concerning carcass traits (Caneque et al., 2004). It is shown that we can estimate genetic principal components directly through a simple reparameterisation of the usual linear mixed model (Meyer and Kirkpatrick, 2004). Karlsson (1992) recommended using principal component analysis to find a smaller set of carcass measurements explaining most of the observed variability in the measurements taken and to examine the relationships between traits and the differences between the groups of animal compared. This technique has been already used to assess relationships between carcass characteristics (Sarti et al., 1992; Laville et al., 1996; Oliver et al., 1997; Hernandez et al., 2000). Similarly, others have applied principal component analysis for carcass characterization and classification (Hernández et al., 1997; Hernandez et al., 1998; Destefanis et al., 2000), for prediction of market specification and to characterise breeds (Mitsumoto, 1972; Thiele, 1986; Butler Hogg and Whelehan, 1987; Eisen, 1987; Zembayashi and Emoto, 1990; Hodgson et al., 1992; Flhacekak, 1997; Silva et al., 1998; Zembayashi, 1999) and in the construction of genetic selection indices (Árnason and Thorsteinsson, 1982; Eisen, 1987; Van Steenbergen, 1989; Karlsson, 1991; Janssens and Vandepitte, 2003).

Generally, carcass quality refers to the composition, or more specifically, proportions of meat, fat and bone of slaughtered animals. Commercially the size of carcass and proportions of meat, fat and bone will affect processing efficiency. Therefore, the main predictor traits considered are carcass weight and fat depth as well as eye muscle area (indicating meat yield) and intra-muscular fat content (meat quality). The present chapter seeks to identify the most important directions of variability in a multivariate data matrix of these four-carcass quality traits.

4.2 Statistical method

Principal components analysis (PCA) of the correlation matrix (see chapter 2) were performed on the hot standard carcass weight (HCWt), rump fat thickness (P8), eye muscle area (EMA) and intramuscular fat percentage (IMF), taken from steers and heifers of seven crossbreds. Also, a linear mixed model was fitted to the dominant principal components (PC scores) for both steers and heifers. The model is

$$\mathbf{PC_n = X}\boldsymbol{\tau} + \mathbf{Zu + e}$$

where:
τ is the vector of fixed effects
$\mathbf{u}$ is the vector of random effect
$\mathbf{e}$ is the vector of random residual effect (temporary environmental effect or measurement error), **NID (0, σ^2)**.

The linear mixed model contains fixed effects of birth month (March or April), sire breed (seven levels) and management group, indicating year effects (a total of 30 levels describing pre- and post-weaning groups, 2 to 6 per year), and random effects of sire. Birth month was fitted to examine age effects rather than a linear covariate of birthday to avoid bias (high leverage) resulting from the small number of very early and very late calves. Sex was not included in the model because PCA and mixed model analyses were performed for heifers and steers, separately.

4.2 Results

Heifers. The first two principal components accounted for 42% and 34% of the total variability in these data sets, respectively, so 76% of the total variance in the four variables is explained by two new variables (Table 4.1). These principal components used as new traits, which have a meaningful biological interpretation, contain information from all of those traits originally measured. Since the analysis has been done on the correlation matrix, the variables in this equation have each been standardized to have a mean of zero and a standard deviation of one. The projection of carcass traits of heifers into ordination space, defined by the first two principal components, indicated that most of the variation in PC1 is due to the EMA and HCWt (Figure 4.1). Results also showed that EMA and HCWt were located on the top right quadrant that is they were positively correlated with PC1. On the contrary, fat traits placed in the top left quadrant were negatively correlated with PC1. It has also shown in the loading plot (Figure 4.1) the cosine of angles among meat traits as well as fat traits were close to each other and that means there were a positive covariance between them. Hence, PC1 could be interpreted as a growth component. The larger the PC1, the larger carcass meat and lower carcass fatness. The second principal component (PC2) accounted for 34% of variation in the data, indicating higher loadings for P8 fat and IMF (Table 4.1 and Figure 4.1). Therefore, it could be described as fatness component. The third component (PC3), accounting, for 16% of the total variance, indicated a major contrast between P8 fat and IMF, consequently it can be interpreted as a fat distribution component (Table 4.1 and Figure 4.1).

Steers. The analysis showed that the first two principal components accounted for 76% of total variability among steers, exactly the same as heifers (Table 4.1). The first and second components (PC1) explained 48% and 28% of the total variation of carcass characteristics, respectively. The first component was mainly determined by fat measures and hot standard carcass weight whereas, the second principal component (PC2) was determined mainly by the high proportion of eye muscle area. So, according to the results given in Table 4.1 the PC1 defined by the fatness characteristics of carcass as illustrated in the loading plot (Figure 4.1). In particular, the fatness characteristics placed to the right in the loading plot are close together and, therefore, positively correlated.

Table 4.1. The eigenvectors and eigenvalues for the correlation matrix of carcass quality traits in heifers and steers

	Heifer				Steer			
	PC1	PC2	PC3	PC4	PC1	PC2	PC3	PC4
HCWt	0.67	0.13	0.28	-0.68	0.63	-0.23	-0.22	0.63
P8	0.07	0.76	-0.64	-0.05	0.52	0.44	-0.54	0.52
EMA	0.70	0.03	0.06	0.71	0.38	-0.74	0.23	0.38
IMF	-0.25	0.64	0.71	0.16	0.43	0.45	0.78	0.43
Eigenvalues	2	1	1	0	2	1	1	2
% of variance	42	27	22	9	48	28	17	48

The PC2 characterised by EMA as an indicator of carcass muscling; as EMA increases, retail cut yield increases. This variable, placed on the right side, far from the origin, in the loading plot showed negative correlation with fatness measures (Figure 4.1 and Table 4.1). PC3 contributed to 17% of total variations, implying P8 fat versus IMF (Figure 4.1). Therefore, as in heifer, PC3 could be defined as a fat distribution (Figure 4.1). The larger PC3, the higher marbling, the lower fat thickness of carcass.

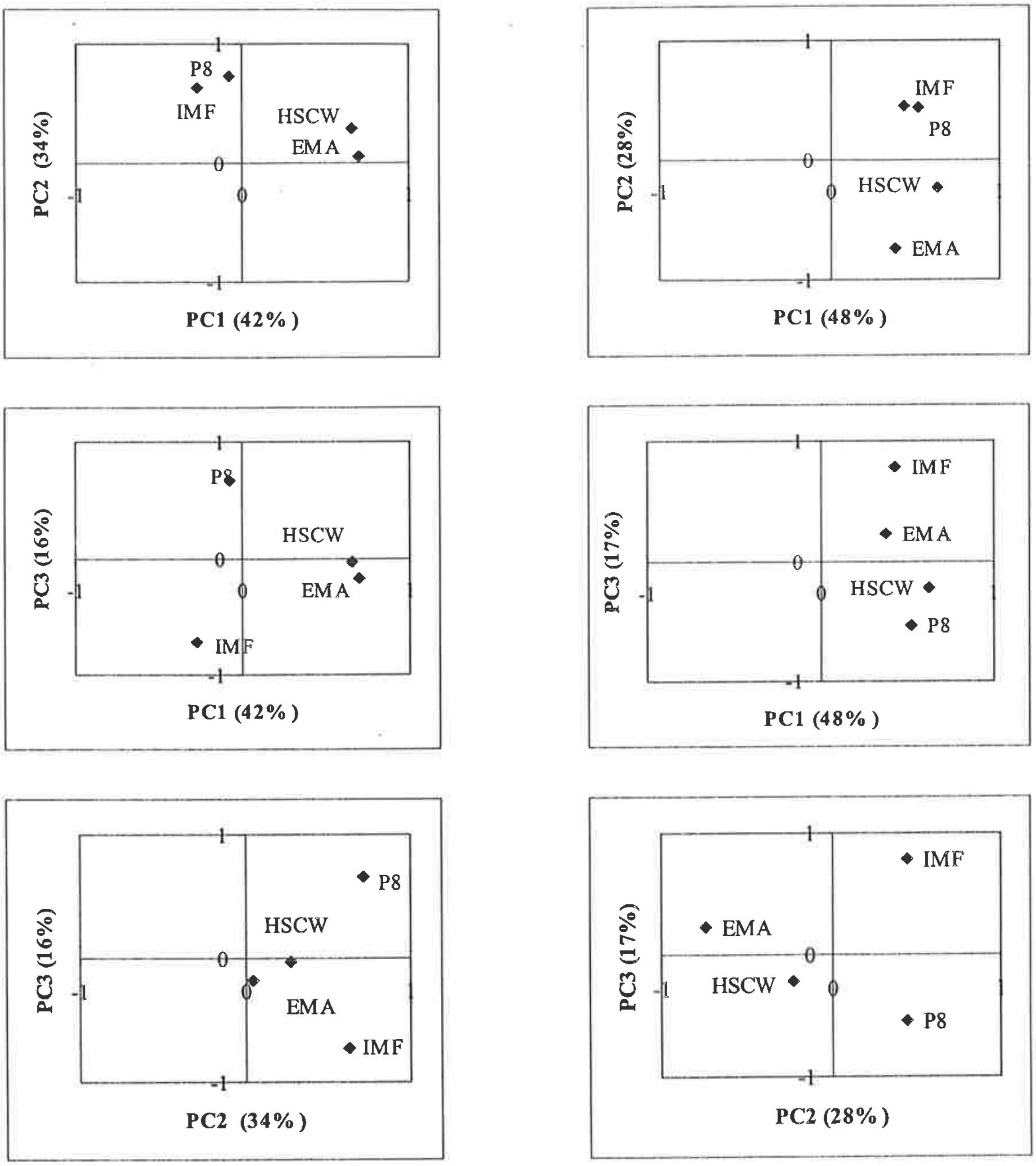


Figure 4.1. The eigenvectors biplot for heifers (left) and steers (right)

Factors affecting principal components of carcass quality traits

Heifers. The effects of year, management groups nested within years, birth month and breed as fixed and the sire nested within breeds as random effects were examined on the three carcass endpoint principal components. Table 4.2 shows the factors fitted in the linear mixed model and the tests of significance applied to the analysis of the growth, fatness and fat distribution for heifers. Year effect (Table 4.2) was highly

(P<0.001) significant in growth, fatness and fat distribution components. Breed differences and year nested within management groups were highly significant (P<0.001) for growth and fatness components, but not for fat distribution. Birth month had no effect on these three components. No differences between either early-March or late-April born calves effects (Table 4.2) were significant in the three components.

Heritabilities for the components were estimated after fitting fixed effects (Year, management group, birth month) and random effects (sire breed) (Table 4.2). The heritability of the growth component was of moderate magnitude (0.46). Heritabilities of the fatness and fat distribution components were extremely low.

Steers. The factors fitted in the linear mixed model procedure, and tests of significance applied to the analysis of the three principal components (PC scores) for steers are given in Table 4.2. Breed differences were significant in market suitability, muscling and fat distribution components among diverse sire breeds of steers (P<0.001). Year effect was also highly significant (P<0.001) for all three components. Year differences (Table 4.2) were largely due to seasonal variation in pasture availability, age of entry into feedlot and time on feed. Management group effects were significant for market suitability component, but it was of low magnitude or non-significant for muscling and fat distribution components. No differences between early-March and late-April born calves (Table 4.2) were observed for all three components.

The variance components, additive genetic variance, phenotypic variance and heritability for the principal components (new indices) were calculated after adjustment for environmental (Year, management group, birth month) fixed effects and sire breed (Table 4.2). Muscling was the most highly heritable component (0.63). The heritability of market suitability and fat distribution were extremely low.

Table 4.2. Analysis of variance, phenotypic variance and heritability of principal components in heifers and steers

	Heifers				Steers			
	df	PC1	PC2	PC3	df	PC1	PC2	PC3
Bmonth	1	0.14	0.72	0.15	1	0.1	0.39	0.66
Year	3	<0.001	<0.001	<0.001	3	<0.001	<0.001	<0.001
Year.LYSP	12	<0.001	<0.001	0.95	9	<0.001	0.17	0.38
Breed	6	<0.001	<0.001	0.42	6	<0.001	<0.001	<0.001
Phenotypic variance		0.32	0.08	0.01		0	0.42	0.05
Heritability		0.46	0.1	0.02		0.07	0.63	0.11

Biplot analysis of management groups

Heifers. Figure 4.2 shows the projection of the management groups into the ordination space. Three groups of management are revealed. The 1994-drop heifers placed on the top right quadrant indicated both high values in growth and fatness. The heifers born in 1995 had high value in growth but low value in fatness. There tended to be a moderate value in growth and fatness for the 1996-drop heifers. The 1997-drop revealed low growth but average value in fatness (Figure 4.2). The prominent features of fat distribution versus growth biplot demonstrated that all 1994 heifers were grouped with high values in growth and fat distribution. The heifers born in 1995 was characterised by a high level of growth but a moderate level of fat distribution. The 1996-drop stood out as being moderate fat distribution and growth. The 1997-drop heifers had a low level of growth and high value in fat distribution (Figure 4.2). There were four groups revealed by the score plot (Figure 4.2) of fatness versus fat distribution. All 1994 heifers were characterised with high fatness and fat distribution. The 1995-drop heifers indicated low value in fatness and moderate on fat distribution. The 1996-drop heifers stood out as being moderate value in fatness and low fat distribution. The heifers born in 1997 nearly parallel to the PC1 axis demonstrated moderate fatness and somehow high fat distribution (Figure 4.2).

Steers.. Thirteen management management groups; a combination of year (1994 to 1997), location of pre-weaning period (Struan and Wandilo), and four post-weaning groups, against their values for market suitability (PC1), muscling (PC2) and fat distribution (PC3) are shown in Figure 4.2.

Figure 4.2 showed a biplot of the management management groups against their values for fat distribution (PC2) versus market suitability (PC1). All 1997 steers with low value in market suitability had a tendency towards moderate value in fat distribution located opposite to steers born in 1996, with high value in market suitability and fat distribution. All steers born in 1995, located on the bottom right quadrant, indicated high market suitability but low value in fat distribution. All the1994-drop, located on the bottom left quadrant, were both low in market suitability and fat distribution (Figure 4.2). Projection of muscling versus fat distribution score plot illustrated two major groups of management groups in steers. The 1997-drop steers, which were the only group not to be feedlot finished, demonstrated a tendency towards moderate muscling and fat distribution. The steers born in 1996 located on the top right quadrant indicated high value of muscling and fat distribution. On the contrary all the steers born in 1994 and 1995 demonstrated low value in muscling and fat distribution (Figure 4.2).

Biplot analysis of breeds

Figure 4.3 shows the projection of the breed means into the ordination space. Breeds were arranged in two groups: the first were Jersey, Wagyu, Angus and Hereford, located on the left side grouped with low values in growth; the second consisting of Belgian Blue, South Devon, and Limousin, located on right side stand out as being high growth. Both groups were characterised by average value of fat distribution (Figure 4.3).

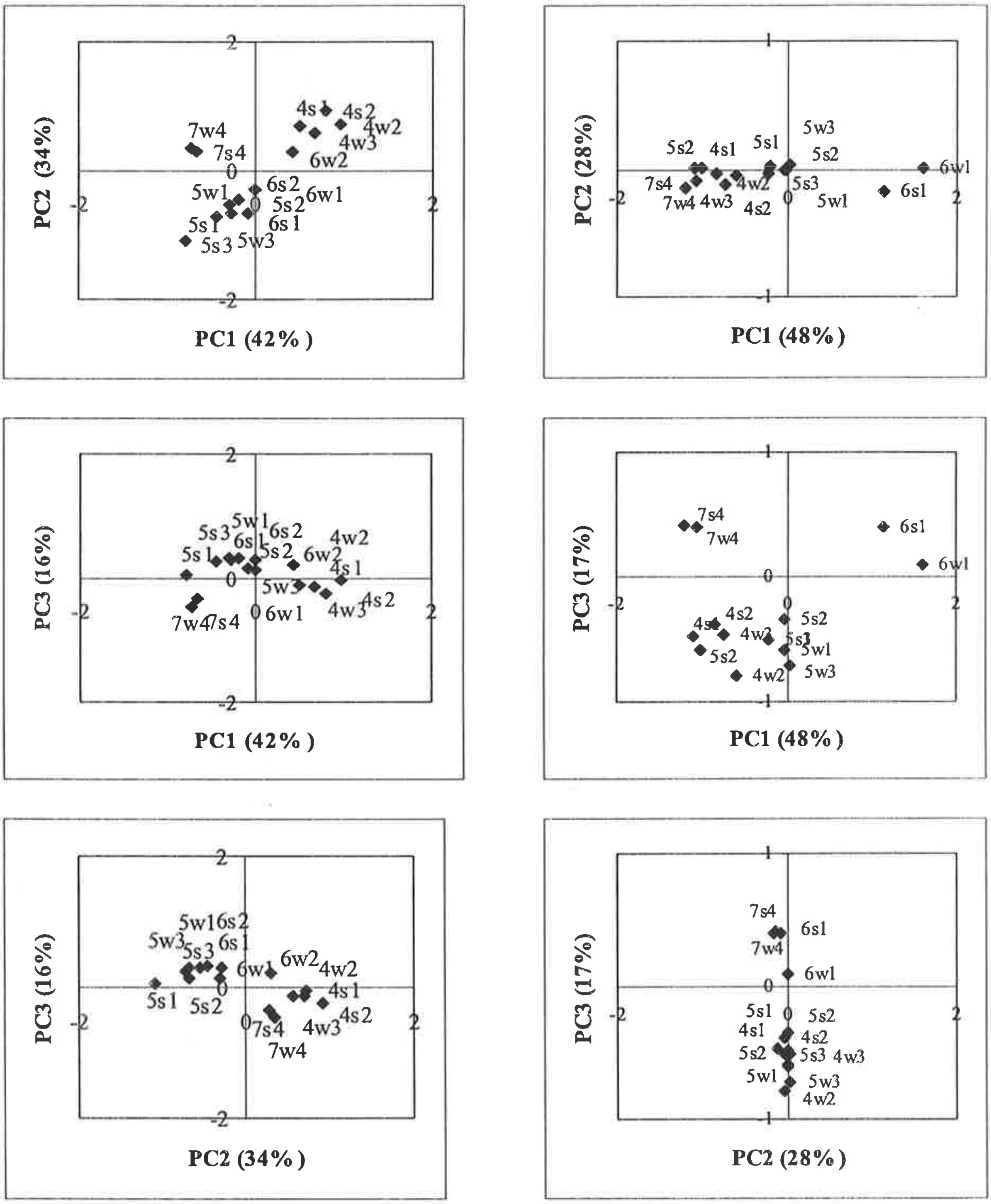


Figure 4.2. Management groups biplot of principal components for heifers (left) and steers (right). For definition of symbols see Figure 3.2

Jersey steers placed on left side have a low value in fatness in contrast to Angus heifers that have a high fatness. Belgian Blue, Limousin and South Devon, Hereford and Wagyu all nearly sited around the origin indicate average values in both fatness and fat distribution (Figure 4.3).

Heifers. Heifers and steers were fairly similar with respect to breed attributes obtained from biplot analysis. The biplots (Figure 4.3) indicated the following features for the crossbred heifers. Jersey and Wagyu grouped with low growth and high fatness. South Devon, Limousin and Belgian Blue characterised by high growth but low fatness. Hereford had medium growth and fatness and Angus grouped with medium growth and high fatness.

Steers. Figure 4.3 illustrates the biplots of seven breeds against their values for muscling (PC2) vs market suitability (PC1), fat thickness (PC3) vs market suitability and fat thickness vs muscling. The Figure 4.3 shows that breeds were substantially arranged in three groups in terms of market suitability: the first - Jersey, Wagyu grouped with low market suitability; the second – Hereford, South Devon, Limousin and Belgian Blue steers with medium market suitability and the third- Angus with high market suitability. The biplots demonstrated the same characterization for steers with respect to muscling component. All heifers and steers characterized by medium fat distribution (Figure 4.3).

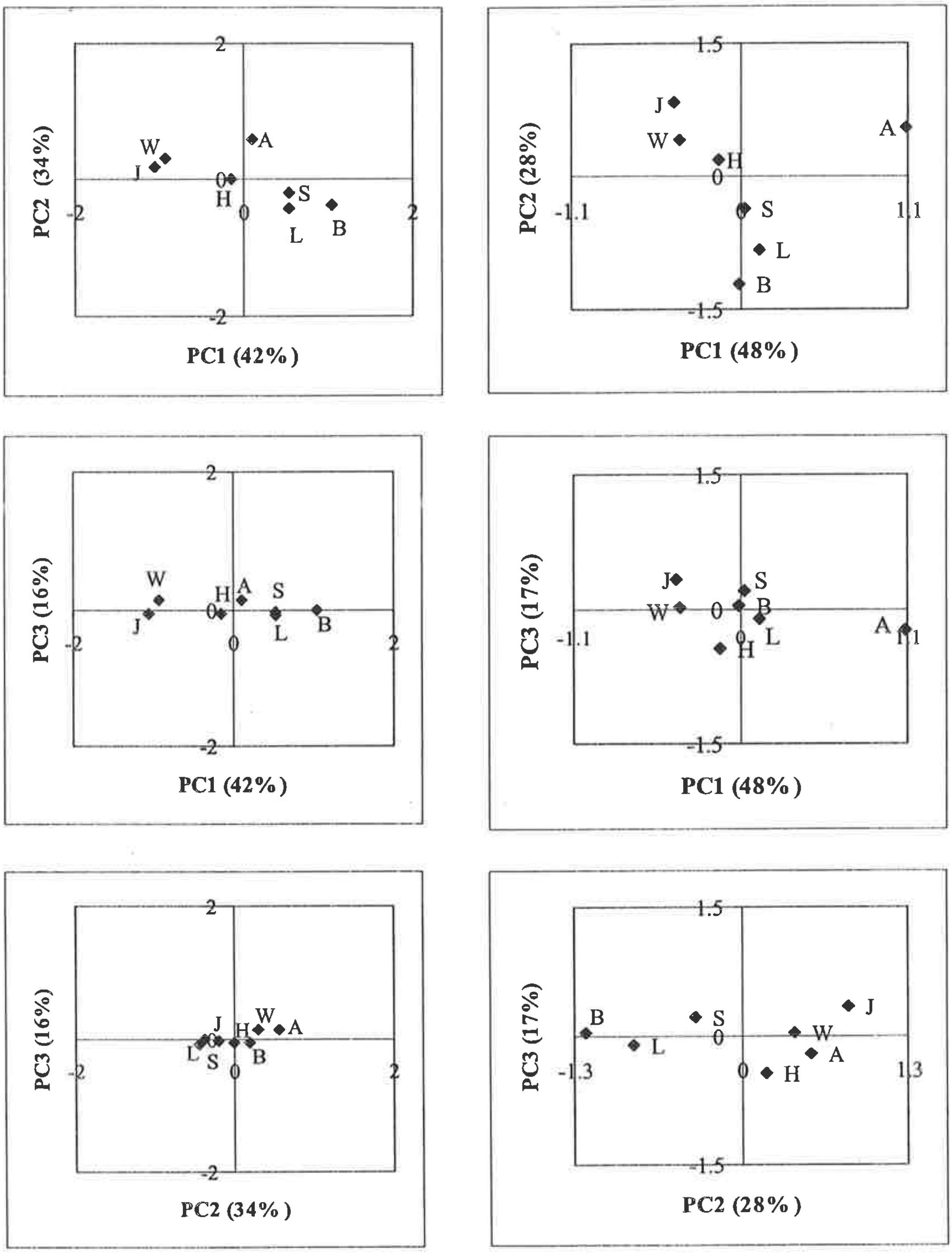


Figure 4.3. Breed biplot of principal components for heifers (left) and steers (right)

4.3 Discussion

PCA made it possible to identify the most important directions of variability in the carcass quality traits considered so that carcass weight and fat thickness are the main determinants of market suitability and eye muscle area identifier of the muscling component. Significant effects of breed of sire indicated that genetic variation is important among breeds for market suitability and fatness. Three categories of sire breeds detected in both steers and heifers were as follows:

Low growth and muscling, high fatness and marbling classes containing Jersey, Angus and Wagyu.

High growth and muscling, low fatness, and low to moderate marbling, including Belgian Blue, Limousin, South Devon and Hereford, implying low variance of fat traits associated with heavy group. Priyanto (1997) have found that if breed corrections for the prediction of carcass composition are required, then these should be addressed primarily in the heavyweight carcasses. They concluded that use of fat thickness, as a general predictor in heavyweight carcasses is associated with low variance and a high prediction error in carcass tissue proportions accounted for by the regression. To this end, the use of fat thickness alone as a general index of carcass composition is not recommended in heavy carcasses. Marshall (1994) reported breed differences for carcass traits, where Charolais ranked first among the sire breeds for carcass weight, and calves sired by Hereford were among those with the thickest fat cover.

It was shown that the proportion of variation in market suitability in steers and fatness in heifers due to year varied considerably across management groups. The effect of climate, e.g. rainfall and temperature, could be reflected by the year and management groups effects.

The notable loadings in the second component in steers were for EMA and HCWt. EMA is an indicator of muscling. As EMA increases, retail cut yield increases. Moreover, it has shown a decrease in the subcutaneous fat thickness/longissimous muscle ratio that may reflect increased carcass muscularity (Owens and Gardner, 1999). Hence, this component was known as a growth component. Muscling (in steers) and growth (in heifers) components have been used as new traits indicating carcass endpoints. Significant effects of year and breeds of sire indicated that not only environmental but also genetic variations are important for growth and muscling in steers and heifers, respectively.

The third components in both steers and heifers were to be an indication of fat thickness versus intramuscular fat. Results obtained from the present study indicated that the larger the fat distribution component the higher the intramuscular fat and the lower the fat thickness. As a strategy for the beef industry, to minimize wastage and maximize meat quality, it would appear to be appropriate to increase marbling relative to fat thickness.

With respect to fat distribution, genetic variation was important for steers but not for heifers. As expected, in both steers and heifers, Jersey, Wagyu and Angus were characterised as high marbling breeds: Hereford and South Devon with medium marbling, Limousin and Belgian Blue with low marbling. The steers born in 1994 and 1995 had a low value in marbling, whereas the heifers' equivalent had high marbling. There tended to be high marbling for 1996-drop steers. However, the heifers born in 1996 had a tendency to be low in marbling. Because they went to feedlot at different ages and they were on feed for different time. The 1997-drop steers tend to have an average value in marbling, but the heifers born in 1997 seem to have a tendency towards high marbling.

Estimated heritabilities for the muscling component trait were generally consistent with most other reported literature for market weight trait (AAABG, 2004). AAABG (2004) reported an average h^2 of 0.51 (age constant and unadjusted basis) for market weight trait. These larger heritability estimates for muscling are due to the larger genetic variance component estimates.

The h^2 estimates of 0.10 (heifer) and 0.07 (steer) for market suitability were lower than estimates (0.18 to 0.63) from the literature (Bertrand et al., 2001). Although the current estimates are dissimilar to the averages, they are not so different from the lower estimates in Table 1.3. The closest estimates were 0.18 (Woodward et al., 1991) and 0.23 for Angus (AAA, 2000). In addition, the h^2 estimates from the present study for market suitability are not very different than the weighted averages of estimates of heritability for unadjusted cutability (0.28) from the review of AAABG (2004). Cutability is a composite trait that is influenced by carcass weight, fat thickness, and ribeye area. In a review by Koots et al. (1994a), average heritabilities of carcass weight ranged from 0.20 (unadjusted) to 0.36 (constant finish). In studies on carcass traits of young bulls of dairy breeds, heritabilities of field-recorded carcass weight and fatness were in the range 0.19–0.26 and 0.12–0.30, respectively (van der Werf et al., 1998; Parkkonen et al., 2000).

Caution should be taken in using many of the literature values for comparisons because of differences in the data sets available for those studies, the use of different breeds of cattle and methods of analysis. Koots et al., (1994a) noted a tendency for heavy continental breeds to have higher heritabilities for age-adjusted backfat than smaller breeds such as Hereford.

4.4 Conclusion

Due to small number of traits, the current PCA could not condense the variations in a few number of PC as much as expected. Moreover, carcass is a very heterogeneous product and in this dataset the carcass traits did not appear highly correlated with each other (Chapter 2). The present PCA also suffered from shortcomings associated with lacking of fixed effects adjustment before the analysis and the small number of carcass traits considered for the analysis. To overcome the latter drawback, it would be worthwhile considering more highly correlated carcass traits using principal component analysis.

PCA described in the chapters 3 and 4 were conducted to explore variations in growth and carcass quality of crossbred cattle. In the subsequent chapters 5-9, the development of a predictive model of carcass quality based on the live measurements is explored.

5.1. Introduction

Growth is continuous during an animal's life and is evaluated by growth rate or by weight and size increases during different stages of the growth path, for example pre- and post-weaning periods. Growth traits change with age and there is evidence that these changes are influenced by genetic and non-genetic factors (e.g. Mrode and Kennedy, 1993; Atchley et al., 1997). From an animal modelling point of view, interest lies in genetic and non-genetic parameters that describe the change of such traits over time.

Several approaches have been proposed to deal with estimating genetic and non-genetic parameters of growth data. Previously, body weights that are measured in time were analysed as a multi-trait model, assuming the phenotypic values at distinct ages as different traits. Recently, random regression models (RRM) have been advocated to fit growth data (Schaeffer and Dekkers, 1994; Jamrozik and Schaeffer, 1997; Kettunen et al., 2000; Schenkel et al., 2002; Hassen et al 2003). Compared to a multivariate model, a RRM provides a more structured and smoother covariance matrix, with less bias (Kirkpatrick et al., 1990). In addition, RRM use fewer parameters to describe the same data as multivariate models (Hassen et al 2003). In beef cattle, the method was applied by Varona et al. (1997) and was used on the weights of mature beef cows by Meyer (1998, 1999, 2000) and by Arango (2000).

In this chapter, a cubic polynomial model was employed to estimate genetic and non-genetic parameters. Thus, the objective was to develop RRM of animal growth from birth to slaughter to address:

How large is the (co)variation of genetic and non-genetic components of growth traits and their genetic and non-genetic relationships ?

Chapter 5

Random regression models of growth

5.2 Statistical method

Data used in this chapter were obtained from the "Southern Crossbreeding Project" (Chapter 2). Data included records of up to thirteen (for steers) and eight (for heifers) sequential weights for cattle measured at ages ranging from birth to about 700 days (for steers) or 500 days (for heifers).

Log transformation, Centering age and scaling. In this analysis, natural logs of the body weights were used rather than the original body weights to achieve homogeneity of variance (Chapter 2).

As illustrated previously (Figure 2.4), a non-linear relationship between weight and age over time is apparent and also high correlations between exist adjacent weights. Age was centered and scaled (from days to years). This was done for both numerical reasons and for prediction. In the former case, (co)variance components were more easily estimated because they were larger, and in the later, changes in one predictor could be gauged by setting others at their mean i.e. at the new origin for centered age.

Random regression analyses

Growth of animals is characterised by

(a) tracking: that is individual animals have their own growth path, and hence these paths vary between animals.

(b) increased variation as animals grow: this is related to tracking in that some animals have a stronger growth rate than others.

The variation in path and in spread over time can be captured by RRM (though not always completely). These models accomodate correlation and also increasing variance and at the same time allow animal specific growth paths. This is achieved by allowing regression coefficients for weight on time to be random effects across individuals, which are correlated within individuals. Thus an animal is viewed as being sampled via these correlated random regression coefficients.

Statistical model for growth

It has shown that growth has an approximately cubic pattern (Figures 2.2 and 2.3). Thus, the cubic polynomial in time forms the basis of the model, but at various levels. The models in this thesis fall into the so-called class of mixed models. These models have a mixture of fixed effects and random effects (that is effects that are assumed to arise from a distribution, usually a normal or Gaussian distribution) including a residual or random variation term.

The growth model considered in this chapter is a mixed model. The response variable is log-body weight. This is traditionally the scale on which weight is analysed, mainly because of the "multiplication" nature of growth. The added benefit is that the heterogeneity in variation is reduced. Finally, the implicit assumption is that the random variation has a log-normal distribution, and various properties can be used to provide results on the original weight scale (Chapter 2).

Let $\mathbf{y}$ be the vector of log-body weights for all animals at all measurement times

The mixed model is

$\mathbf{y} = X\tau + Z\mathbf{u} + \mathbf{e}$

where τ is the vector of fixed effects

$\mathbf{u}$ is the vector of random effects

$\mathbf{e}$ is the vector of residual errors

The matrices X and Z contain covariate values and indicators (factors) specific to each animal and sometime to each measurement time. They extract the appropriate elements of τ and $\mathbf{u}$ for each animal and time.

General assumptions are that **u** ~ N(0, G) and **e** ~ N(0, R) for some (co)variance matrices G and R. In addition, u and e are assumed independent. The form for **G** and R depend on the actual model. We turn to the specification of the growth models considered in this chapter.

Note that under the above general mixed model,

$E(\mathbf{y}) = X\boldsymbol{\tau} = \boldsymbol{\mu}$, say and var $(\mathbf{y}) = R + ZGZ^T$

The mean $\boldsymbol{\mu}$ depends on the fixed effects included in the model. The parameters associated with the fixed effects are given by $\boldsymbol{\tau}$.

Two models were considered; the animal and sire models. We consider the sire model in some detail. The animal model is similar with sire effects replaced by an animal (pedigree and hence additive) effect. Firstly the fixed effects involve breed, sex, age (time) and interactions between breed and sex with age. As the cubic polynomial forms the basis of time or age growth trends, breeds and sexes are allowed to differ in their cubic growth path.

Let i denote breed, k sire nested within breed, j sex, l dam, m management and r animal at time t.

$$\begin{aligned}\mu_{ijklmrt} = {} & \alpha_0 + b_{0i} + s_{0j} \\ & + \alpha_1 \, Age_t + b_{1i} \, Age_t + s_{1j} \, Age_t \\ & + \alpha_2 \, Age^2_t + b_{2i} \, Age^2_t + s_{2j} \, Age^2_t \\ & + \alpha_3 \, Age^3_t + b_{3i} \, Age^3_t + s_{3j} \, Age^3_t\end{aligned}$$

when $\mu_{ijklmrt}$ is formed into a vector,

$\tau = [\alpha_0 \, \alpha_1 \, \alpha_2 \, \alpha_3 \, b_{01} \, b_{12} \, b_{21} \, b_{31} \ldots b_{0,97} \, b_{1,97} \, b_{2,97} \, b_{3,97} \, s_{02} \, s_{12} \, s_{22} \, s_{32}]$

The initial $b_{01} \ldots b_{31}$ and $s_{02} \ldots s_{32}$ are zero by constraint. The matrix X is formed accordingly.

The random effects **u** consist of random cubic regression for Sire, Dam, Management

$\mathbf{u} = [\mathbf{u}^T_1 , \mathbf{u}^T_2 , \mathbf{u}^T_3 , \mathbf{u}^T_4]^T$

Where $\mathbf{u}^T_1$ is a 388X1 vector of 97 Sire random polynomial coefficients (4 for each sire). Thus

$\mathbf{u}^T_1 \sim N(\mathbf{0} , G_1 \otimes I_{97})$

where G_1 is a 4x4 unstructured variance-covariance matrix.

To provide an explicit model for the **u**'s is possible. For example, for Sire k the effect is $\mathbf{u}_{01k} + \mathbf{u}_{11k}\, t + \mathbf{u}_{21k}\, Age^2_t + \mathbf{u}_{31k}\, Age^3_t$.

This structure is the same for Dam, Management and PE effects. Thus

$$\mathbf{u} \sim N(\mathbf{0} , \begin{bmatrix} \mathbf{G}_{\mathbf{Sire}} \otimes I_{97} & 0 & 0 & 0 \\ 0 & \mathbf{G}_{\mathbf{M}} \otimes I_{581} & 0 & 0 \\ 0 & 0 & \mathbf{G}_{\mathbf{Mg}} \otimes I_{28} & 0 \\ 0 & 0 & 0 & \mathbf{G}_{\mathbf{PE}} \otimes I_{1141} \end{bmatrix})$$

The matrix Z has the constant and t, t^2, t^3 values for each observation.

Lastly it is assumed that $R = \sigma^2 I$. This may seem an unusual assumption for growth or repeated measures data. However, we are using the random regression to allow

(a) for time-changing variances and

(b) correlation between sucssessive time points.

Growth data often exhibits increasing variance. A log-transformation has been used to stabilise the variance, but even on this scale, if variances change, the random regressions will attempt to accommodate that change in a quadratic fasion.

An effective way to represent the full model is a pseudo analysis of variance table. Table 5.1 presents all the terms and their associated degrees of freedom for fixed effects or variance (covariance) parameter numbers for random effects. This is given for both the sire and animal models.

Table 5.1. Effects, their status (F=fixed, R=random), degrees of freedom (df) and variance parameters (V.P.) for maximal sire and animal models

	Status	df	Sire (V.P)	Animal (V.P)
Animal				
Breed	F	6	-	-
Sex	F	1	-	-
Sire	R	-	1	1
Animal (additive)	R	-	-	1
Dam	R	-	1	1
permanent environmental (PE)	R	-	1	1
Management	R	-	1	1
Time				
Age	F	1	-	-
Age2	F	1	-	-
Age3	F	1	-	-
Animal.Time	F	1	-	-
Breed.Age	F	1	-	-
Breed.Age2	F	1	-	-
Breed.Age3	F	1	-	-
Sex.Age	F	1	-	-
Sex.Age2	F	1	-	-
Sex.Age3	F	1	-	-
Sire.Age	R	-	1	-
Sire.Age2	R	-	1	-
Sire.Age3	R	-	1	-
Sire covariances	R	-	6	-
Dam.Age	R	-	1	1
Dam.Age2	R	-	1	1
Dam.Age3	R	-	1	1
Dam covariances	R	-	6	6
Management.Age	R	-	1	1
Management.Age2	R	-	1	1
Management.Age3	R	-	1	1
Management covariances	R	-	6	6
Animal.Age	R	-	-	1
Animal.Age2	R	-	-	1
Animal.Age3	R	-	-	1
Animal covariances	R	-	-	6
PE.Age	R	-	1	1
PE.Age2	R	-	1	1
PE.Age3	R	-	1	1
PE covariances	R	-	6	6
Residual	R	-	1	1

In the animal model, the effects involving animal have an associated relationship matrix (Henderson, 1950) to reflect the pedigree structure. Estimation of fixed effects and variance parameters is via residual per restricted maximum liklihood (Patterson and Thompson, 1971). Prediction of random effects is via Best Linear Unbiased Prediction (BLUP) (Robinson, 1991). The ASReml package is used for analysis. Gilmour et al. (1995) provided the details of the algorithms.

Relative growth rate (RGR)

In order to investigate relative growth rate changes over time, the first derivatives of growth function (differentiation) was calculated as follows:

Suppose growth is exponential, that is

(without the stochastic random error)

$$y(t) = e^{Rt}$$

Then for two times t_1 and t_2

$$\frac{y(t_2)}{y(t_1)} = \frac{e^{Rt_2}}{e^{Rt_1}}$$

or

$$\ell n \frac{y(t_2)}{y(t_1)} = R(t_2 - t_1)$$

$$\frac{\ell ny(t_2) - \ell ny(t_1)}{t_2 - t_1} = R$$

R is the relative growth rate (RGR). In fact

$$R = R(t) = \frac{d\ell ny(t)}{dt}$$

For the growth model presented above, the base model is (at various level)

$$\ell ny(t) = \beta_0 + \beta_1 t + \beta_2 t^2 + \beta_3 t^3$$

Thus

$$\frac{d\ell ny(t)}{dt} = \beta_1 + 2\beta_2 t + 3\beta_3 t^2$$

In the case of cubic model, RGR can be calculated as the first derivative of the function as follow:

$$= \frac{d\ell ny(t)}{dt}/y(t)$$

Thus R = R(t) is actually the instantaneous rate of change of the log-weight at time t, and also the rate of change of weight, relative to that weight.

5.3. Results

As stated earlier, the cubic model was fitted with either sire or animal genetic components. Log-likelihood, number of parameters, observations, fixed effects and error variances for the two models are shown in Table 5.2. The residual variation of the sire model was 3% lower than that of the animal model. The random effects accounted for approximately 65% [(0.02462-0.00833)/0.02462] of the residual variation after only fixed effects were fitted (Table 5.2). Some components could not be estimated in the animal model leading to a poorer fit (Table 5.5).

Table 5.2. Summary descriptions of the sire and animal models

	Sire	Animal
Loglikelihood (fixed+random effects)	20722.8	20686.3
Loglikelihood (fixed effects)	16004.5	16004.5
Number of model parameters[a]	22	18
Number of observations	11936	11936
Number of fixed effects	12	12
Error variance	0.00833	0.008548

[a] Number of variance components

The mixed model contained the fixed breed and sex effects and their interactions with first (linear), second (quadratic) and third (cubic) order of age. Table 5.3 shows the ASReml *F* values to test the significance of fixed effects considered in the model. Differences due to breed group were significant ($P < 0.01$). The third order of age and breed by Age^3 interactions as well as sex by Age^3 interactions were significant ($P<0.01$), indicating the importance of cubic form of the growth model (Table 5.3).

Table 5.3. ASReml F-Value to test the fixed effects

Fixed effects	df	F Value
Mean	1	176183.87
Breed	**6**	**42.78**
Sex	**1**	**145.89**
Age	1	17513.72
Age^2	1	1056.80
Age^3	**1**	**1555.57**
Breed.Age	6	11.41
Breed.Age^2	6	8.31
Breed.Age^3	**6**	**6.52**
Sex.Age	1	23.85
Sex.Age^2	1	4.57
Sex.Age^3	**1**	**3.57**

The comparison of the fitted vs fitted and fitted vs observed body weights obtained from both models are shown in the Figure 5.1. The plots of the fitted vs observed body weights were evenly distributed around the 45^0 line. It seems that the models fitted the data reasonably well. Also the plots of fitted vs fitted exhibited evenly distribution around the 45^0 line, indicating agreement of the sire and animal models There appears to be little difference between the animal and sire models.

Breed effects

The estimated mean weight of animal based on the fixed effects was obtained for both models (Table 5.4). In terms of comparing breeds, Hereford, Angus, South Devon Limousin and Belgian Blue were not significantly different from each other but they were approximately 10% heavier than Jersey and Wagyu calves (Table 5.4).

Table 5.4. Estimates (mean±SE) of sex and breed effects

Table 5.4. Estimates (mean±SE) of sex and breed effects

	Mean	Age	Age^2	Age^3
Sex				
Steer	5.67	0.86	-1.27	0.99
Heifer	5.61	0.92	-1.28	0.92
Standard error	±0.01	±0.01	±0.03	±0.04
Breed				
Jersey	5.58	0.88	-1.35	1.07
Wagyu	5.58	0.84	-1.30	1.05
Angus	5.68	0.90	-1.33	1.04
Hereford	5.67	0.86	-1.27	0.99
South Devon	5.69	0.88	-1.26	1.00
Limousin	5.69	0.84	-1.27	1.02
Belgian Blue	5.69	0.87	-1.27	0.98
Standard error	±0.02	±0.03	±0.04	±0.03

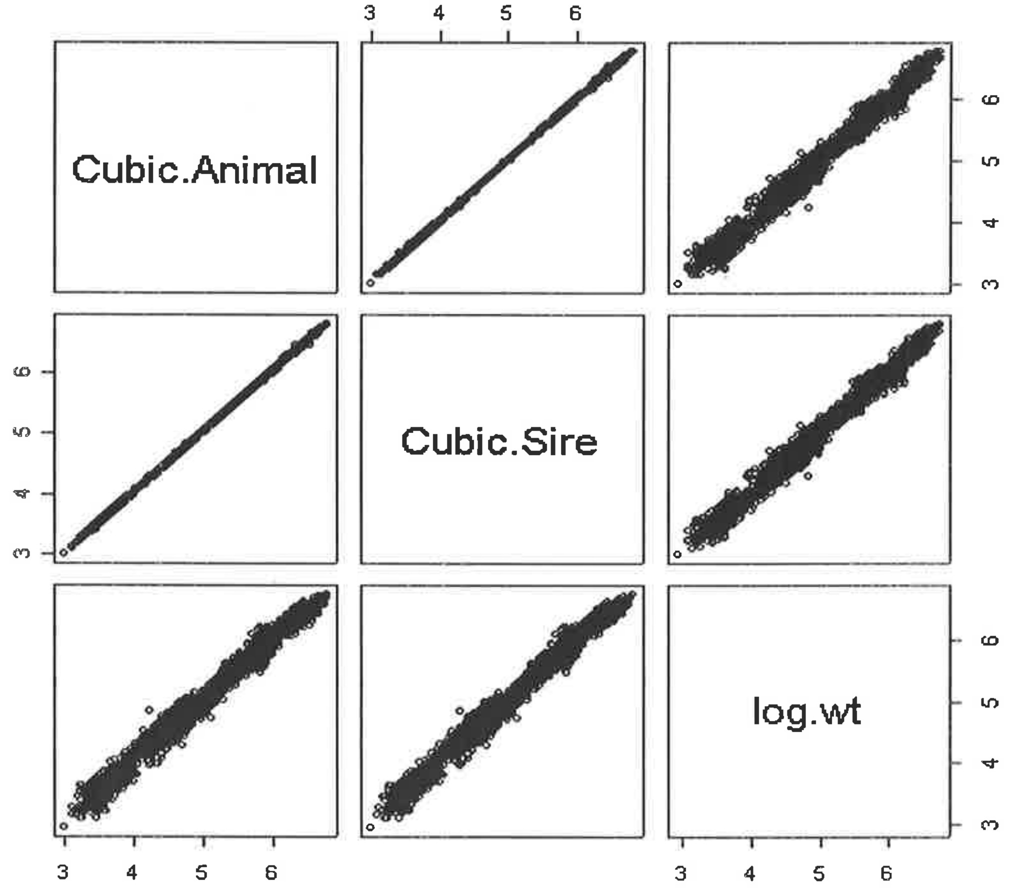
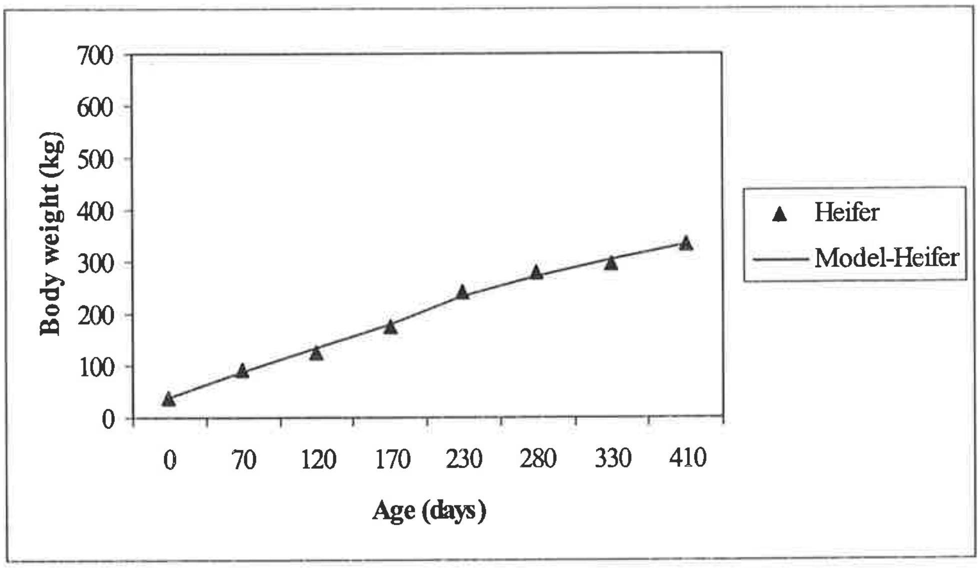


Figure 5.1. Scatter plot of fitted vs fitted and fitted vs observed body weights from sire and animal models

The results revealed similarities between the actual body weights and predicted body weights of heifers and steers (Figure 5.2), emphasizing fitting the cubic model on the body weights in the current study.



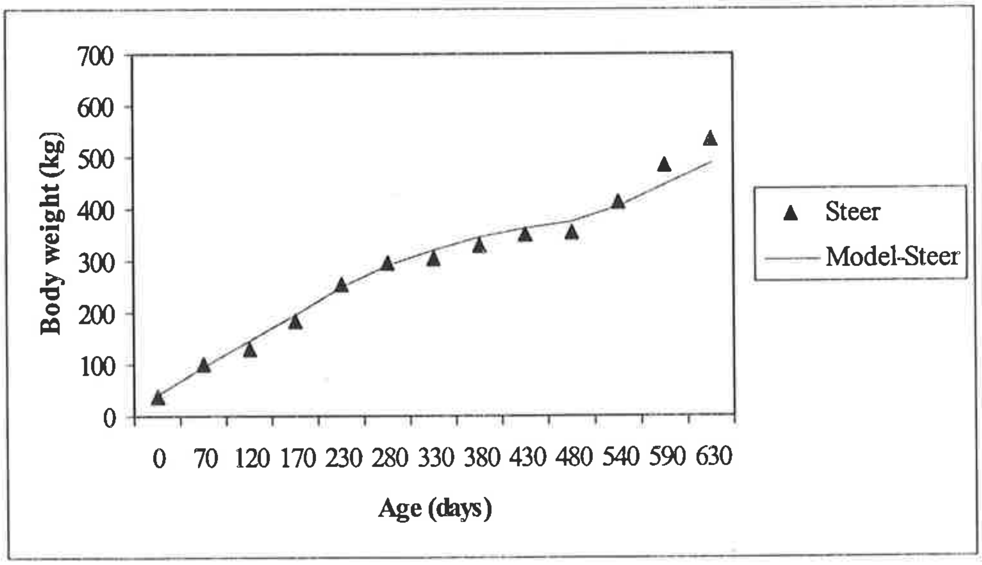


Figure 5.2. Actual and predicted weight-age curves for heifers (top) and steers (bottom)

The estimated monthly body weights from birth to slaughter for seven breeds are displayed in Figure 5.3. Body weights of all breeds increased over pre-weaning period, held fairy steady (slightly flattening) over the dry season, then increased again toward the end of the feedlot period.

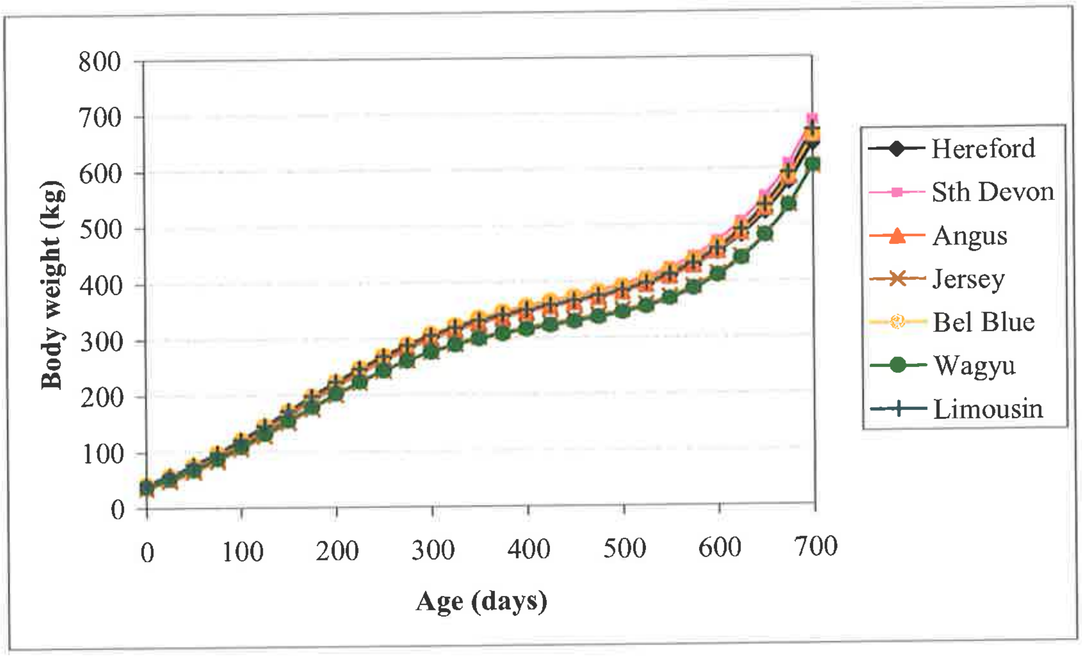


Figure 5.3. Growth curves (birth to slaughter) for seven crossbreeds derived from the growth model

Crossbred comparisons with purebred Hereford. Figure 5.4 illustrates the percentage deviation of estimated average weight of crossbreds from purebred Herefords at various ages. Although the magnitude of the percentage of deviation among breeds was variable over time, South Devon, Belgian Blue and Limousin calves were consistently heavier and Jersey and Wagyu were lighter than Hereford calves, as expected. Basically, breed differences were consistent across ages except that Jersey and Angus were relatively lighter in the first 200 days than 200-700 days. The magnitude of the percentage of deviation during pre-weaning period was approximately -20 to -10% and -12 to -8% for Jersey and Wagyu, respectively. After weaning they remained steady at about –10%, however, the magnitude of the percentage of deviation for Jersey became smaller than Wagyu (Figure 5.4). During pre-weaning the percentage of deviation of Angus cross calves increased dramatically, it was clearly lighter than the Hereford calves. Obviously, after weaning the direction of the deviation changed, so Angus calves became heavier than Hereford calves. Breed ranking at the post-weaning period were the same as the pre-weaning period (Figure 5.4).

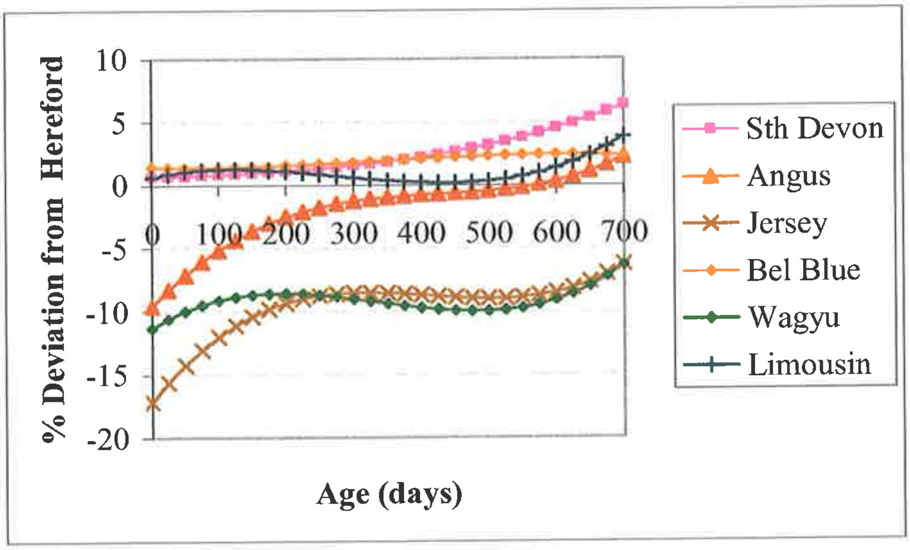


Figure 5.4. Deviation of estimated body weight of six crossbreds from purebred Hereford

Relative growth rate

As can be seen in Figures 5.5, the slope of individual rates of change clearly indicated three stages. First, growth rate during the pre-weaning period was increased, and approximately three month before weaning (the last 40% of the pre-weaning) a change in the rank of breeds was observed (Figure 5.5). Second, a reduction in growth rate at weaning up to feedlot that remains stable but low throughout. Third, In contrast, the slopes of individual rates of change for the feedlot period tend to rise (Figure 5.5).

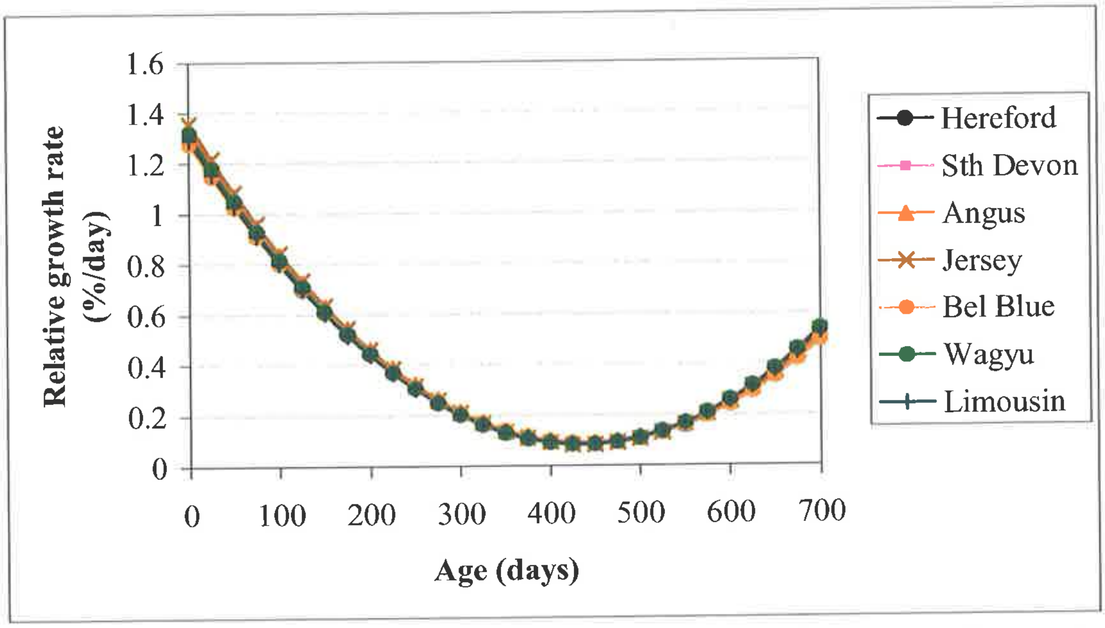


Figure 5.5. Average growth rate of breeds utilizing first derivatives of estimated coefficients of mean and slopes against time

Genetic and non-genetic (co)variance components

Cubic random coefficients models were postulated for Sire (and Animal), Dam, Permanent environmental and Management effects. In many cases the data did not support inclusion of all terms because the model failed to converge in estimations. Table 5.5 presents the variance components (excluding covariances for simplicity) that were able to be fitted. Estimated components that are listed as zero were estimated to be on the boundary; that is they converged to zero. A quadratic random effect for sire and dam were in the model, but had to be removed because the algorithm failed to converge. The covariance between sire constant and linear was not able to be estimated (Table 5.6). Finally, twenty-two (co)variance components were able to be estimated (Table 5.6).

Table 5.5. Variance components derived from the sire and animal growth models

	Sire	Animal
Sire (Animal)[a]	0.000465	0.003969
Maternal	0.004380	0.009273
Management	0.005820	0.007879
Permanent environmental	0.003550	0.002753
Sire.Age (Animal.Age)[b]	0.000089	0.001959
Maternal.Age	0.001610	0.001535
Management.Age	0.013000	0.045651
Management.Age^2	0.020700	0.076682
Management.Age^3	0.009240	0.009454
Permanent environmental.Age	0.001940	0
Permanent environmental.Age^2	0.002470	0
Residual	0.008330	0.008548

[a] Sire for sire model and Animal (additive) for animal model
[b] Sire.Age for sire model and Animal.Age for animal model
[c] Sire variance expected to be ¼ of animal variance

Table 5.6. Estimated variance components (on diagonal) and covariances (off diagonal) from the cubic sire model. Ticks mark indicate the components that were able to be estimated

	1	2	3	4	5	6	7	8	9	10	11	12
1. Sire constant	✓											
2. Sire linear		✓										
3. Maternal constant			✓									
4. Maternal linear			✓	✓								
5. Management.constant					✓							
6. Management.linear					✓	✓						
7. Management.quadratic					✓	✓	✓					
8. Management.cubic					✓	✓	✓	✓				
9. Permanent environmental.constant									✓			
10. Permanent environmental.linear									✓	✓		
11. Permanent environmental.quadratic									✓	✓	✓	
12. Residual												✓

Components of parameters of growth in beef cattle include sire (additive), dam, permanent environmental and environmental effects variances across ages. Estimates of total variance for each random component were plotted on a continuous scale (Figure 5.6). Genetic variances increased steadily over time, though with a small amount. Maternal variance declined with age, indicating tendency to be higher at younger ages (Figure 5.6). The shape of the permanent environmental variance was generally similar to dam variance. However, it should be noted that all of those components were pretty small. The remarkable changes occurred where management variances increased rapidly from 500-700 days, so all driven by steer feedlot phase (Figure 5.6).

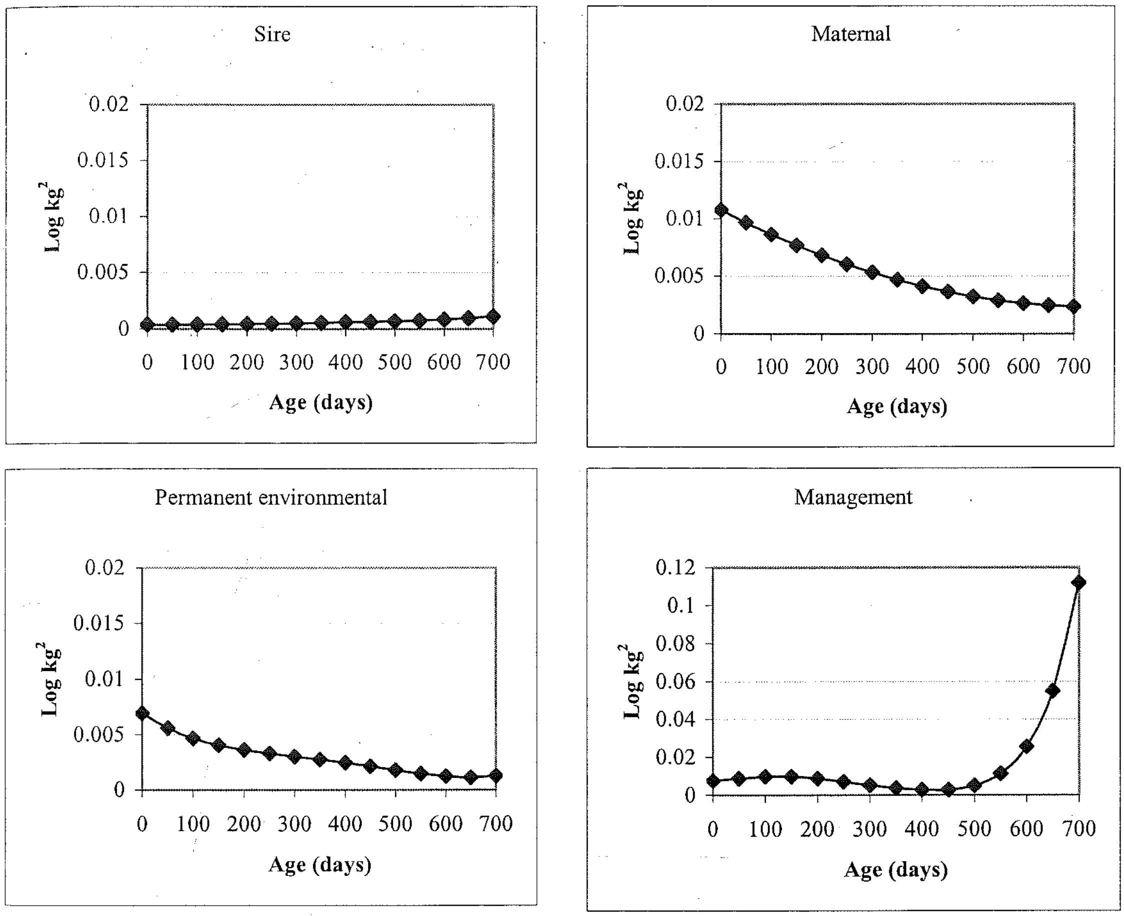


Figure 5.6. Variance components for sire, dam, permanent environmental and management groups effects at different ages derived from the sire growth model

Figure 5.7 shows a plot of the heritability of body weights at different ages derived from the sire model. Heritability increased steadily with age, ranging from 0.08 at birth to 0.92 at 700 days of age. Maternal heritability was moderate at all ages, ranging from 0.50-0.63 (Figure 5.7).

5.4. Discussion

The RRM coefficients were predicted for each calf, i.e. each calf had its own slope, quadratic and cubic coefficients. The sire model seemed to be the simplest and best

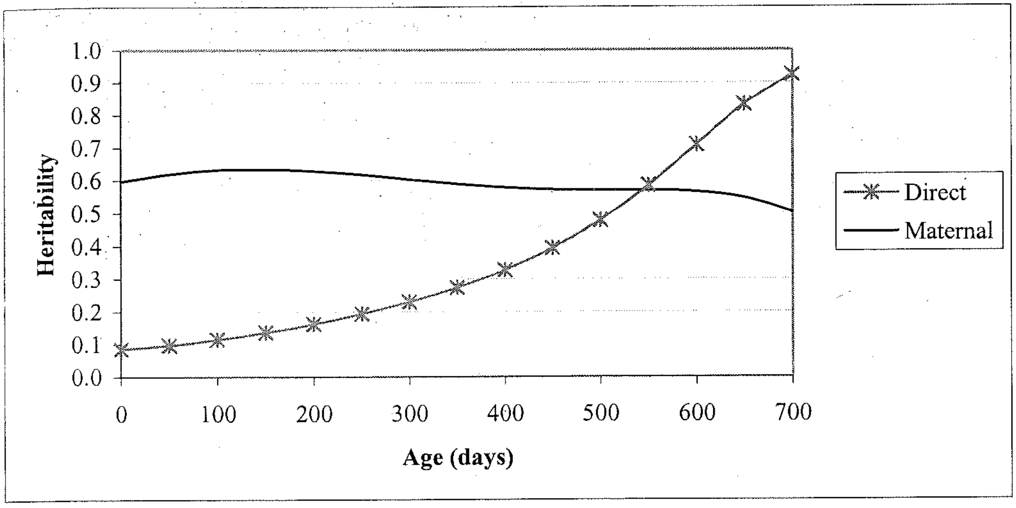


Figure 5.7. Estimates of additive and maternal heritabilities at different ages

performing (stable) model. Not all variances and covariances listed in table 5.1 could be fitted. Thus a formal model reduction process using likelihood ratio tests not possible or appropriate. In any case, the term attempted to be fitted constituted both the maximal and minimal model. It should be noted that due to the limitations imposed by the data set all terms could not be fitted in the models. It should also be pointed out that the terms in the model are included if only they can be estimated. That is a variance or covariance exists. Therefore, significant test within the model is NOT an issue.

Breed effects

The weight of an average animal at any time point for the combination of fixed effects was obtained from the solution of model to plot average growth path, average deviation of crossbred cattle from purebred Hereford and then average growth rate (first derivative with respect to age). Generally, results of relative contribution of variance components from all random regression growth models in this study indicated that non-genetic variation accounted for the larger proportion of the total variation. Likewise, the management variation contributed to the largest proportion of non-genetic as well as total variation in body weight. The results showed that differences between heifers and steers increased up to weaning. It then decreased again when steers remained in background phase while heifers went to feedlot, grew faster and caught up the steers at around 450-500 days (Figure 5.2). Hence, the pattern of difference at birth weight between steers and heifers, already observed, remained up to the feedlot period. Generally however, a similar growth pattern was observed for both sexes throughout pre-weaning and post-weaning periods (Figures 5.3). Body weights of all breeds increase over pre-weaning period, increased only slightly during the dry season (December to March) and then went up again during June to October (wet season).

Environmental effects accounted for a large proportion of the total variation in the body weights of calves as nutrition in the current study was based on the pasture. The seasonal pattern (growth curves) of green herbage mass and senesced residues (dead and litter) at Wandilo and Struan demonstrated that the dry matter of available green herbage mass and senesced residues (dead and litter) increased over June to October (Figure 2.1). It also exhibited declining levels of green herbage mass (but high levels of senesced residues) in spring and low levels of green herbage mass in summer through autumn, i.e. the approximate period between 250 days (December) to 350 days (March), which corresponded with dry season. For the period March-April total pasture availability still decreased. Also, based on the seasonal pattern of *in vitro* digestibility and energy content for the green and senesced fractions of herbage mass at Wandilo and Struan, the digestibility of green herbage mass progressively declined in summer through autumn from 0.77 to 0.58, remained relatively constant over autumn at 0.57–0.60 and was uniformly high in winter and spring at 0.75 to 0.78. The digestibility of the senesced fraction remained in the range 0.45–0.55 digestibilities.

Figure 2.1 illustrates occurrence of a summer–autumn feed-gap due to the sub-optimal nutritive value of green herbage mass from late spring through summer–early autumn. Thus, the seasonal pattern of quantity and quality of pastures at Struan and Wandillo indicated the limitations of the feed year include a feed gap in summer–early autumn due to low herbage mass associated with dry season, and a feed gap in summer–autumn associated with only moderate pasture quality (digestibility) of secondary regrowth pasture. Growth body weights of calves were significantly higher on pre-weaning (pasture growth) than during the post-weaning period (Figure 2.1) although they were high during the feedlot phase (Figure 5.5). The higher gains of calves on pasture can be due to the higher availability of nutrients from their dams, particularly at the start of the grazing season and if they had been undernourished during backgrounding as part of the post-weaning period. Thus, the significance of these feed gaps for the post-weaning growth of steers and heifers is highlighted through the backgrounding period from average growth path. All seven sire breeds showed the similar growth patterns during the pre-weaning period. However, during the post-weaning period two groups of sires, heavy and light, showed different growth patterns (Figure 5.3 and 5.4).

Breed differences in performance characteristics are an important genetic resource for improving efficiency of beef production. Diverse breeds are required to exploit heterosis and complementarity through crossbreeding to match genetic potential with diverse markets, feed resources and climates. The percentage deviation of estimated average weight of crossbreds relative to purebred Herefords from birth to slaughter indicated that, as might be expected, the South Devon, Belgian Blue and Limousin calves were consistently heavier and Angus Jersey and Wagyu were lighter than

Hereford calves (Figure 5.4). Jersey and Angus demonstrated the best combination of minimum birth weight and maximum growth rate over time (Figure 5.4).

Relative growth rate

One aspect of growth that is considered in the literature is relative growth rate (RGR) (Fitzhugh and Tylor, 1971; McWhir and Wilton, 1986; Ahunu and Makarechain, 1987; Kemp, 1990; Johnston et al., 1992; Liu and Makarechian, 1993; Bailey et al., 1994; Kimiaki et al., 1998; Holloway et al., 2002; Nkrumah et al., 2004). Relative growth rate increased during the pre-weaning period, then essentially held steady during the follow-up period and increased through the feedlot period (Figure 5.5). The decrease in the rate of growth after weaning during the dry period was due to decreased milk availability and decreasing quality of pasture as the season progressed. No breed differences existed with respect to average growth rate of the seven breeds.

Genetic and non-genetic estimation of (co)variance components

Genetic analysis of growth curves has been applied to body weight-age curves in beef cattle (DeNise and Brinks 1985; Rekaya et al. 1999). Determining the genetic control of growth curves is important because they correct for irregularities in the data caused by human error or random environmental effects and allow for prediction of growth at ages where measurements are missing.

Components of parameters of growth in beef cattle include additive, maternal, permanent environmental and temporary environmental variances across ages (van der Werf et al., 1998; Meyer, 2001; Meyer, 2002; Albuerque and Meyer, 2004).

The estimates of genetic variance generally exhibit expected trends. Maternal variance is a component of the phenotypic variance that arises from maternal differences between dams, e.g., nursing ability, maternal care, etc. Maternal variance tends to be constant throughout the trajectory, consistent with Fischer et al. (2004)

who reported constant maternal variances over growth path (500 days) for sheep. Other studies have shown that maternal variance declines with age (Meyer, 2001, 2002). Perhaps, the discrepancy found in various studies may be attributed to partitioning problems between maternal genetic and permanent environmental effects. The variance partitioning is similar to that shown in studies which estimated these random components for beef cattle growth data (Meyer, 2002). However except for additive genetic variance, the shapes of the variance component graphs were generally different from those reported by Albuquerque and Meyer (2002).

The notable pattern for management variances beyond 500 days of age indicates the importance of management group during feedlot period, particularly for steers (Figure 5.6). Heifers were slaughtered after a short feedlot period (~70 days) up to 500 days of age.

Generally, the estimated heritabilities (h^2) were low due to low contribution of sire and animal variances to the total variation of body weights. These estimates were under the range of the average estimates for pre-weaning and post-weaning weights reviewed by Koch et al. (1994) and Meyer (1999). This difference could be associated with the model of analysis or sampling (co)variances (Meyer, 1992). The current result demonstrated that the additive heritability (h^2) increased steadily with age. It should also be noted that heritability has been used to reflect additive genetic variance. Thus any changes in genetic variance are expressed as a proportion of phenotypic variance that was low herein so that changes in heritability indicate changes in additive genetic variance relative to those in phenotypic variance.

Quite obviously, there is a definite systematic change over time and additive heritability increased steadily with age. This is probably an artefact because the mean profile (Figure 5.2) did not fit well at these late stages. An alternative explanation is that there may be changes in the environmental variance (management and permanent environmental) over time, which would affect the heritability. The additive heritabilities were 0.08, 0.19 and 0.27, at birth, weaning (250 days of age) and yearling (350 days of age), respectively. AAABG (2004) report 0.35 for the estimate of additive h^2 of birth weight using 172 estimations. The average estimates summarize by Mohiuddin (1993) for male and female were 0.46 and 0.39, respectively and 0.24 being across sexes. The average estimates of h^2 (Table 1.2) for weaning weight are 0.26, 0.27 in steers, 0.23 in females and 0.20 across sexes (Mohiuddin, 1993). Mohiuddin (1993) reported wide range of h^2 estimates from –0.13-0.84 in steers and 0.00-0.64 in females. The average estimates of h^2 for yearling weight are 0.35 and range between 0.04-0.73 in males, 0.16-0.71 in females and 0.14-0.48 across sexes (Mohiuddin, 1993). Estimates of additive and maternal heritabilities in Australian breeds for birth, weaning, yearling and 600 days weights were estimated to be 0.35, 0.20, 0.24 and 0.25, respectively, for additive effects and 0.08, 0.09, 0.06 and 0.04 for maternal effects (Robinson, 1996). The current result was consistent with literature values summarised by Benyshek (1982), who proposed additive heritability estimates of 0.17, 0.33 and 0.34 for birth, weaning, and yearling weights. Moreover, Arnason and Kassa-Mersha (1987) obtained heritability estimates of 0.11 and 0.22 for weights taken at birth and weaning weights. Phocas and Laloe (2004) and Demeke et al. (2003) have observed 0.08 and 0.10 for heritability of birth weight, respectively.

In general, these results except for the beginning and the end of the trajectory, were in the range of most values seen in the literature (Mohiuddin, 1993; Koots et al., 1994a; Gregory et al., 1995; Robinson, 1996 and Carnier et al., 2000; AAABG, 2004). The heritability estimates, were unexpected for birth weight and beyond 650 days. The estimates of additive heritabilities for birth weight was smaller than previously reported in the literature. In contrast additive heritability beyond 650 days were higher than others. As mentioned, it seems that, the discrepancy found in various studies could be attributed to partitioning problems between maternal genetic and permanent environmental effects. Another reason for this could be that both additive and maternal effects were fitted in the current study, whereas many past estimates were from models that only fitted additive genetic effects. According to Meyer (1992b), models that do not account for additive maternal effects may yield substantially higher estimates of additive genetic variance, and as a result, higher estimates of additive heritability.

It is possible that the fit is the worst for traits with the smallest variances. Kettunen et al. (1998) concluded that the overestimation of the genetic variances at the edges of the defined lactation curve trajectory was likely due to the mathematical characteristics of the sub-model, i.e. the function chosen within the test day model. This result was consistent with Meyer (1998) who observed that data points at the beginning and end of the lactation trajectory for which an animal has records have a relatively large impact on the regression coefficient estimates, when polynomials are used as the covariance function. To ensure that evaluation of body weights by RRM is optimal, it may be necessary to "adjust" RRM parameters so they would equal those of multi-trait model for birth weight. In addition, to overcome the above problem, some workers have applied another type of function, Legendre polynomials (Kirkpatrick et al., 1990) because they expected a relatively smooth covariance function based on polynomials underlying the lactation curve. However, similar behaviour of covariance function estimates for ages where the least data is present has been shown even when legendre polynomials has been used (Meyer, 2002 and van der Werf et al., 1998) and even when data are evenly spread across the trajectory (Fischer and van der Werf, 2002). This remains a shortcoming for models that utilise polynomials; hence making use of functions other than polynomials may solve this problem. Although the choice of which type of function to use might not have a large effect on the parameter estimates within the interval that data was collected, the function might be more important as soon as data are extrapolated (Kirkpatrick et al., 1990).

The maternal effects on growth traits are defined as any environmental influence that the dam contributes to the phenotype of her offspring that starts during prenatal life and extends to the time until the young individual becomes independent. As indicated by Koch (1972) and Willham (1972) the contribution of the dam is environmental with respect to the calf (mothering ability, milk production, environment, dam instinct). The effect of the milk yield of the dam on calf growth traits is considered in breeding schemes by including maternal genetic effects and permanent maternal effects. Maternal effects are important during the nursing period with diminishing effects through post-weaning. However, maternal effects are related to factors that affect all progeny of a dam and their influence on post-weaning weights, probably are due to effects on pre-weaning weights. Robinson et al. (1981) stated that optimum improvement programs for early growth traits require knowledge of parameters involving the joint influence of genetic and environmental effects on additive growth potential and dam ability.

Maternal estimates of linear growth were similarly low. In the current study, estimates of maternal heritabilities derived from cubic sire model are moderate at all ages (0.50-0.63), fairly constant during the trajectory. Meyer (2002) reported that maternal effects decrease as time lapses post-weaning. The magnitude of present estimates was higher than some past estimates reported in the literature. The heritability estimates due to maternal effects on birth weight in order range between 0.03-0.82 in different breeds, 0.1 being the average (Mohiuddin, 1993). The average of c^2 on weaning weight is 0.13 respectively. Baker (1980) reported the average estimates of genetic parameters due to maternal effects on growth traits higher than those reviewed by Mohiuddin (1993). For example, the average of maternal heritability reported by Baker (1980) is 0.19 for birth weight and 0.30 for weaning weight. Contrary to previous literature in general, maternal heritabilities were higher than additive heritabilities, indicating that growth traits were determined more by the environmental conditions than by those of the genetic characteristics of the calf. However, the pattern of estimates are in agreement with others, where they are highest for birth and weaning weights, followed by yearling, implying importance of maternal effects for birth and weaning weights rather than others. Difficulties in separating additive genetic (both additive and maternal) and environmental maternal effects (Willham, 1972 and Meyer, 1992) using field data continue to exist. Meyer (1992) concluded that when only one of these effects (maternal genetic or permanent environmental) is considered in the model of analyses, most of maternal variation is likely to be accounted for. In many situations, the knowledge of the behaviour of total maternal effects (genetic plus permanent environmental) at early ages, obtained by univariate analyses can be of interest and may represent the best compromise (Albuquerque and Meyer, 2001). Considering the difficulties in obtaining reliable estimates of the correlation between additive and maternal genetic effects, in the present study, this correlation was assumed to be zero.

Several strategies may be used for obtaining "better" estimates. One could be to use larger, more carefully selected data. Another strategy would be to use functions other than polynomials that are less susceptible to artifacts i.e. fractional polynomials as applied by Robert-Granié et al. (2002, 2004). In yet another strategy, multiple-trait (MT) parameters could be "smoothed" and converted to an RRM scale (Lidauer et al., 1999). Misztal et al. (2000) have described the so-called "constructive approach" for artifact-free estimates of parameters by RRM. Other studies have applied parametric covariance structures, such as structured ante-dependence models, to longitudinal data to eliminate this problem (Albuerque and Meyer, 2004; Meyer, 2001).

5.5. Conclusion

In conclusion, the sire model seemed to be the simplest and best performing (stable) model. Interestingly, management variation was fairly high, emphasising the importance of management effects. Estimates of environmental effects on growth curves and of individual variation of parameters could be used for the modelling of pre-weaning and post-weaning calf performance in simulations of management alternatives. The low genetic variances and consequently low heritability estimates obtained for all traits indicate the need for improved and uniform animal management over years to increase the precision of parameter estimates as well as animal performance. Results in this study should be viewed as trends rather than absolute values, and no definite "true" parameters should be expected.

The second part of the thesis is concerned with prediction of carcass quality from growth measurements. The work described in the current chapter was aimed at providing estimation of growth measurement parameters, which are needed to develop the predictive model. The next chapter applies similar models to the carcass quality traits.

Chapter 6

Multivariate models for analysis of carcass quality traits

6.1. Introduction

Beef producers face the challenge of using diverse resources to produce cattle that are profitable to all segments of the industry and to produce meat products that target consumer demand (Marshall, 1994). To accomplish these goals, producers and breeders need information from a broad spectrum of marketing end points to implement effective breeding and management plans. The information required includes genetic and non-genetic (co)variation for all economically important traits of interest. In this chapter estimation of genetic and non-genetic (co)variation for four economically important carcass quality traits is presented through the multi-trait models. Practically, there are some advantages in estimating variance components from a multi-trait model instead of separate uni-variate models, especially in breeding programme. Generally, carcass quality traits used for animal breeding programs are correlated, so that considering only one trait will likely result in a physiological imbalance for instance (Wheeler et al., 1994). Therefore, it makes sense to analyse those traits together.

6.2. Statistical method

Multivariate sire and animal models were fitted using ASREML (Gilmour et al., 2000), estimating multi-trait (co)variance components including genetic and non-genetic parameters of carcass quality traits (Table 6.1). Variation in the four carcass quality traits (HCWt, P8, EMA and IMF) was considered in terms of the same fixed and random factors as the growth models. The following mixed model was fitted using REML:

$\text{Ln (carcass)} = X\tau + Z\mathbf{u} + \mathbf{e}$

where τ is the vector of fixed effects

$\mathbf{u}$ is the vector of random effect

$\mathbf{e}$ is the vector of random residual effect (temporary environmental effect or measurement error), NID $(0, \sigma^2)$.

The structure of the model follows similar lines to the growth model. However, this is a multivariate model with traits measured once (at slaughter).

The model considered partitions the variability in each carcass quality trait into its genetic (sire or animal), maternal, management groups and environmental components. For carcass traits, permanent environment is confounded with the temporary environment because there is only one measurement for each animal, therefore it is called “environmental” component. All components were estimated by fitting the multi-trait model except for the maternal variance of P8 fat and the maternal covariance between P8 fat and carcass weight (in animal model) because the model failed to converge when they were included.

6.3. Results

Summary descriptions of the fitted sire and animal models are given in Table 6.1. The residual variation of the sire model was smaller than the animal model. But, the log likelihood of the sire model was higher than the animal model. Hence, based on the above criteria, the sire model seemed to be the best performing (stable) model (Table 6.1).

Table 6.1. Summary descriptions of the sire and animal carcass models

	Sire	Animal
Loglikelihood (random+fixed effects)	5088.10	4974.08
Loglikelihood (fixed effect)	4601.46	4601.46
Number of model parameters[a]	40	40
Number of observations	1141	1141
Number of fixed effects	4	4
Error variance	0.26	0.28

[a]number of variance components,

Estimated means and standard errors of different effects for carcass quality traits are presented in Table 6.2. Sire breed, sex, and slaughter age nested within sex were significant for all traits (Table 6.2). Estimated means and confidence intervals for carcass traits resulting from a multi-trait sire model are shown in Table 6.3. Predictably, carcass weights of South Devon, Belgian Blue and Limousin and unexpectedly, Angus were the heaviest on the average (Table 6.5 and Figure 6.3). It also illustrated that Hereford calves were intermediate, and Jersey and Wagyu were lighter on the average than others (Figure 6.1). A rather similar pattern followed for EMA. Similar patterns were observed for fat traits (Figure 6.1). With respect to fat traits, roughly three groups were detected. First, carcasses of the Belgian Blue and Limousin had low P8 and IMF, second carcasses of Hereford and South Devon were intermidiate and third Angus, Jersey and Wagyu had high P8 and IMF. Interesting results observed for Angus crosses in where they exhibited highest P8, IMF as well as HCWt amongst breeds (Figure 6.2). In the current study, much of the difference among carcass traits in muscle mass and fat traits may have been due to breed effects.

Table 6.2. Estimated mean and standard error of the fixed effects derived from the multi-trait carcass model

Effects	HCWt		P8		EMA		IMF	
Fixed								
Constant	5.77	±0.02	2.72	±0.08	4.24	±0.03	1.36	±0.01
Sex.slage (Heifer-Steer)^{a***}	0.04	±0.03	0.36	±0.04	1.20	±0.08	1.47	±0.13
Sex***								
Sex (Steer)	0.42	±0.02	0.56	±0.03	0.56	±0.08	-0.22	±0.12
Sex (Heifer)	-0.41	±0.01	-0.29	±0.02	-0.13	±0.01	-0.29	±0.02
Sire breed ^{a***}								
JxH	-0.13	±0.02	-0.12	±0.06	-0.06	±0.02	0.23	±0.05
WxH	-0.10	±0.02	-0.06	±0.06	0.01	±0.02	0.17	±0.05
AxH	0.05	±0.02	0.15	±0.06	0.05	±0.02	0.22	±0.05
SxH	0.05	±0.02	-0.21	±0.06	0.11	±0.02	0.04	±0.05
LxH	0.04	±0.02	-0.18	±0.06	0.15	±0.02	-0.15	±0.05
BxH	0.07	±0.02	-0.38	±0.06	0.21	±0.02	-0.22	±0.05

[a] Sex.sla. age, slaughter age nested within sex, [b] Management groups include location, year and post-weaning groups combination, ***P<0.001

Table 6.3. Median and confidence intervals (CI, 95%) for carcass traits resulting from the multi-trait carcass model

Breed	HCWt (kg)	±CI[a]	P8 (mm)	±CI	EMA (cm^2)	±CI	IMF (%)	±CI
JxH	236.98	223.12	11.68	10.85	61.15	59.66	4.25	3.82
		232.63		12.51		62.63		4.67
WxH	240.44	231.38	12.42	11.57	65.49	63.96	3.98	3.59
		240.84		13.26		67.03		4.38
HxH	265.52	254.56	13.16	12.17	65.16	63.50	3.37	3.02
		265.90		14.14		66.81		3.72
AxH	283.55	268.87	15.28	14.18	68.68	67.00	4.21	3.78
		280.47		16.38		70.37		4.63
SxH	278.85	269.11	10.67	9.93	72.71	70.96	3.50	3.15
		280.35		11.41		74.46		3.86
LxH	275.15	264.83	10.94	10.19	75.33	73.55	2.89	2.60
		275.77		11.70		77.11		3.18
BxH	287.82	273.97	8.99	8.37	80.19	78.27	2.70	2.43
		285.34		9.62		82.11		2.97

[a] Lower and upper Confidence intervals

Figure 6.2 illustrates the percentage deviation of estimated average carcass traits of crossbreds from purebred Herefords. South Devon, Belgian Blue and Limousin calves had higher and Jersey and Wagyu lighter HCWt and EMA than Hereford calves, as expected. Angus cross calves were higher for P8 fat than Hereford. Jersey had highest and Belgian blue lowest IMF deviations from Hereford (Figure 6.2). On the contrary, as might be expected, the Belgian blue had the highest and Jersey the lowest EMA deviations from Hereford.

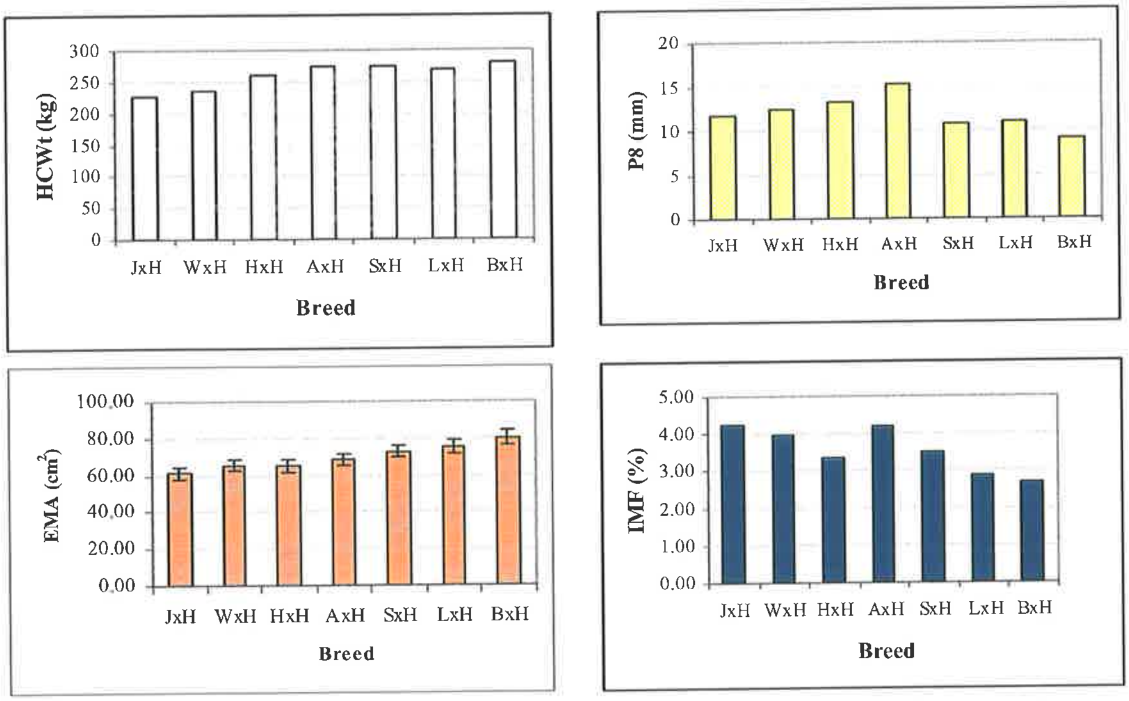


Figure 6.1. Median and confidence intervals (CI, 95%) of carcass quality traits for seven sire breeds

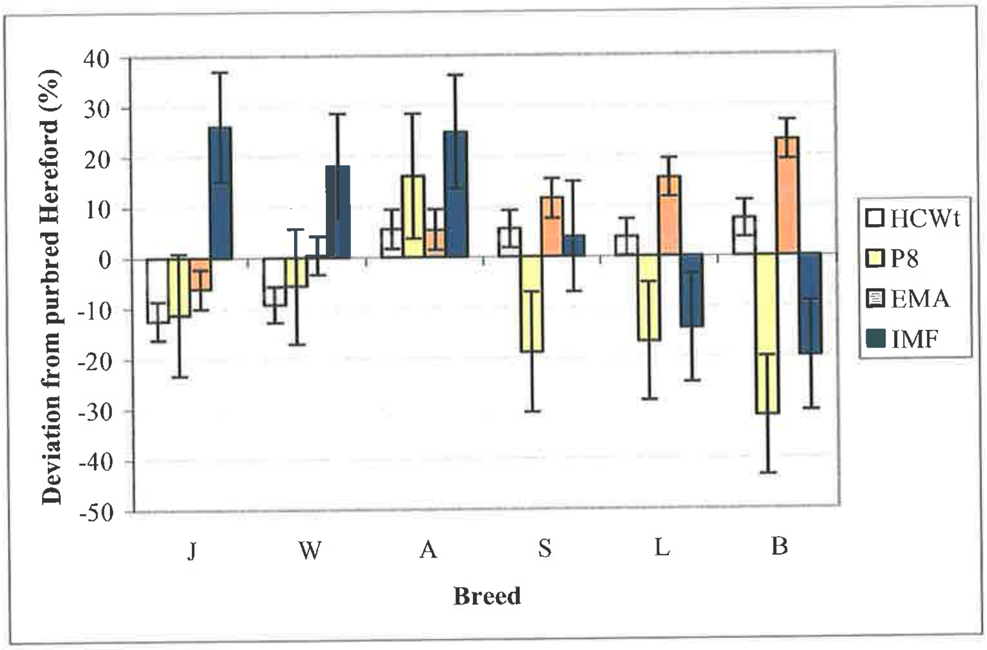


Figure 6.2. Deviation of the median of carcass quality traits for six crossbreds from purebred Hereford

Genetic and non-genetic (co)variance components

Multi-trait models were postulated for Sire (and Animal), Maternal, environmental and Management effects. Fortunately, in all cases the data support inclusion of all terms. Table 6.4 presents 40 (co)variance components that were able to be fitted by the multi-trait sire model.

Table 6.4. Estimated variances (on diagonal) and covariances (off diagonal) components for carcass traits obtained from the the multi-trait sire carcass model

	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28
HCWt (kg)																
13. Sire (animal)	✓															
14. Maternal		✓														
15. Management			✓													
16. Environment[a]				✓												
P8 (mm)																
17. Sire (animal)	✓				✓											
18. Maternal		✓				✓										
19. Management			✓				✓									
20. Environment				✓				✓								
EMA (cm^2)																
21. Sire (animal)	✓				✓				✓							
22. Maternal		✓				✓				✓						
23. Management			✓				✓				✓					
24. Environment				✓				✓				✓				
IMF (%)																
25. Sire (animal)	✓				✓				✓				✓			
26. Maternal		✓				✓				✓				✓		
27. Management			✓				✓				✓				✓	
28. Environment				✓				✓				✓				✓

[a]For carcass traits environment component = PE + TE

The relative contributions of variance components to the total variance of carcass traits are shown in Figure 6.3. Four independent components: additive genetic, maternal, management and error components were estimated for each carcass quality trait in both the sire and animal models. As in previous chapter, the management variance has not been included in the calculation of phenotypic variance. Overall, 81-96% (in the sire model) and 69-92% (in the animal model) of the total variances in carcass quality traits was non-genetic. Management variation was considerable and accounted for about 28-57% (in sire model), 29-51% (in animal model) of the total variance (Figure 6.3). The residual or error variance accounted for roughly half of the variation in carcass quality traits. The sire variation represented in Figure 6.4 was about 6%, 6%, 4% and 2% of total variation for sire model. The sire component describes ¼ of the genetic variance. The additive variation ranged from 8% to 26% of all variation of carcass quality traits. As illustrated a large proportion of the phenotypic variance, especially for EMA and IMF, are non-genetic (Figure 6.3).

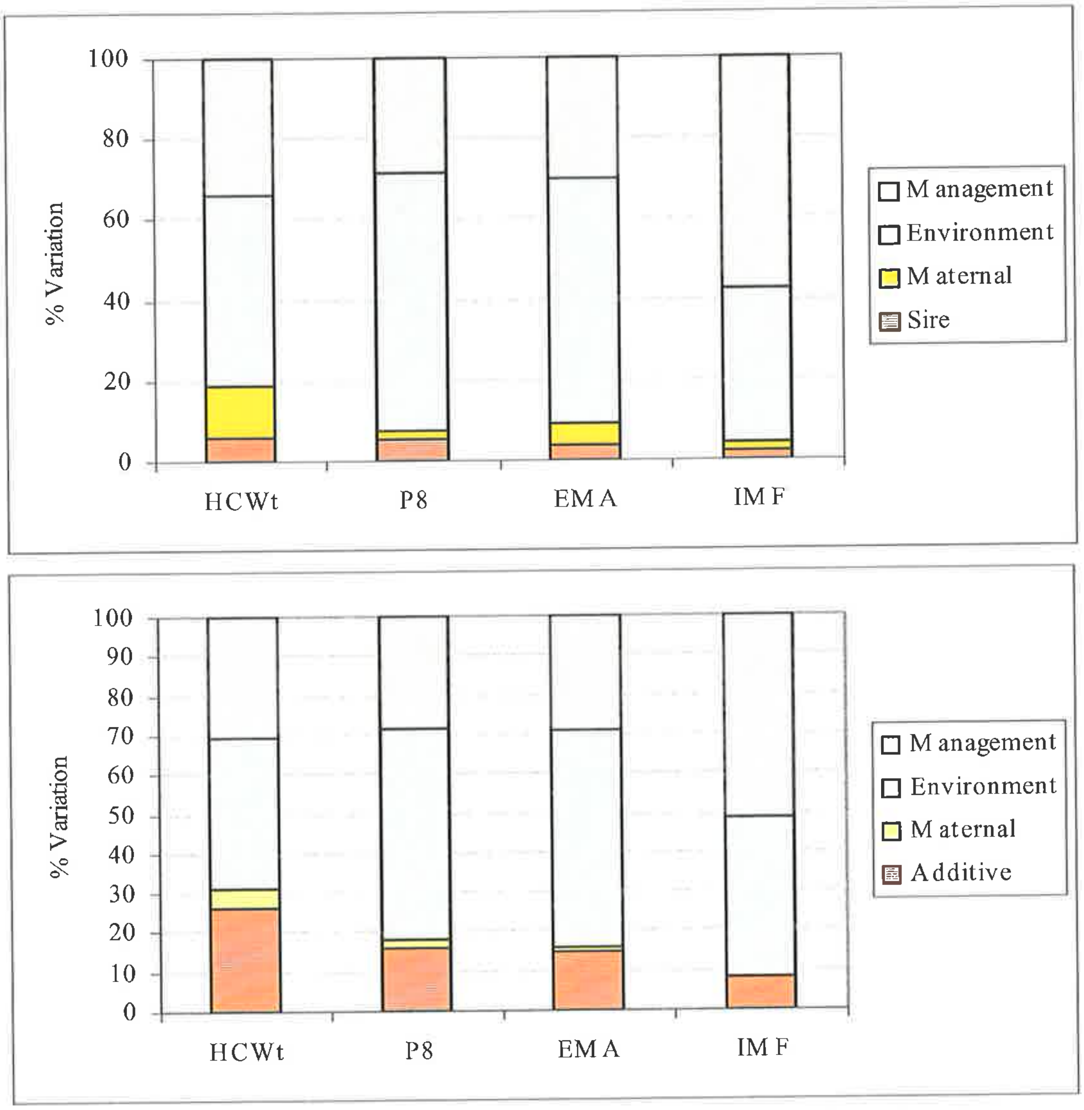


Figure 6.3. Variance components of carcass traits as the proportion of total variance derived from the sire (top) and animal (bottom) models

Tables 6.5 shows the sire variance components for carcass traits derived from the multivariate model. The sire covariance between the fat traits was lower than expected in both models. However, the sire covariance between the quantity traits (HCWt and EMA) was as might be expected (Table 6.5). The sire covariance between EMA and IMF was negative. Estimated maternal (genetic and environmental) variance components for carcass traits are presented in Table 6.5. As expected, the maternal covariance component was low for all carcass traits. The maternal components in the animal model were lower than sire model (Table 6.5). Estimates of management (co)variances are reported in Table 6.5. The management covariance between all carcass traits were reasonably high which means environment had a big effect on the relationships between carcass traits. The management variances and covariances observed in the sire model were slightly higher than the animal model (Table 6.5). The variance and covariance of the environment for carcass traits were higher than genetic and maternal components (Table 6.5). Among the carcass traits considered, environmental variances for P8 fat and IMF were higher than others (Table 6.5).

Table 6.5. (Co)variance components* of carcass quality traits derived from the multi-traits sire and animal models

	Sire model				Animal model			
	HCWt	P8	EMA	IMF	HCWt	P8	EMA	IMF
Sire								
HCWt	**0.86**				**3.60**			
P8	-0.37	**10.47**			-1.47	**30.78**		
EMA	0.60	-1.14	**0.79**		2.45	-3.54	**3.21**	
IMF	-0.17	1.93	-0.86	**5.22**	-0.66	4.33	-3.44	**18.40**
Maternal								
HCWt	**1.82**				**0.65**			
P8	1.26	**3.89**			0.14	**4.33**		
EMA	0.70	0.37	**1.22**		0.00	0.10	**0.32**	
IMF	0.39	-1.40	-0.54	**5.05**	0.02	-0.28	0.04	**0.03**
Management group								
HCWt	**4.86**				4.23			
P8	11.60	**52.50**			11.30	**56.00**		
EMA	5.16	15.70	**6.69**		4.79	15.80	**6.48**	
IMF	21.50	17.90	18.30	**140.60**	17.50	14.10	16.20	**115.10**
Environment								
HCWt	**6.70**				5.28			
P8	6.92	**119.10**			8.52	**104.20**		
EMA	4.36	1.68	**13.55**		3.19	3.19	**12.20**	
IMF	3.11	10.30	-0.12	**94.10**	5.13	11.00	1.71	**90.50**

* Note that all variables were log transformed, slaughter age was in years, and these components have been multipled by 10^3 to ease reporting.

EMA and IMF was negative. Estimated maternal (genetic and environmental) variance components for carcass traits are presented in Table 6.5. As expected, the maternal covariance component was low for all carcass traits. The maternal components in the animal model were lower than sire model (Table 6.5). Estimates of management (co)variances are reported in Table 6.5. The management covariance between all carcass traits were reasonably high which means environment had a big effect on the relationships between carcass traits. The management variances and covariances observed in the sire model were slightly higher than the animal model (Table 6.5). The variance and covariance of the environment for carcass traits were higher than genetic and maternal components (Table 6.5). Among the carcass traits considered, environmental variances for P8 fat and IMF were higher than others (Table 6.5).

Table 6.5. (Co)variance components* of carcass quality traits derived from the multi-traits sire and animal models

	Sire model				Animal model			
	HCWt	P8	EMA	IMF	HCWt	P8	EMA	IMF
Sire								
HCWt	**0.86**				**3.60**			
P8	-0.37	**10.47**			-1.47	**30.78**		
EMA	0.60	-1.14	**0.79**		2.45	-3.54	**3.21**	
IMF	-0.17	1.93	-0.86	**5.22**	-0.66	4.33	-3.44	**18.40**
Maternal								
HCWt	**1.82**				**0.65**			
P8	1.26	**3.89**			0.14	**4.33**		
EMA	0.70	0.37	**1.22**		0.00	0.10	**0.32**	
IMF	0.39	-1.40	-0.54	**5.05**	0.02	-0.28	0.04	**0.03**
Management group								
HCWt	**4.86**				4.23			
P8	11.60	**52.50**			11.30	**56.00**		
EMA	5.16	15.70	**6.69**		4.79	15.80	**6.48**	
IMF	21.50	17.90	18.30	**140.60**	17.50	14.10	16.20	**115.10**
Environment								
HCWt	**6.70**				**5.28**			
P8	6.92	**119.10**			8.52	**104.20**		
EMA	4.36	1.68	**13.55**		3.19	3.19	**12.20**	
IMF	3.11	10.30	-0.12	**94.10**	5.13	11.00	1.71	**90.50**

* Note that all variables were log transformed, slaughter age was in years, and these components have been multipled by 10^3 to ease reporting.

Estimates of heritabilities (h^2), phenotypic (r_P) and genetic (r_G) correlations between carcass quality traits are shown in Tables 6.6. These correlations were based on a constant (adjusted) slaughter age. All phenotypic correlations were positive, although not large. The largest phenotypic correlations were for HCWt and EMA. HCWt was lowly correlated with IMF, moderately correlated with P8, and highly correlated with EMA. P8 was lowly correlated with IMF and moderately correlated with EMA (Table 6.6). EMA was lowly correlated with IMF. Some genetic correlations were different to phenotypic correlations. Hot carcass weight was highly positively correlated genetically with EMA (0.73) as expected, slightly negatively correlated genetically with P8 fat, and moderately genetically correlated with intramuscular fat. The genetic correlation between the two fat depots was not as high (0.18) as expected. EMA was negatively genetically correlated with intramuscular fat (-0.43). The genetic correlations between carcass longissimus muscle area and carcass fat thickness was -0.08 (Table 6.6).

Table 6.6. Estimates of heritabilities (h^2), phenotypic (r_P) and genetic (r_G) correlations between carcass quality traits derived from the multi-traits sire and animal models

	Sire model				Animal model			
	HCWt	P8	EMA	IMF	HCWt	P8	EMA	IMF
HCWt	**0.37**	0.38	0.61	0.26	**0.38**	0.36	0.60	0.24
P8	-0.12	**0.31**	0.42	0.13	-0.14	**0.22**	0.40	0.14
EMA	0.73	-0.08	**0.20**	0.23	0.72	-0.08	**0.20**	0.21
IMF	-0.40	0.26	-0.43	**0.20**	-0.36	0.18	-0.45	**0.17**

Heritability (h^2) on diagonal, Phenotypic correlations above diagonal,
Genetic correlations below diagonal

Table 6.7 shows the estimates of the maternal, environmental (PE+TE) and management correlations between carcass traits. Maternal effects were low for carcass traits. Management correlations were very high for most traits (except between P8 and IMF). In general, management correlations were higher than random environmental correlations.

Similar patterns to the genetic correlations were observed for management correlations between fat traits and quantity traits. Management correlation between HCWt with P8 (0.72) and IMF (0.84) were higher than the corresponding genetic correlations. HCWt had the highest association among carcass traits with EMA (0.91). There was a high positive management correlation (0.82) observed between P8 and EMA (Table 6.7). The value and direction of the correlation between EMA and IMF for management component (0.60) was different from that in the genetic correlation (-0.43). In general, management correlations were high between all traits except P8 and IMF where the correlation was only 0.21 (Table 6.7). Most of these correlations obtained from sire model were consistent with coefficients derive from the animal model (Table 6.7).

Table 6.7. Estimates of maternal, environmental and management correlations between carcass quality traits derived from the multi-traits sire and animal models

	Sire model				Animal model			
	HCWt	P8	EMA	IMF	HCWt	P8	EMA	IMF
HCWt	0.19	0.25	0.46	0.04	0.07	0.36	0.40	0.09
P8	**0.72**	0.03	0.12	0.10	**0.73**	0.03	0.23	0.11
EMA	**0.91**	**0.82**	0.08	0.00	**0.92**	**0.79**	0.02	0.05
IMF	**0.84**	**0.21**	**0.60**	0.05	**0.83**	**0.18**	**0.59**	0.00

Maternal effect on diagonal, Environmental correlations above diagonal
Management correlations below diagonal (bold)

6.4. Discussion

Multi-trait mixed sire and animal models were conducted to estimate variance, covariance of four economically important carcass traits. Random effects accounted for considerable proportions of total variation and caused much improvement in reducing error variance for both models. Results of analysis indicated that non-genetic variation accounted for more than half of total variations of carcass quality traits. Likewise, management variation was considerably higher than other components. Results related to breed comparisons illustrated that at the point of slaughter, carcasses of Jersey and Wagyu (as early-maturing breeds) were lighter than South Devon, Belgian Blue and Limousin (as late-maturing breeds) breeds. Heavier carcasses tended to have greater EMA and less P8 and IMF than lighter carcasses. Koch et al. (1976) and Gregory et al. (1994) stated that carcasses of large-framed steers (South Devon, Belgian Blue and Limousin crosses) had less fat at the 12th /13 th rib interface than carcasses of either smaller medium-framed steers (i.e. Angus, Hereford, Jersey and Wagyu crosses) at any given feeding period. Summarizing the Meat Animal Research Center Germ Plasm Evaluation study, Marshall (1994) indicated that generally, smaller-framed breeds of cattle tend to yield carcasses with higher degrees of marbling on an age-constant basis. This was due to more muscling and less fat in the late–maturing breeds.

Historically, carcass traits have been reported as being moderately to highly heritable (Koots, et al., 1994a; Marshall, 1994). In the current study carcass traits indicated low to moderate heritability. Heritability estimates in the current study were computed at a constant age for carcass quality traits. Nowadays, meat scientists work "at a constant weight", while animal breeders work "at a constant age". Although age is seldom the primary criterion determining slaughter date in today's production systems, most breed associations currently adjust carcass traits to a constant age when computing breeding values or expected progeny differences (Shanks et al., 2001). Koch et al. (1995) notice that slaughter end point can alter the expression of genetic and environmental differences; however, Shanks et al. (2001) observed that in general, adjustment to different slaughter end points had minor effects on phenotypic correlations. They also concluded that genetic evaluations of carcass traits conducted on an age-, weight-, or marbling-constant basis produced similar rankings. Amer et al. (1994), Wilton and Goddard (1996a, 1996b) and Wilton (2003) concluded that when management variables are optimized, economic weights are equivalent regardless of the end point considered. This means that economic weights and selection indexes can be conveniently calculated for age constant end points even though commercial production may use weight or fat depth constant slaughter end points.

Carcass weight derived from the current animal model was moderately heritable (0.38), in accordance with several previous studies (Koots et al., 1994a; Marshall, 1994; Shanks, 2001; Bertrand et al., 2001; Pitchford et al., 2002; AAABG, 2004). In contrast, Cundiff et al. (1971), Koch (1978), and MacNeil et al. (1984) found carcass weight to be highly heritable and Wheeler et al. (1996) found it to be lowly heritable. Differences between heritabilities for carcass traits based on age and weight covariates were small, in agreement with Cundiff et al. (1971), Veseth et al. (1993) and AAABG (2004). Shanks et al. (2001) obtained weight-constant heritabilities of 0.22 and 0.14 for EMA area and fat depth, respectively, which are smaller than those published by Cundiff et al. (1971), Wilson et al. (1976), and Arnold and Bennett (1991).

The heritability estimate for P8 (0.22) was similar to those reported by Wilson et al. (1993); Gregory et al. (1995); Robinson et al. (1998); AAA (2000). However, it was smaller than some estimates reported (Koots et al., 1994a; Marshall, 1994; Bertrand et al., 2001; AAABG, 2004).

Heritability for EMA (0.20) was in agreement with several previous findings as reported in reviews by Koots et al. (1994a), Marshall (1994) and Shanks et al. (2001). Also the estimated value is not far from the estimates reported by Gregory et al. (1995) and AAA (2000). However, moderate to high range estimates have been reported (Bertrand et al., 2001, AAABG, 2004).

For IMF, the heritability estimate (0.17) was generally smaller than marbling score, summarized by Koots et al. (1994a), Marshall (1994), Bertrand et al. (2001), and AAABG, (2004). The heritability estimate for IMF in this study agreed favorably with those published for marbling score by Woodward et al. (1992) and Robinson et al. (1998) who reported a heritability of 0.23 and 0.15 respectively. Estimates of genetic parameters of marbling are dependent upon the method used to measure the trait, the method of finishing cattle, and age and weight at the time of measurement. In a data set where different measures of marbling were made on the same carcasses, the estimate of heritability of marbling assessed by the Australian AusMeat system was 0.15, compared to 0.32 for the Meat Standards Australia and USDA system, and 0.43 for measure of intramuscular fat by chemical extraction from the visually assessed site (Johnston, 1999).

In general, specific correlations estimated here were quite similar between sire and animal models. All significant correlations in sire model were of the same direction and magnitude as corresponding values in the animal model. All phenotypic correlations were positive and the largest was between HCWt and EMA.

The phenotypic correlations between HCWt-P8 fat, HCWt-EMA and HCWt-IMF obtained from animal model, herein, were 0.36, 0.60 and 0.24, respectively and their corresponding genetic correlations averaged across all the studies were 0.32, 0.41 and 0.09, respectively (Bertrand et al., 2001, AAABG, 2004). Similar estimates between carcass weight and fat thickness have been found by other researchers (Koch, 1978; Lamb et al., 1990).

The phenotypic correlations between carcass weight and eye-rib area was moderate and large (0.60), in agreement with the finding of Cundiff, et al. (1971), Lamb et al. (1990) and Owens and Gardner (1999) who observed that longissimus muscle area increased as carcass weight increased. Owens and Gardner (1999) concluded that the covariance adjustment of longissimus muscle area for only carcass weight is invalid. They explained that the decrease in longissimus muscle area in relation to carcass weight may stem from several factors. "First, longissimus muscle area is a surface measurement, whereas carcass weight is volumetric, and longissimus muscle length may increase without a change in surface area. Second, muscle size may reach a plateau (maturity) before body weight, reflecting the natural progression from lean to fat deposition with maturity".

Lamb et al. (1990) and Koots et al. (1994b) reported correlations of 0.27 and 0.15 between carcass weight and marbling score. Owens and Gardner (1999) also reported that fat thickness and marbling scores increased slightly with carcass weight.

The phenotypic correlations between P8-EMA and P8-IMF were 0.40 and 0.14, respectively. However, the phenotypic correlations of marbling with fat thickness reported consistently in the direction of an antagonism and were small to moderate in magnitude (Gilbert et al., 1993; Koots et al., 1994b; Marshall, 1994; Pitchford et al., 2002), averaged -0.14 (Bertrand et al., 2001; AAABG, 2004). The phenotypic correlation between EMA and IMF was, 0.21 in agreement with Lamb et al. (1990).

The average phenotypic association between EMA and IMF reported is 0.07 (Bertrand et al., 2001; AAABG, 2004).

The genetic correlation between HCWt and P8 fat depth was low and negative (-0.14). Shanks et al. (2001) also found similar correlation on age-constant basis. Based on studies reviewed by Koots et al. (1994b) and Marshall (1994), there is considerable evidence that the genetic correlation between HCWt and P8 fat depth is positive in British cattle on an age-constant basis. In two studies that included both British and Continental breeds, the correlation between HCWt and P8 fat depth was smaller, though still positive (0.13) (Gregory et al., 1995; Crews and Kemp, 1999).

The most notable relationship was between carcass weight and EMA which are highly genetically correlated (0.72), indicating that selection for higher carcass weight should also lead to greater EMA. In a comparison among crossbreeds used in this study with the pure breed Hereford, Limousin crosses had less intramuscular fat and higher EMA, and Jersey crosses had low EMA but high IMF. Previous estimates for the genetic correlation between EMA and HCWt on an age-constant basis ranged from 0.02 to 0.80 (Koots et al., 1994b; Marshall, 1994; Bertrand et al., 2001; AAABG, 2004).

The genetic correlation between P8 fat and IMF was positive but lower than expected, consistent with the averaged estimate reviewed by Bertrand et al. (2001) and AAABG (2004), indicating opportunity to make improvement in both traits, i.e. decreased P8 fat depth and increased IMF, thus causing a change in fat distribution rather than total fatness *per se*. Pitchford et al. (2002) with the same data set as that herein with respect to relationships between P8 and IMF implied that there appears to be prospect to select breed combinations that enable IMF to be maximized relative to subcutaneous. On an age-constant basis, other researchers have found the association to be high and positive (Dunn et al., 1970; Koch, 1978; Lamb et al., 1990), moderate and positive (Dinkel and Busch, 1973; Koch et al., 1982; Gregory et al., 1994, 1995), near zero (Wheeler et al., 1996), or low and negative (Wilson et al., 1976). At a constant weight, P8 fat depth and marbling score were positively correlated (Wilson et al., 1976; Arnold and Bennett, 1991).

The genetic correlations between P8 fat and EMA was -0.08 (Table 6.5), tend to agree with several studies conducted at a constant age, whereas other studies have reported stronger negative relationships between P8 fat and EMA (Koots et al., 1994b; Marshall, 1994). Studies conducted at a constant weight (Wilson et al., 1976; Arnold and Bennett, 1991) or constant fat thickness (Gilbert et al., 1993) also found larger negative correlations. Brackelsberg et al. (1971) suggested a small negative association between EMA and fat thickness on a marbling-constant basis. Moser et al. (1998) cited an estimate for the relationship between longissimus muscle area and fat depth, in Brangus seedstock, of -0.05. This indicates that selecting for a decrease in fat thickness would correspond to selection for an increase in EMA. However, this result was lower than that of reported by Koots et al. (1994b). Arnold and Bennett (1991) summarized that selection for a decrease in fat thickness was related to larger EMA and a reduction in marbling. Therefore, it is important to take more than one carcass trait into consideration when selecting sires for genetic improvement.

This result exhibits a negative genetic relationship between EMA and IMF in agreement with the literature (Koots et al., 1994b; Marshall, 1994; van der Werf et al., 1998), but Lamb et al. (1990), Veseth et al. (1993), Shanks et al. (2001) found positive values. Studies based on constant quality grade (Brackelsberg et al., 1971) or weight (Wilson et al., 1976; Arnold and Bennett, 1991) also reported negative correlations between EMA and marbling score. However, at a fat-constant end point, Gilbert et al. (1993) and Wulf et al. (1996) found positive correlations. The negative genetic correlation between these traits indicates that high marbling is generally associated with unfavourable genetics for carcass muscularity.

Beef cattle grow, develop, mature, and fatten at different chronological ages, and the differences among individuals are often discussed in terms of physiological maturity (e.g., Berg and Butterfield, 1976). Therefore, further investigation seems necessary to determine the effects of maturity or mature size on the correlation between carcass traits. Aass (1996a, 1996b) and Piles et al. (2000) suggested that breeds might differ in carcass composition and meat quality at the same market weight due to differences in degree of maturity.

It should be noted that consistent estimation of genetic parameters requires good data, i.e. sufficient amounts of reliable measurements and good pedigree structure (Meyer and Kirkpatrick, 2004c). The wide range of reported estimates seems to indicate that the genetic relationships among carcass traits may vary with the breed or population, or simply may be due to sampling variance because most studies, including this study, have relatively few observations. Differences in the model used and the use of age- weight- and fat-constant end points may have caused these differences. Therefore, the genetic relationships reported in other studies are hardly extrapolated to the current discussion. Genetic comparisons are only logical if the cattle are treated similarly. Overall, management relationships among carcass traits reported herein were higher than the genetic associations among them.

However, estimates of genetic correlations for carcass traits suffered from the small number of records available for these traits and problems associated with a sample of sires that might not have been fully representative of the population for these traits.

Hence,- Estimates involving these traits should hence be regarded with caution, and estimation should be repeated when more data for these traits become available.

6.5. Conclusion

Management variation contributed a large proportion of the total carcass variation. Knowledge about the non-genetic determinant of carcass quality traits would be of interest for optimising management practices to meet market specifications. Comparatively, the error variance and log likelihood of both sire and animal models indicated a better fit for the sire model, hence, the sire model was selected for joint analysis (Chapter 7). Analysis also revealed that specific correlations were quite similar between the two models.

Results from this study suggest that strategies to increase genetic potential for HCWt, which is the greatest determinant of carcass value at a constant age at slaughter, would increase the genetic potential for EMA but may reduce marbling and tend to slightly increase P8. A slight genetic antagonism may exist between EMA and marbling. Today in the beef industry, a major goal for beef cattle breeding seems to be to maximize muscle tissue and minimize fat. To this end, any strategies that maximize profit need to balance genetic potential for carcass yield with adverse correlated changes in the quality of the product. Therefore, it is important to take more than one carcass trait into consideration in the analysis of carcass quality when selecting sires for genetic improvement. In general, selection for carcass weight, carcass fatness, longissimus muscle area, and marbling could yield genetic progress. Selection for improved carcass quality might be possible without sacrificing lean growth.

The work described in this chapter provided estimates of carcass quality parameters required for building a predictive model. The next chapter of this thesis deals with the joint modeling of growth and carcass quality traits, which is the ultimate step for building a comprehensive predictive model.

6.6. Connection between multi-trait mixed model and PCA

So far the phenotypic principal component analysis (Chapter 4) and multi-trait mixed model (current chapter) have been conducted to examine variation in carcass traits. PCA conducted in chapter 4 lacked the fixed effects (e.g., breed and sex) adjustments incorporated in the multi-trait mixed model so that the correlation structure and variation involving these traits should be regarded with caution. Hence, it would be worthwhile conducting principal component analysis on estimated correlation structures for sire, maternal, management and environment obtained from multi-trait mixed model with the hope of obtaining quality information. The aim of this part is to investigate the decomposition of a square matrix (4×4) of the sire, maternal, management and environment into eigenvalues and eigenvectors (PCA) for the four carcass traits obtained from multi-trait mixed model. The determination of the eigenvectors and eigenvalues of those components aids in understanding the important sources of variation in carcass quality traits and to appreciate how the fitting of fixed factors affect the linear combinations of the original variables.

PCA results herein permit a description of the simultaneous or multivariate patterns of covariation among the various carcass quality traits within each variance components matrix. These eigenvectors were orthogonally rotated to facilitate more interpretable results, i.e. statistically independent vectors exhibiting either high or low eigenvector coefficients or few intermediate values. The four patterns of covariation (eigenvectors) summarize the common information among these four carcass quality traits.

PC1 and PC2 accounted for the major proportions of the total management variation (98%). The first eigenvector has large loading for HCWt, EMA, P8 fat and IMF respectively, presenting market suitability. The second orthogonal vector had a large coefficient for the P8 fat and IMF with different sign, indicating fat distribution.

PC1 and PC2 of contributed up to 77% of total sire and maternal variability. PC1 of sire component indicated a major contrast between quantity and fat traits. PC2 of sire component respects mean (weighted) values for carcass traits with less attention to EMA, presenting market suitability. The third component accounting, for 18% of the total variance, indicated a major contrast between P8 and IMF, consequently it can be interpreted as a fat distribution component (Figure 6.4).

PC1 of the maternal component was similar to the other components in major patterns of covariation among carcass quality traits, presenting market suitability. PC2 (28%) showed much more emphasis on the IMF (marbling characteristic). PC3 (20%) demonstrated contrast between P8 fat and EMA.

The first two principal component accounted for 65% of total environmental variation in considered carcass quality traits. PC1 of environment component, as in management, could be defined as a market suitability component. PC2 exhibited large value on fat traits, interpreted as a fatness component. PC3 PC1 could be defined as a fat distribution component, as in sire component.

The following points can be noticed from comparison between phenotypic (unadjusted) principal component analysis (Chapter 4) and the principal component analysis of the 4×4 sire, maternal, management and environmental (co)variance matrices derived from multi-trait carcass model (current chapter).

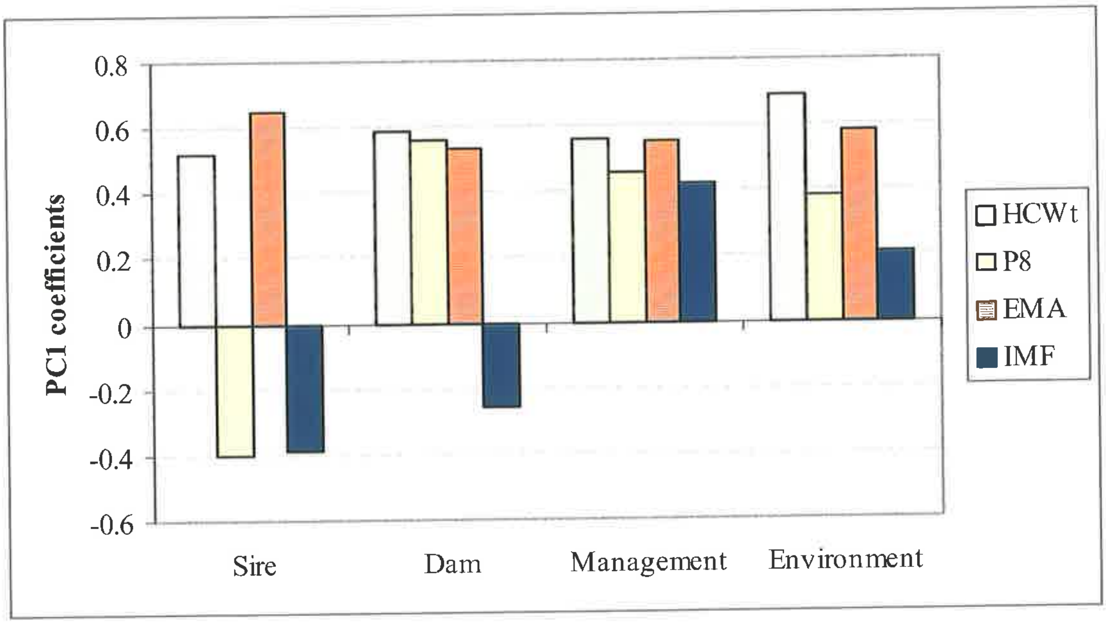
Overall, the first two principal components accounted for approximately 70% of total variation like the analyses conducted for heifers and steers (Chapter 4). As in steers

(Chapter 4), PC1 exhibited large correlations with HCWt, P8 fat and EMA. PC2 quite obviously correlated with fat traits (P8 and IMF), as observed in heifers (Chapter 4). PC3 of sire and environment components interpreted as a fat distribution component similar to heifers and steers. Generally some differences detected in variation of carcass traits herein might be due to the fixed effects adjustments, even though it was not as much as hypothesised. Moreover, some researcher reported that carcass traits in cattle may vary with genotype (Truscott et al., 1983; Kempster et al., 1986) and sex (Mukhoty and Berg, 1971; Johnson et al., 1994).

Table 6.8. The eigenvectors and eigenvalues of the sire, maternal, management and environmental components derived from 4x4 correlation matrices

	PC1	PC2	PC3	PC4
Sire				
HCWt	0.52	-0.62	0.00	-0.59
P8	-0.40	-0.50	-0.75	0.18
EMA	0.65	-0.17	-0.05	0.74
IMF	-0.39	-0.58	0.66	0.26
%variance	52	25	18	4
Maternal				
HCWt	-0.59	0.49	-0.12	0.64
P8	-0.56	-0.19	-0.65	-0.49
EMA	-0.53	0.09	0.74	-0.41
IMF	0.26	0.85	-0.15	-0.43
%variance	45	28	20	6
Management				
HCWt	-0.56	0.14	-0.35	0.74
P8	-0.46	-0.64	-0.44	-0.43
EMA	-0.55	-0.18	0.82	0.00
IMF	-0.42	0.73	-0.12	-0.52
%variance	77	21	2	0
Environment				
HCWt	0.69	-0.10	0.02	0.72
P8	0.38	0.50	-0.73	-0.27
EMA	0.58	-0.47	0.21	-0.63
IMF	0.21	0.72	0.65	-0.13
%variance	39	26	22	12

Values in bold are indicative of high loading values



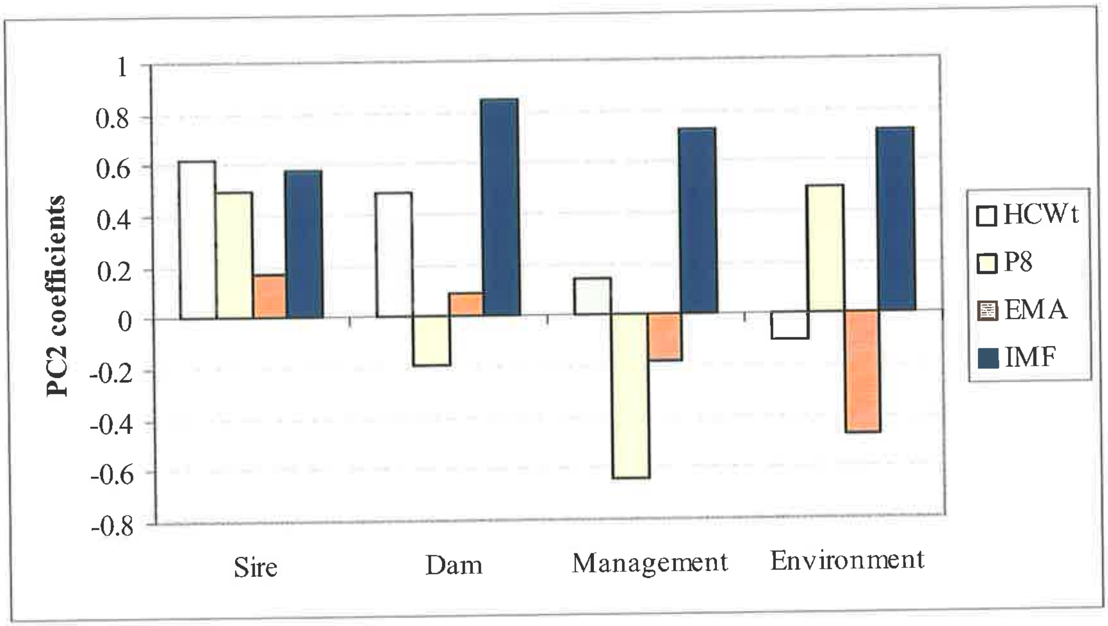


Figure 6.4. Comparisons amomg PC1 (top) and PC2 (bottom) of the sire, maternal, management and environmental components

Chapter 7

Joint modeling of growth and carcass quality

7.1. Introduction

Variability in the growth of cattle is important to the economic costs and returns of both the cattle producer and processor. The optimisation of cattle production systems including the evaluation of alternative management and marketing strategies requires knowledge of the variation in body weights, carcass traits and the association between them. A successful prediction of the carcass quality of cattle following specific growth path depends as much on a correct estimation of (co)variance components of its genotype parameters as on a detailed description of its environment (Chapters 5 and 6). These (co)variances and parameters have to be known because they are critically important for the model. It is then possible to use these models to estimate the correlations between growth and carcass quality traits over the entire growth period. Moreover, knowledge of these relationships will allow producers to optimise management practices to meet market specifications. In much of the published work, correlations between growth and carcass traits at specific (discrete) ages are provided (Koots, 1994a; Marshall, 1994; Bertrand et al., 2001; Mohiuddin, 1993) and essential information relating to estimation of correlations between longitudinal growth data and carcass quality traits is often lacking. Therefore, the main objective of this chapter was to estimate genetic and non-genetic correlations between longitudinal body weights and carcass quality traits using the joint growth-carcass sire models with random regression.

7.2. Statistical method

A joint growth-carcass sire model with random regression was conducted using ASREML (Gilmour, 2000) to estimate the correlations between genetic and environmental components of the body weights and carcass quality traits. The mixed model fitted was of the form

$$\mathbf{y} = \mathrm{X}\tau + \mathrm{Z}\mathbf{u} + \mathbf{e} \qquad \textbf{(7.1)}$$

where

X is the incidence matrix of fixed effects;

τ is the vector of fixed effects

Z is the incidence matrix for random effects;

u is the vector of random effects

e is the vector of random errors (temporary environmental effect or measurement error), NID $(0, \sigma^2)$.

The vector **y** contains both the growth and carcass measurements. The fixed effects are as for the individual analysis of growth and carcass traits. Thus

$$\mathrm{X} = \begin{bmatrix} \mathrm{X}_1 & 0 \\ 0 & \mathrm{X}_2 \end{bmatrix}$$

where X_1 is the design matrix for the growth fixed effects and X_2 is the design matrix for the carcass fixed effects.

The fixed effects fitted are listed in Table 7.1 and the final random effects fitted are listed in Table 7.2.

Table 7.1. Fixed effects and their degree of freedom (df) for the growth and carcass models

Growth model	df	Carcass model	df
Animal			
Breed	6	Breed	6
Sex	1	Sex	1
-	-	Sex. Slaughter age	2
Time			
Age	1	-	-
Age^2	1	-	-
Age^3	1	-	-
Animal.Time	1		
Breed.Age	1	-	-
Breed.Age^2	1	-	-
Breed.Age^3	1	-	-
Sex.Age	1	-	-
Sex.Age^2	1	-	-
Sex.Age^3	1	-	-

Table 7.2. Structure of random effects used in joint model. Estimated variance components on diagonal and covariances off diagonal from sire model. Ticks mark indicate the components that were able to be estimated

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28
Growth																												
1. Sire constant	✓																											
2. Sire linear	✓	✓																										
3. Dam constant			✓																									
4. Dam linear			✓	✓																								
5. Management constant					✓																							
6. Management linear					✓	✓																						
7. Management quadratic					✓	✓	✓																					
8. Management cubic					✓	✓	✓	✓																				
9. Residual between constant									✓																			
10. Residual between lin									✓	✓																		
11. Residual between qua									✓	✓	✓																	
12. Overall residual												✓																
Carcass weight (HCWt)																												
13. Sire	✓	✓											✓															
14. Dam			✓	✓										✓														
15. Management					✓	✓	✓	✓							✓													
16. Residual																✓												
Fat depth (P8)																												
17. Sire	✓	✓											✓				✓											
18. Dam			✓	✓										✓				✓										
19. Management					✓	✓	✓	✓							✓				✓									
20. Residual									✓	✓	✓					✓				✓								
Eye muscle area (EMA)																												
21. Sire	✓	✓											✓				✓				✓							
22. Dam			✓	✓										✓				✓				✓						
23. Management					✓	✓	✓	✓							✓				✓				✓					
24. Residual									✓	✓	✓					✓				✓				✓				
Intramuscular fat (IMF)																												
25. Sire	✓	✓											✓				✓				✓				✓			
26. Dam			✓	✓										✓				✓				✓				✓		
27. Management					✓	✓	✓	✓							✓				✓				✓				✓	
28. Residual									✓	✓	✓					✓				✓				✓				✓

In the model (7.1) we have for the ith animal

$\mathbf{u_i} \sim \mathrm{N}\,(\mathbf{0}, \mathbf{G})$

where $\mathbf{u_i}$ is the 16 X 1 vector of random effects, which consist of constant, linear, quadratic and cubic terms for each of the four component random effects (Sire, Maternal, Management and Permanent environmental).

The matrix **G** is of size 32x32 and has the form

$$\mathbf{G} = \begin{bmatrix} \mathbf{G}_{\mathbf{Sire}} & 0 & 0 & 0 \\ 0 & \mathbf{G}_{\mathbf{M}} & 0 & 0 \\ 0 & 0 & \mathbf{G}_{\mathbf{Mg}} & 0 \\ 0 & 0 & 0 & \mathbf{G}_{\mathbf{PE}} \end{bmatrix}$$

and each $\mathbf{G_j}$ (j=S (Sire effect), M (Maternal effect), Mg (Management effect), PE (permanent environmental effect) is 8 x 8. Hence, the **G** structure of the sire effect describes a 8 x 8 matrix contains variances-covariance between body weights at times t and HCWt (cw), P8 (P), EMA (E) and IMF (I).

$$\mathbf{G}_{\mathbf{sire}} = \begin{bmatrix} S^2_{con} & S_{con,Age} & S_{con,Age^2} & S_{con,Age^3} & S_{con,CW} & S_{con,P} & S_{con,E} & S_{con,I} \\ & S^2_{Age} & S_{Age,Age^2} & S_{Age,Age^3} & S_{Age,CW} & S_{Age,P} & S_{Age,E} & S_{Age,I} \\ & & S^2_{Age^2} & S_{Age^2,Age^3} & S_{Age^2,CW} & S_{Age^2,P} & S_{Age^2,E} & S_{Age^2,I} \\ & & & S^2_{Age^3} & S_{Age^3,CW} & S_{Age^3,P} & S_{Age^3,E} & S_{Age^3,I} \\ & & & & S^2_{CW} & S_{CW,P} & S_{CW,E} & S_{CW,I} \\ & & & & & S^2_{P} & S_{P,E} & S_{P,I} \\ & & & & & & S^2_{E} & S_{E,I} \\ & & & & & & & S^2_{I} \end{bmatrix}$$

where $S^2_{con}, S^2_{Age}, S^2_{Age^2}, S^2_{Age^3}, S^2_{CW}, S^2_{P}, S^2_{E}, S^2_{I}$ are the genetic variances of constant, linear, quadratic, cubic, HCWt, P8, EMA and IMF, respectively. All off diagonal terms are the sire covariances.

The maternal variance and covariances among body weights and carcass quality trait is given similarly by,

$$G_M = \begin{bmatrix} M^2_{con} & M_{con,Age} & M_{con,Age^2} & M_{con,Age^3} & M_{con,CW} & M_{con,P} & M_{con,E} & M_{con,I} \\ & M^2_{Age} & M_{Age,Age^2} & M_{Age,Age^3} & M_{Age,CW} & M_{Age,P} & M_{Age,E} & M_{Age,I} \\ & & M^2_{Age^2} & M_{Age^2,Age^3} & M_{Age^2,CW} & M_{Age^2,P} & M_{Age^2,E} & M_{Age^2,I} \\ & & & M^2_{Age^3} & M_{Age^3,CW} & M_{Age^3,P} & M_{Age^3,E} & M_{Age^3,I} \\ & & & & M^2_{CW} & M_{CW,P} & M_{CW,E} & M_{CW,I} \\ & & & & & M^2_{P} & M_{P,E} & M_{P,I} \\ & & & & & & M^2_{E} & M_{E,I} \\ & & & & & & & M^2_{I} \end{bmatrix}$$

where $M^2_{con}, M^2_{Age}, M^2_{Age^2}, M^2_{Age^3}, M^2_{CW}, M^2_{P}, M^2_{E}, M^2_{I}$ are the genetic variances of constant, linear, quadratic, cubic, HCWt, P8, EMA and IMF, respectively. All terms off diagonals are the covariances between growth and carcass trait for maternal effect.

The G structure of management effect are given as below:

$$G_{Mg} = \begin{bmatrix} Mg^2_{con} & Mg_{con,Age} & Mg_{con,Age^2} & Mg_{con,Age^3} & Mg_{con,CW} & Mg_{con,P} & Mg_{con,E} & Mg_{con,I} \\ & Mg^2_{Age} & Mg_{Age,Age^2} & Mg_{Age,Age^3} & Mg_{Age,CW} & Mg_{Age,P} & Mg_{Age,E} & Mg_{Age,I} \\ & & Mg^2_{Age^2} & Mg_{Age^2,Age^3} & Mg_{Age^2,CW} & Mg_{Age^2,P} & Mg_{Age^2,E} & Mg_{Age^2,I} \\ & & & Mg^2_{Age^3} & Mg_{Age^3,CW} & Mg_{Age^3,P} & Mg_{Age^3,E} & Mg_{Age^3,I} \\ & & & & Mg^2_{CW} & Mg_{CW,P} & Mg_{CW,E} & Mg_{CW,I} \\ & & & & & Mg^2_{P} & Mg_{P,E} & Mg_{P,I} \\ & & & & & & Mg^2_{E} & Mg_{E,I} \\ & & & & & & & Mg^2_{I} \end{bmatrix}$$

where $Mg^2_{con}, Mg^2_{Age}, Mg^2_{Age^2}, Mg^2_{Age^3}, Mg^2_{CW}, Mg^2_{P}, Mg^2_{E}, Mg^2_{I}$ are the genetic variances of constant, linear, quadratic, cubic, HCWt, P8, EMA and IMF, respectively. All terms off diagonals are the covariances between growth and carcass trait for management effects.

The permanent environmental (co)variance components are:

$$\mathbf{G}_{\mathbf{PE}} = \begin{bmatrix} \mathrm{PE}^2_{\mathrm{con}} & \mathrm{PE}_{\mathrm{con,Age}} & \mathrm{PE}_{\mathrm{con,Age^2}} & \mathrm{PE}_{\mathrm{con,Age^3}} & \mathrm{PE}_{\mathrm{con,CW}} & \mathrm{PE}_{\mathrm{con,P}} & \mathrm{PE}_{\mathrm{con,E}} & \mathrm{PE}_{\mathrm{con,I}} \\ & \mathrm{PE}^2_{\mathrm{Age}} & \mathrm{PE}_{\mathrm{Age,Age^2}} & \mathrm{PE}_{\mathrm{Age,Age^3}} & \mathrm{PE}_{\mathrm{Age,CW}} & \mathrm{PE}_{\mathrm{Age,P}} & \mathrm{PE}_{\mathrm{Age,E}} & \mathrm{PE}_{\mathrm{Age,I}} \\ & & \mathrm{PE}^2_{\mathrm{Age^2}} & \mathrm{PE}_{\mathrm{Age^2,Age^3}} & \mathrm{PE}_{\mathrm{Age^2,CW}} & \mathrm{PE}_{\mathrm{Age^2,P}} & \mathrm{PE}_{\mathrm{Age^2,E}} & \mathrm{PE}_{\mathrm{Age^2,I}} \\ & & & \mathrm{PE}^2_{\mathrm{Age^3}} & \mathrm{PE}_{\mathrm{Age^3,CW}} & \mathrm{PE}_{\mathrm{Age^3,P}} & \mathrm{PE}_{\mathrm{Age^3,E}} & \mathrm{PE}_{\mathrm{Age^3,I}} \\ & & & & \mathrm{PE}^2_{\mathrm{CW}} & \mathrm{PE}_{\mathrm{CW,P}} & \mathrm{PE}_{\mathrm{CW,E}} & \mathrm{PE}_{\mathrm{CW,I}} \\ & & & & & \mathrm{PE}^2_{\mathrm{P}} & \mathrm{PE}_{\mathrm{P,E}} & \mathrm{PE}_{\mathrm{P,I}} \\ & & & & & & \mathrm{PE}^2_{\mathrm{E}} & \mathrm{PE}_{\mathrm{E,I}} \\ & & & & & & & \mathrm{PE}^2_{\mathrm{I}} \end{bmatrix}$$

where $\mathbf{PE}^2_{\mathbf{con}}, \mathbf{PE}^2_{\mathbf{Age}}, \mathbf{PE}^2_{\mathbf{Age^2}}, \mathbf{PE}^2_{\mathbf{Age^3}}, \mathbf{PE}^2_{\mathbf{CW}}, \mathbf{PE}^2_{\mathbf{P}}, \mathbf{PE}^2_{\mathbf{E}}, \mathbf{PE}^2_{\mathbf{I}}$ are the genetic variances of constant, linear, quadratic, cubic, HCWt, P8, EMA and IMF, respectively. All terms off diagonals are the covariances between growth and carcass trait for permanent environmental.

An important point for this joint model is that the PE effects for carcass traits correspond to the residual term for these traits. The overall residual modelled as σ^2I (that is constrant variance and uncorrelated) can in fact only be estimated from the growth data. Nonetheless this term is part of the carcass traits variation. Thus the variance-covariance matrix for PE for carcass traits must be adjusted by adding σ^2 to the four traits variances. Again, REML and BLUP are approximate and ASReml is the package used.

7.3. Results

Relationships between growth traits and carcass quality traits

Estimates of sire (genetic), maternal (genetic and environmental), management group variance components and permanent environmental for the growth, carcass quality traits and correlations between them are given in Table 7.2. Carcass quality included quantity traits (HCWt and EMA) and fat traits (P8 and IMF). Management components consisted of constant, linear and all (co) variance components associated with the quadratic and cubic of polynomial.

Genetic variances and correlations

Fat traits (P8 and IMF) had higher variance than quantity traits (HCWt and EMA). Table 7.3 shows the genetic correlations between growth and carcass quality traits. The quantity traits were most highly correlated with the constant and P8 was most highly correlated with the linear growth parameter. Constant and linear growth were highly positive correlated with HCWt, whereas linear growth was not correlated with EMA. Genetic correlations between constant and P8 was low (Table 7.3), however the association between linear growth rate and P8 was positive and moderate (0.48).

Maternal variances and correlations

Expectedly, maternal effects were more substantial in young animals and decreased with age (Table 7.3). The magnitude of the estimated maternal variance constant was approximately twice that of the variance of linear growth. The correlation between fat traits was higher than for quantity traits. Maternal correlations were also significant between constant and eye muscle area (0.51). Linear growth and IMF (0.26) had low maternal association. The mean (growth) exhibited strong and linear growth rate indicated poor maternal relationships with HCWt. Therefore, no maternal influences on growth rate of carcasses were observed. The maternal correlations between constant and P8 was 0.49 (Table 7.3). However, an antagonistic genetic correlation between linear growth rate and P8 existed though very low maternal correlations between constant and linear growth rate with EMA were 0.51 and -0.11. The maternal correlations between IMF with constant and linear growth rate were 0.26 and -0.08, respectively.

Management variances and correlations

There was a negative and high association between constant and linear growth (Table 7.3). The relationships between linear growth and second (quadratic) and third (cubic) order of the age was high. In general, constant and linear growth rate had unfavourable management correlations with carcass traits. The management correlations between constant and carcass quality traits were not estimated. There was an antagonistic management correlation between P8 and linear growth rate. The management correlation between linear growth rate and IMF was 0.32 (Table 7.3).

Permanent environmental variances and correlations

The permanent environmental correlations between constant, linear and quadratic with carcass quality traits appear to be low. However, the permanent environmental correlations between constant, linear and quadratic with HCWt were not able to be estimated (Table 7.3).

Inter-relationships between carcass quality traits

The genetic correlations between the fat traits was lower than expected (0.29), indicating opportunity to make improvement in both traits, i.e. causing a change in fat distribution rather than total fatness *per se.* Associations of HCWt with P8 and IMF were very low (Tables 7.3). The most notable relationship was with HCWt and EMA (0.99), indicating that selection for heavier HCWt should also lead to greater EMA (Tables 7.3). The genetic correlation between P8 and EMA was -0.22, indicating that reduced fat thickness was associated with larger longissimous muscle area (Tables 7.2). EMA and IMF also exhibited a similar antagonistic genetic relationship (-0.14). The negative genetic correlation between these traits indicates that high marbling genetics are generally associated with unfavorable genetics for carcass muscularity, however; the genetic correlations were relatively low. This explains to some extent the difficulty in attaining high quality in combination with superior quantity, or vice versa.

The maternal correlations were similar to sire correlations for fat traits and quantity traits. Correlation between the fat traits was close to sire and lower than expected. Management correlation of HCWt with P8 (0.82) and IMF (0.77) were higher than the corresponding additive genetic coefficients. HCWt had a positive and high association with EMA (0.90). There was a high positive management correlation (0.83) observed between P8 and EMA. The value and direction of the correlation between EMA and IMF for management component (0.56) was different from that in the genetic component.

Table 7.3. Estimated variances (on diagonal) and correlations (off diagonal) for growth and carcass quality traits derived from the joint model. Zero means that traits were not able to be estimated

	Con	Age	Age^2	Age^3	HCWt	P8	EMA	IMF
Sire								
Constant (Con)	**5**							
Age	0.80	**1**						
Age^2	0	0	**1**					
Age^3	0	0	0	**0**				
HCWt	0.99	0.90	0	0	**11**			
P8	0.03	0.41	0	0	0.08	**107**		
EMA	0.90	0.03	0	0	0.99	-0.22	**8**	
IMF	-0.12	0.90	0	0	0.14	0.29	-0.14	**50**
Maternal								
Constant (Con)	**55**							
Age	-0.76	**20**						
Age^2	0	0	**0**					
Age^3	0	0	0	**0**				
HCWt	0.99	-0.15	0	0	**36**			
P8	0.49	-0.02	0	0	0.99	**114**		
EMA	0.51	-0.11	0	0	0.99	0.40	**35**	
IMF	0.26	-0.08	0	0	0.58	-0.01	0.05	**51**
Management group								
Constant (Con)	**56**							
Age	-0.74	**139**						
Age^2	-0.48	0.43	**170**					
Age^3	0.40	-0.67	0.18	**370**				
HCWt	0	0	0.73	0.49	**43**			
P8	0	-0.23	0.71	0.64	0.82	**631**		
EMA	0	0	0.70	0.29	0.90	0.83	**58**	
IMF	0	0.32	0.51	0.10	0.77	0.26	0.56	**796**
Permanent environmental (growth) and environmental (carcass)								
Constant (Con)	**31**							
Age	-0.39	**22**						
Age^2	-0.35	-0.58	**23**					
Age^3	0	0	0	**0**				
HCWt	0	0	0	0	**82**			
P8	0.16	0.22	-0.18	0	0	**1210**		
EMA	0.29	0.07	-0.14	0	0	-0.01	**134**	
IMF	-0.03	0.07	0.12	0	0	0.12	-0.02	**994**

* Variances on diagonal have been multipled by 10^4 to ease reporting, correlations below diagonal and note that all variables were log transformed and age was in years (not days).

7.4. Discussion

In addition to the previous analyses (univariate growth and multi-trait carcass models), the joint growth-carcass model also indicated the importance of management variation. Likewise, the magnitudes of the management correlations were significantly higher than genetic, maternal and permanent environmental correlations. However, the management correlations between constant and HCWt were not estimated. As expected, there were high associations between growth traits and HCWt. The genetic correlation between constant and P8 was low but the association between linear growth rate and P8 was positive and moderate, close to those reported by Koots et al. (1994b). Therefore, in the present study, high genetic associations of growth rate with HCWt and P8 fat indicated that high growth will lead to heavier carcasses with more fat depth. Koch (1978), Koch et al. (1982) and Lamb et al. (1990) reported positive genetic correlations between fat thickness and pre-weaning growth of Hereford cattle. Arnold and Bennett (1991) reported that fat thickness had positive association with post-weaning gain. This may be expected because on one hand, total body fat (TBF) at birth being only 6.5% of empty body weight (or 2% of body weight) and subcutaneous fat accounted for about 6% of TBF (Robelin, 1986) and there is no adipose tissue at two months of age. On the other hand, as the cattle progress from birth to mature weight, there is a large increase in the percentage of fat. Koots et al. (1994b) reported genetic correlations of 0.24, 0.32 and 0.19 between fat depth with weaning, yearling weights and post-weaning gain, respectively. The genetic correlation between the constant and IMF was low. This might be due to brown adipose tissue at birth and the fact that fat is mainly deposited in the abdominal cavity and visceral organs at birth. The high genetic associations of growth rate and

IMF in this study imply that selection for fast growth is likely to change IMF in breeding animals. Koch, (1978), Koch et al. (1982), Lamb et al. (1990), Reynolds et al. (1991), Woodward et al. (1992) and Veseth, et al. (1993) reported that the average genetic correlation between pre-weaning growth and marbling score of Hereford and Simmental cattle was 0.39, indicating a favourable relationship between selection for increased weaning weight and increased marbling. However, Arnold and Bennett (1991) asserted that marbling was uncorrelated with weaning weight and also stated that marbling was positively correlated with post-weaning gain on a weight-constant basis. The most notable relationship was between HCWt and EMA. In other studies, Moser et al. (1998) and Kemp et al. (2002) have reported genetic correlations of 0.60 and 0.45, respectively, between yearling weight and ribeye area.

7.5. Conclusion

The current analysis was performed to examine genetic, maternal, management and permanent environmental relationships between growth and carcass measurements using a joint with RRM. These correlations and parameters were critically important for establishment of the carcass correlation curves over time (Chapter 8) as well as development of a predictive model (chapter 9). A successful prediction of the carcass quality of cattle following specific growth path depends as much on a correct estimation of (co) variances components of its genotype parameters as on a detailed description of its environment. Fitting the joint model resulted in estimation of 99 parameters required for the prediction carcass quality from live body weights. However, some components were not able to be estimated. These limitations may have been caused by the size of data set, the nature of relationships between traits and number of parameter estimated could influence on the possibility of estimations. The size of data set is important because it provides information for the algorithms used in the model, so lack of enough information may affect the capability of the model for estimation of the parameters. The relationship between the number of parameters and the size of data set is also important. The power of the analytical program also may affect estimation. However, through the process, as many parameters as possible were estimated. The results of this chapter, namely a joint growth-carcass model allow the examination of characteristics of carcass quality in terms of various growth parameters. This is considered in the next chapter.

Chapter 8

Correlation between carcass quality and growth characteristics

8.1. Introduction

The potential for change in carcass quality traits is largely dependent on their genetic variation and correlation with growth path. Producers need to be aware of where these correlations are positive and optimum as well as possible negative relationships among traits during specific period of growth so that they may account for them in their management strategies and breeding programs. Numerous studies have reported estimates of genetic or phenotypic parameters for growth (at specific ages), or carcass traits (Mohuiddin, 1993; Koots et al., 1994b; Bertrand et al., 2001), but few have reported estimates of relationships among carcass traits and growth characteristics. Hence, a major point of interest within this study was to answer a basic question. If growth traits and carcass quality traits were correlated, did that correlation change over time, and if so, then how did it vary? The previous chapter (7) reported estimated (co)variances associated with longitudinal growth and carcass traits. This chapter expands on these findings to develop a set of functions to visualize time-dependent covariances and correlations between growth path and carcass quality traits for different genetic and non-genetic effects.

8.2. Statistical method

A least squares model, which consistently estimate overall mean effect, is useful for an exploratory analysis of longitudinal data. However, it does not take into account the serial correlations possibly present within each time series. Under a RRM, observations within animals are assumed to be correlated, with correlation arising in part from an animal's deviation from overall effects. As described in the previous chapter, variances and covariances among growth and carcass traits are given by the covariances among the random effects (sire, maternal, management and permanent environmental) and carcass traits, and random effects were assumed uncorrelated.

There are several aims in this chapter. We begin by exploring the correlation between growth path and a carcass trait. Thus

$$\rho(\ln c_{ij}, \ln g_{ijt}) = \frac{\operatorname{cov}(\ln c_{ij}, \ln g_{ijt})}{\sqrt{\left(\operatorname{var}(\ln c_{ij})\operatorname{var}(\ln g_{ijt})\right)}} \qquad \textbf{(8.1)}$$

where ln c_{ij} is log of ith carcass trait of jth calve, lng_{ij} is log of ith body weight of jth calve at time t, $\operatorname{var}(\ln g_{ijt})$ is the variance of growth components, var lnc_{ij} is the variance of growth components and cov ln c_{ij}, lng_{ij} is the covariance between growth and carcass quality traits. In fact, the model is in term of log-weights and log-carcass trait. Using properties of the log-normal distribution (Aitchison and Brown, 1963; Crow and Shimizu, 1988; Johnson et al., 1994; Limpert et al., 2001).

$$\rho(c_{ij}, g_{ijt}) = \frac{(e^{\operatorname{cov}(\ln c_{ij}, \ln g_{ijt})} - 1)}{\sqrt{\left((e^{\operatorname{var}(\ln c_{ij})} - 1)(e^{\operatorname{var}(\ln g_{ijt})} - 1)\right)}} \qquad \textbf{(8.2)}$$

Thus the variance of growth components ($\operatorname{var}(\ln g_{ijt})$), the variance of carcass quality traits (var lnc_{ij}) and the covariance between growth and carcass quality traits (cov (ln c_{ij}, lng_{ij})) need to be determined from the joint model of Chapter 7.

First, the variance of each component can be shown to be

$$\begin{aligned}\operatorname{var}(\ln g_{ijt}) = {} & V^2{}_{\mathrm{CON}} + t^2.V^2{}_{\mathrm{Age}} + t^4.V^2{}_{\mathrm{Age}^2} + t^6 V^2{}_{\mathrm{Age}^3} + 2.t.\mathrm{COV}_{\mathrm{CON,Age}} + 2.t^2.\mathrm{COV}_{\mathrm{CON,Age}^2} \\ & + 2.t^3.\mathrm{COV}_{\mathrm{CON,Age}^3} + 2.t^3.\mathrm{COV}_{\mathrm{Age,Age}^2} + 2.t^4.\mathrm{COV}_{\mathrm{Age,Age}^3} + 2.t^5.\mathrm{COV}_{\mathrm{Age}^2,\mathrm{Age}^3}\end{aligned} \qquad \textbf{(8.3)}$$

Second, the variance of carcass (var (lnc_{ij})) is independent of time and estimated by joint model (Chapter 7).

Third, the covariance between body weights and each carcass trait, that is $\operatorname{cov}(\ln c_{ij}, \ln g_{ijt})$, is given by

$$\mathrm{cov}(\ln c_{ij}, \ln g_{ijt}) = \mathrm{COV}_{\mathrm{CON,CARCASS}} + t.\mathrm{COV}_{\mathrm{Age,CARCASS}} + 2.t^2.\mathrm{COV}_{\mathrm{Age^2,CARCASS}} + t^3.\mathrm{COV}_{\mathrm{Age^3,CARCASS}} \quad \mathbf{(8.4)}$$

The correlation between relative growth rate and carcass traits is also of interest. This is given by

$$\rho(\ln c_{ij}, \frac{\partial \ln g_{ijt}}{\partial t}) = \frac{\mathrm{cov}(\ln c_{ij}, \frac{\partial \ln g_{ijt}}{\partial t})}{\sqrt{\left(\mathrm{var}(\ln c_{ij})\mathrm{var}(\frac{\partial \ln g_{ijt}}{\partial t})\right)}} \quad \mathbf{(8.5)}$$

the variance of relative growth rate, $\mathrm{var}(\frac{\partial \ln g_{ijt}}{\partial t})$

$$= V^2{}_{\mathrm{Age}} + 4t^2 V^2{}_{\mathrm{Age^2}} + 9t^4 V^2{}_{\mathrm{Age^3}} + 4t\mathrm{COV}_{\mathrm{Age,Age^2}} + 6t^2\mathrm{COV}_{\mathrm{Age,Age^3}} + 12t^3\mathrm{COV}_{\mathrm{Age^2,Age^3}} \quad \mathbf{(8.6)}$$

the variance of carcass (var (lnc_{ij})) is also independent of time and estimated by joint model (Chapter 7).

and the covariance between relative growth rate and each carcass trait, that is

$\mathrm{cov}(\ln c_{ij}, \frac{\partial \ln g_{ijt}}{\partial t})$, is given by

$$= 2\mathrm{COV}_{\mathrm{Age^2,CARCASS}} + 6t\mathrm{COV}_{\mathrm{Age^3,CARCASS}} \quad \mathbf{(8.7)}$$

8.3. Results

Genetic and non-genetic (co)variance components derived from the joint model (Chapter 7) were used to estimate corresponding correlations between body weights and carcass quality traits (Figure 8.1). The Figure depicts chronological changes of those correlations over the growth trajectory. Overall, the phenotypic and genetic correlations between body weight and carcass traits were positive. The genetic correlations between body weight and P8 were negative and close to zero (Figure 8.1). Genetic correlations were generally higher than the corresponding phenotypic ones except for P8 fat. Genetic correlations between body weights and EMA at pre-weaning as well as phenotypic correlations between body weights and HCWt during feedlot period were 0.99-1.03, although it seems reasonable to assume there was a strong relationship (Figure 8.1). Phenotypic correlations between body weight with HCWt and EMA increased from birth up to feedlot period where it plateaus. The rate of change in phenotypic correlations between body weight and IMF, (Figure 8.1), increased as age increased from birth to feedlot. However, those genetic correlations declined as the calves approached feedlot period.

Figure 8.1 presents the maternal correlation component of carcass traits over time. Overestimated and positive maternal correlations between body weight and HCWt were observed during the post-weaning period. Similar to HCWt coefficients maternal correlations between body weight and P8 fat and EMA increased as age increased. Maternal correlations between body weight and IMF were the lowest.

Figure 8.1 also relates permanent environmental correlation of body weight and carcass traits over the growth trajectory. Permanent environmental correlations for all other carcass traits with body weight were very low (Figure 8.1).

In the current study, management variation made an important contribution to total variation. Thus, of special interest were management correlations between growth and carcass quality traits. Figure 8.1 presents the general trend of management correlations between growth traits (body weights and growth rate) and carcass quality traits at different ages from birth to slaughter. Management correlations between body weight and carcass traits during the pre-weaning period were positive except for IMF. The magnitude of those correlations decreased from birth to weaning, then went dramatically up for the feedlot period, where they plateaud (except for IMF which decreased from 500-700 days). The pattern of changes in management correlations of HCWt and P8 with BW were similar from birth to slaughter, shown in Figure 8.1.

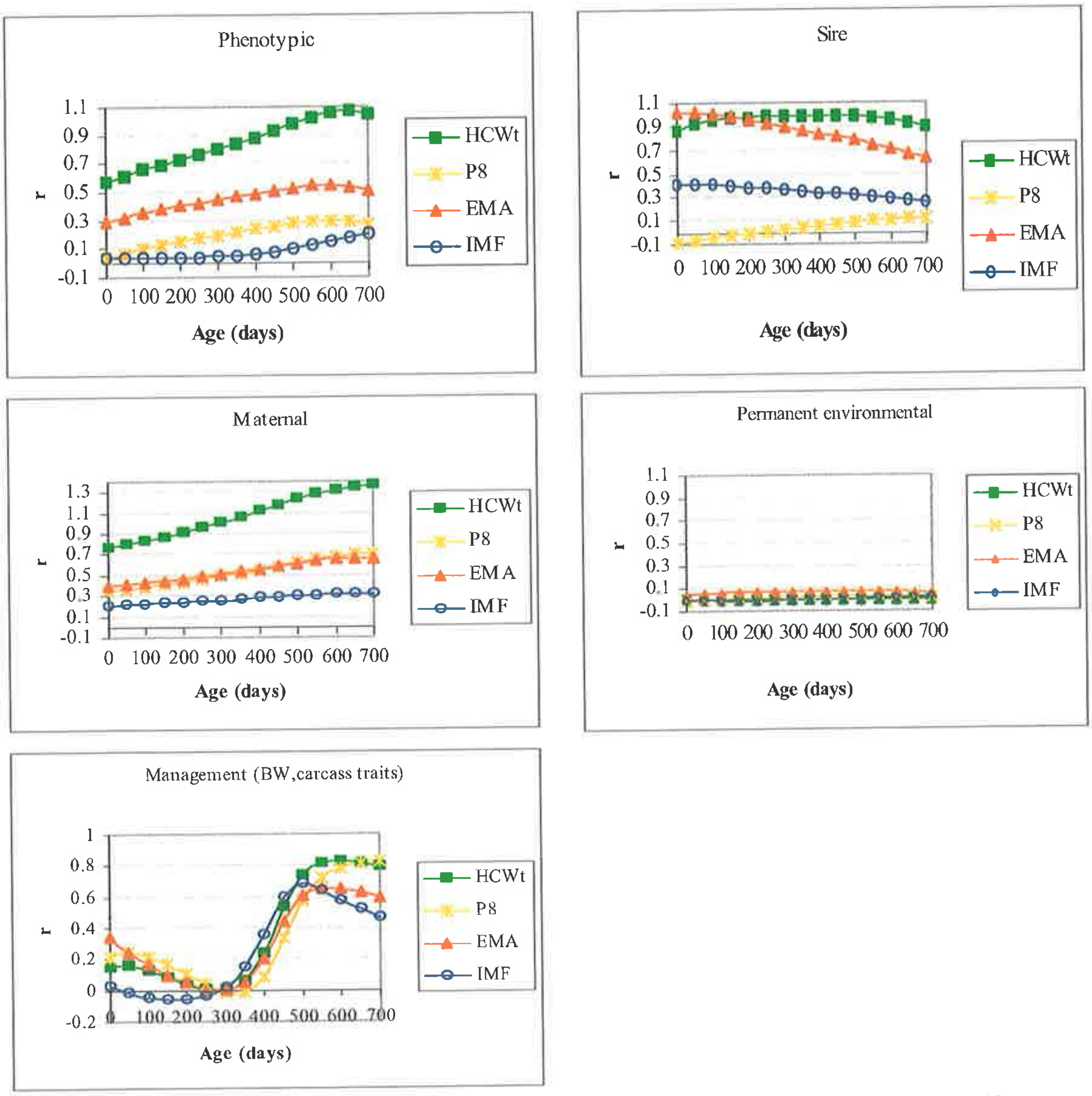
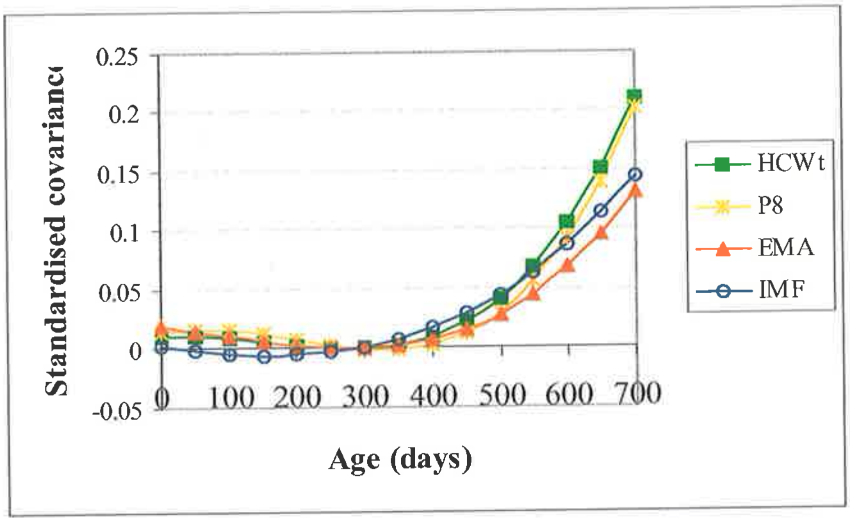


Figure 8.1. Correlations between body weights and carcass quality traits at different ages derived from the joint model

The estimates of correlations between RGR and carcass traits during the pre-weaning period were generally negative (Figure 8.2). At birth, management correlations between RGR and HCWt and P8 were positive but those of EMA and IMF were negative. Unexpectedly, all carcass traits were negatively correlated (-0.05 to –0.65) with RGR at 150 days. However, the negative and high correlations were likely due to the negative covariances between carcass traits and body weights during this period as well as very low variance for carcass traits and RGR at that period (Figure 8.2). Moderate to high management correlations were observed for P8 fat and EMA at about 150 days of age. IMF had a negative relationship with birth weight (-0.11) and at early growth (200 days of age), gained positive management association with RGR up to weaning. The shape of correlations for HCWt, P8 and EMA except IMF followed a rather similar pattern over the growth trajectory, particularly for correlations involving ages greater than 300 days up to 500 days of age, where it declined (Figure 8.2). This result indicated that the highest correlation between RGR with HCWt and P8 occurred at slaughter age.



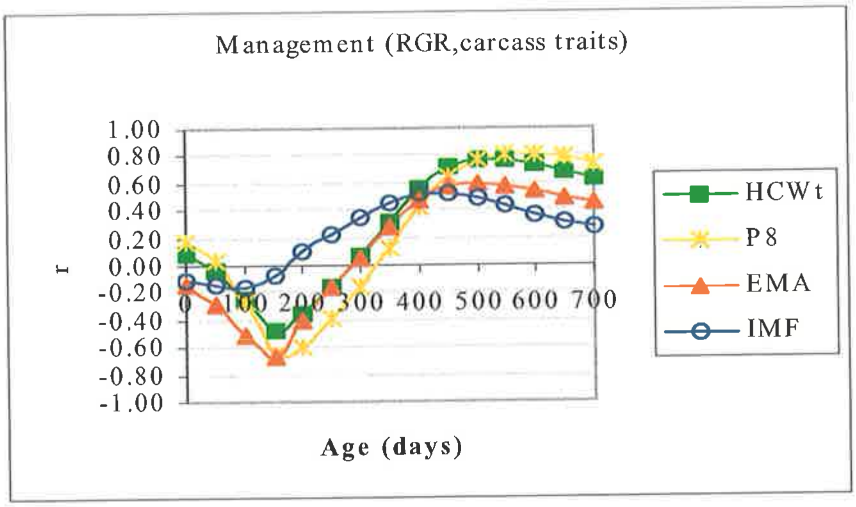


Figure 8.2. Management covariances (top) and correlations (bottom) between relative growth rate and carcass quality traits at different ages derived from the joint model

8.4. Discussion

The main goal of this chapter was the description of how continuous growth traits and carcass quality traits were correlated over time to identify which part of the growth path had a significant effect on the carcass quality traits. The correlations between growth traits (body weights and RGR) and four considered carcass traits will be discussed seperately for the pre-weaning and post-weaning periods.

8.4.1. Pre-weaning correlations between body weights and carcass traits

Correlations between birth weight and carcass quality traits

Correlations between birth weights and HCWt. The phenotypic, genetic and maternal correlations of birth weight with HCWt, were positive and moderate to high (Figure 8.1). However, the environmental correlations between birth weight and HCWt were very low, implying that environmental effects on HCWt were independent of those influencing birth weight. The average phenotypic correlation between birth weight and carcass traits was lower than the genetic correlations. The genetic correlation between birth weight and HCWt was highest among estimates of the other components, in general agreement with other researchers (Mohuiddin, 1993; AAABG, 2004).

Correlations between birth weight and P8 fat. Birth weight had very low phenotypic and genetic correlations with fat depth, indicating there are very few genes that affect both traits and that there will be little correlated change in one trait as a result of selection for the other trait, consistent with values reported by Koch et al., (1982) and AAABG, (2004). Maternal and environmental associations between birth weight and P8 fat was moderate and low, respectively (Figure 8.1).

Correlations between birth weights and EMA. The associations between birth weight and EMA were phenotypically low, but genetically very high. However, Koch et al.,

(1982) reported both phenotypic and genetic correlations between birth weight and rib eye area to be low (Table 1.5). Maternal and environmental correlations between birth weight and EMA was moderate.

Correlations between birth weights and IMF. The phenotypic, maternal and environmental correlations between birth weight and IMF were positive and low, but the genetic correlation was moderate. This tends to be consistent with that of Koch et al. (1982) who reported an estimate of 0.3.

Correlations between weaning weight and carcass quality traits

Correlations between weaning weights and HCWt. Weaning weight and HCWt had favorable phenotypic and genetic correlations (Figure 8.1), and may represent opportunities for increased productivity. This is in strong agreement with other literature (Koch, 1978; Koots et al., 1994b; Reynolds et al., 1991; AAABG, 2004). Crews and Kemp (1999) and Splan et al. (2002) obtained positive estimates of genetic correlation between direct genetic effects for weaning weight and hot carcass weight (0.28 and 0.70, respectively). Likewise, the estimate of the genetic correlation between the maternal component of weaning weight and direct component for hot carcass weight reported by Crews and Kemp (1999) and Splan et al. (2002) was smaller (0.64 and 0.61, respectively) than the present estimate (1.07). Gregory et al. (1995) found a moderate positive genetic correlation between weaning weight and carcass weight (0.42) from data involving both purebred and composite animals. Arnold and Bennett (1991) reported a small but positive genetic correlation between weaning weight and carcass weight. Hennessy et al. (2001); Hennessy and Morris (2003) reported that those animals that had higher pre-weaning growths, had heavier carcasses although they also tended to be fatter than carcasses from animals that had low pre-weaning growth rates. Several authors have estimated correlations between growth and carcass traits, but without fitting maternal effects to the models for growth traits. As with birth weight, the environmental estimates of correlation between weaning weight and HCWt were low, indicating independency of the environments that affect both traits.

Correlations between weaning weights and P8 fat. Estimates of correlations for phenotypic, genetic and environmental effects of weaning weight with P8 were low and for maternal effects were moderate and positive (Figure 8.1). The estimates of phenotypic correlation between weaning weight and fat depth range between 0.19-0.26 while the genetic correlations varies from –0.01 to 0.13 (Mohuiddin, 1993). AAABG, (2004) reports those estimates averages across studies 0.15 and 0.07, respectively. Gregory et al. (1995) and Splan et al. (2002) and reviews by Koots et al. (1994) and Marshall (1994b) report a positive genetic correlation between weaning weight and fat depth (0.15 and 0.23, respectively). Direct weaning weight and pre-weaning body weights in the present study were negatively related genetically with P8 fat depth (Figure 8.1), in general agreement with Dinkel and Busch (1973); Wilson et al. (1976) and Arnold and Bennett (1991) and Crews and Kemp (1999). Koch et al. (1982) and Gregory et al. (1995) reported a genetic correlation of 0.15 between weaning weight-fat thickness (Table 1.5). The negative relationship between weaning weight and P8 fat depth could be related to maturing rate. Animals that are heavier at weaning may mature slowly and consequently could have increased amounts of lean muscle tissue relative to external fat.

Correlations between weaning weights and EMA. An estimate of genetic correlations between weaning weight and EMA was high and positive (Figure 8.2). The estimates of phenotypic and maternal correlations between weaning weight and EMA were moderate but the environmental correlations was low. Crews and Kemp (1999) and Gregory et al. (1995) estimated genetic correlations between direct and maternal components of weaning weight and EMA to be positive (0.34 and 0.45, respectively). Splan et al. (2002) reported that correlations between direct weaning weight and EMA were moderate and positive at age, marbling, and fat-thickness end points. At constant carcass weight, this correlation decreased, probably reflecting reduced variation in EMA when weight was constrained. On a weight-constant basis, Arnold and Bennett (1991) obtained positive but Wilson et al. (1976) reported negative genetic correlations between weaning weight and EMA.

Correlations between weaning weights and IMF. The environmental correlation between the direct effect of pre-weaning and weaning weight with IMF was low (-0.04), while the estimate of genetic correlation for pre-weaning and weaning weight and direct effect for IMF was positive and moderate (Figure 8.2). Gregory et al. (1995) and Splan et al. (2002) reported a positive genetic correlation between weaning weight and marbling (0.12 and 0.21, respectively). Wilson et al. (1976) found a negative genetic correlation between weaning weight and marbling score, but Arnold and Bennett (1991) found little association (Table 1.5). Estimates of correlations for phenotypic and maternal effects of pre-weaning and weaning weight with IMF were low, in agreement with Koch et al. (1982) and Splan et al. (2002). Arnold and Bennett (1991) found that marbling was uncorrelated with weaning weight. Likewise, AAABG (2004) reports the phenotypic and genetic correlations averaged across studies to be positive and low between pre-weaning gain and marbling, but negative and low genetic correlations between weaning weight-marbling. However, others observed positive and moderate genetic correlation between pre-weaning growth and marbling score, indicating a favourable relationship between selection for increased weaning weight and increased marbling (Koch, 1978; Koch et al., 1982; Lamb et al., 1990; Reynold et al., 1991; Woodward et al., 1992; Veseth et al., 1993). Cundiff and MacNeil (1986) observed that between breed additive genetic variation was of comparable magnitude to that found within a breed, and that 0.37 for weaning weight-marbling score, whereas, average genetic correlation between weaning weight and marbling score was found to be negative by Koots et al. (1994b). The subjective nature of assessing marbling score may account for the inconsistent estimates.

8.4.2. Post-weaning correlations between body weights and carcass traits

Correlations between post-weaning weights and HCWt. Phenotypic, genetic and maternal correlations were found to be positive and high for post-weaning body weights with HCWt (Figure 8.2). The phenotypic and genetic correlations of yearling weight, yearling gain and post-weaning growth rate with carcass weight averaged across studies are positive and high (AAABG, 2004). Reynolds et al. (1991) and Shackelford et al. (1994) observed the values of 1.26 and 1.10 for genetic correlations between post-weaning growth rate with carcass weight. However, management correlations between yearling body weight and carcass weight was low but as age increased it sharply increased towards post-weaning period.

Correlations between post-weaning weights and P8 fat. The phenotypic correlations between yearling weight and P8 fat depth was positive and low (Figure 8.2), in agreement with Dickerson et al. (1974), Koch et al. (1978), Mavrogenis et al. (1978), Neely et al. (1982) and McWhir and Wilton (1987). Mohuiddin (1993) reported that the phenotypic and genetic correlations between yearling weight and fat depth are positive and low to moderate. Likewise, the phenotypic and genetic correlations between post-weaning growth rate and P8 fat was low, as supported by Dickerson et al. (1974), Neely et al. (1982), Dijkstra et al. (1990), Lamb et al. (1990) and Arnold and Bennett (1991). Mavrogenis et al. (1987) and Kuchida et al. (1990) reported low and negative correlation between post-weaning growth rate and P8. The phenotypic correlations between post-weaning growth rate and carcass fat thickness is positive (averaged 0.31) (Marshall, 1994; AAABG, 2004). However, the genetic correlations between those traits is quite variable (ranged from -0.20 to 0.62, averaging .13 (Marshall, 1994). Arnold and Bennett (1991) reported that fat thickness was positively associated with post-weaning gain (0.17). Although the estimated management correlation between yearling weight and P8 fat was low, the estimates between post-weaning body weights and P8 fat increased over the post-weaning period.

Correlations between post-weaning weights and EMA. There was a moderate to high, positive genetic correlation between post-weaning growth and EMA in the present study (Figure 8.1), indicating that selection for higher growth should also lead to more total muscle mass as reflected in the size of the EMA. On a theoretical basis, faster-gaining animals will be fatter if they have capacity to dispose of more calories by fat accretion. This, in turn, should reduce mature size. If animals that gain less rapidly have lower energy intakes, they may be physiologically younger and thereby leaner than rapidly gaining cohorts (Owens et al., 1995). The genetic correlation between post-weaning growth rate and eye-rib area varies widely, from –0.7 (Benyshek, 1981) to 0.82 (Shackelford et al., 1994). Koch, (1978) found that EMA was uncorrelated with post-weaning growth rate but Arnold and Bennett (1991) observed positive and high genetic correlation between them. Moser et al. (1998) and Kemp et al. (2002) have reported genetic correlations of 0.60 and 0.45, respectively, between yearling weight and EMA. Likewise, the estimates of correlations for maternal and management effects were positive and moderate to high with EMA.

Correlations between post-weaning weights and IMF. There were a low phenotypic and management and a moderate genetic and maternal relationships between yearling weight and IMF (Figure 8.1). The pattern of phenotypic correlations between body weight and IMF as the animal grew (Figure 8.1) were similar to those observed from animal developmental studies in that IMF is later developing than subcutaneous fat (Vernon, 1981; Pethick et al., 2004). This result indicated that during the early growth phase (about 50 kg HCWt at 50 days) IMF correlations with body weights remained low and constant, then followed by a phase of almost linear coefficient as the carcass begins to fatten more rapidly (starting at ~250 days). Finally, it is assumed that as mature body size is reached (~450 kg HCWt) the increase in IMF is reduced as growth rate decline (not seen in the current report where average HCWt for heifer and steers were 218 and 324, respectively).

AAABG (2004) reports that marbling score is positively phenotypically but negatively genetically associated with yearling weight, 0.14 and -0.36, respectively. The average genetic correlation between post-weaning gain and marbling was 0.05, although estimates varied widely across studies (ranged from -.62 to .48). Arnold and Bennett (1991) asserted that marbling was positively correlated with post-weaning gain (0.54) on a weight-constant basis.

8.4.3. Correlations between RGR and carcass quality traits

Correlations between pre-weaning RGR and carcass quality traits

Relative growth rate (Fitzhugh and Taylor, 1971) is an economically important growth trait that used to determine the energetic efficiency of beef cattle (Nkrumah et al., 2004). Unexpectedly, in the present study, the negative estimates of management correlations between RGR and carcass traits during pre-weaning period occurred as the variances of management during this period were very poor when the covariance between RGR and carcass traits were negative and close to zero (Figure 8.2). This means that those calves that had slower growth up to weaning produced higher values of carcass quality. Hennessy and Arthur, (2004) reported relative growth rates of –0.51 –0.48 –0.19, –0.24 –0.49, for carcass weight (kg), dressing percentage, rib fat (mm), P8 fat (mm) and eye muscle area (cm^2), respectively. Smith et al. (1979) and McWhir and Wilton (1987) found low associations between RGR and HCWt, RGR and P8 fat, RGR and EMA and RGR and marbling score. AAABG (2004) reports low and negative relationships between RGR and cutability.

Correlations between post-weaning RGR and carcass quality traits

Over post-weaning period, all carcass quality traits were favourably correlated to the post-weaning RGR, implying that management is a key component in the production of faster growing animals of high carcass quality. Selection for higher RGR should also lead to heavier and fatter carcasses during this period (Figure 8.2). The general shape of the curves matches most of the relationships from the literature indicating that mass of fat increased quadratically with weight whereas protein mass increased more linearly. However, this change in body composition can be ascribed to degree of maturity and should not be extrapolated to suggest that rate of weight gain alters composition of gain (Owens et al., 1995). It was also observed by Owens et al. (1995) that as empty body gain increased up to approximately 1.3 kg/d, the rate of fat accretion increased. But with gains higher than 1.3 kg/d, similar to gains expected for feedlot cattle, fat accretion reached a plateau at approximately 550g daily. Comparatively, the correlations between RGR and HCWt were lower in magnitude compared to fat traits correlations. P8 was positively associated with post-weaning growth (0.12 to 0.61), indicating that faster-gaining cattle were fatter.

IMF showed positive and favourable relationships with post-weaning period RGR (Figure 8.2), which is most frequently used in selection programs (0.42 to 0.71). The highest management association was found between IMF and RGR at about 350 days of age; it declined with increasing age.

8.5. Conclusion

It seems that selection for increased direct genetic value for pre-weaning and weaning body weights would be expected to increase HCWt, EMA, IMF (to some extent). Genetic correlations between body weight and fat traits were low. Maternal correlations between body weight and HCWt were high, but they were lower for other traits. So, emphasis on maternal milk or maternal effects on pre-weaning and weaning and post-weaning body weights may lead to positive correlated responses in HCWt and EMA. However, because most of the correlations between maternal genetic effects for weaning weight are not large in magnitude, selection for carcass fat traits would not be expected to result in important changes in maternal ability. All genetic correlations with carcass traits that were positive for direct genetic effects for pre-weaning and weaning body weights were also positive for maternal genetic effects, except for P8, which had small negative estimates of genetic correlations with direct effects for weaning weight. To meet demand for quality beef, seed stock and commercial producers need to consider not only growth efficiency but also carcass traits in selection decisions.

9.1. Introduction

Today, in the beef industry, it is a challenge to design the "best" management strategy for individual breeder, backgrounder and finisher operations to get optimum end products under different circumstances. In the face of these issues, it is suggested to develop a flexible and feasible model to predict carcass quality resulting from specific growth path under a variety of management regimes that will lead to those cattle being marketed at the optimum time. Oltjen et al. (1986) stated that these models are necessary to predict performance and also to examine alternative feeding or management strategies.

There are two possible approaches to develop a beef growth model, the empirical and the mechanistic approach. The empirical model consists of a function that fits the data. The graph of the function goes through the data points approximately. Therefore, although an empirical model cannot be used to explain a system, it could be used to intrapulate behaviour of the system where data do not exist. Alternatively, the mechanistic approach attempts to simulate the biological processes and gives a real understanding of the system under study. However, application of the latter is limited by availability of suitable data and its complexities. Therefore, it is believed that empirical models give more practical solutions to the development of a predictive model for the growth of beef cattle.

Many attempts have been made in developing empirical and mechanistic models to estimate beef cattle growth and body composition (Chapter 2). However, so far in much of the published work, there is a lack of information to address predicting carcass quality when the growth path is known. Hence, according to the literature cited, the empirical models to predict carcass quality based on the longitudinal body weights at various stages of growth have not been published. Whereas, it has been shown that as animals grow their carcass composition changes (Robelin et al., 1990) and that composition is almost controlled by age and weight (Reid et al., 1968). Live weight is an easy and inexpensive measurement and market cattle often are sold on a live basis and so the live animal evaluation could be very beneficial indication of most desirable animals for meeting market specifications. Thus, the objective of this study was to develop an empirical model to predict carcass quality traits based on breed, sex and growth performance. This model can be useful in answering basic questions and examining "what-if" scenarios that may apply to many different circumstances in beef production.

9.2. The Model

A successful prediction of the carcass quality following specific growth path requires estimation of variation in growth traits (Chapter 5), carcass traits (Chapter 6) and association between both of them over growth path (Chapter 7).

Consider the growth and carcass traits both modelled on the log-scale. The underlying normal distribution used in the modelling mean that if $\mathbf{y}_w$ is log-weight for an animal and $\mathbf{y}_c$ is the log-carcass quality

$$\begin{bmatrix} y_w \\ y_c \end{bmatrix} \sim N\left(\begin{bmatrix} \mu_w \\ \mu_c \end{bmatrix}, \begin{bmatrix} \Sigma_{ww} & \Sigma_{wc} \\ \Sigma_{cw} & \Sigma_{cc} \end{bmatrix} \right)$$

where

$$\mu_w = E(y_w)$$
$$\mu_c = E(y_c)$$

and Σ_{ww} is the variance-covariance matrix for log-weight, Σ_{cc} is the the variance-covariance matrix for log-carcass traits and Σ_{wc} ($=\Sigma_{cw}^{T}$) is the cross-covariance matrix between log-weight and log-carcass traits. Of interest is to"predict" y_c given y_w at the first level, this is to consider the distribution of $y_c | y_w$, namely

$$\mathrm{y_c}|\mathrm{y_w} \sim \mathrm{N}\left(\mu_\mathrm{c} + \Sigma_\mathrm{cw}\Sigma_\mathrm{ww}{}^{-1}(\mathrm{y_w} - \mu_\mathrm{w}), \Sigma\mathrm{cc} - \Sigma_\mathrm{cw}\Sigma_\mathrm{ww}{}^{-1}\Sigma_\mathrm{wc}\right)$$

Thus we can provide an estimate of the mean log-carcass quality by

$$\mu_\mathrm{cw} = \mu_\mathrm{c} + \Sigma_\mathrm{cw}\Sigma_\mathrm{ww}{}^{-1}(\mathrm{y_w} - \mu_\mathrm{w})$$

We have estimates of μ_c , Σ_{cw}, Σ_{ww} and μ_w from the joint model of Chapter 7. Thus given a growth path specified by $\mathrm{y_w}$, we can estimate the log-carcass traits by

$$\hat\mu_\mathrm{cw} = \hat\mu_\mathrm{c} + \hat\Sigma_\mathrm{cw}\hat\Sigma_\mathrm{ww}{}^{-1}(\mathrm{y_w} - \hat\mu_\mathrm{w})$$

This is also our prediction.

A confidence interval for μ_{cw} can be found as follows.

Firstly $$\hat\mu_\mathrm{c} = \mathrm{X_c}\hat\tau_\mathrm{c} \quad \text{and} \quad \hat\mu_\mathrm{w} = \mathrm{X_w}\hat\tau_\mathrm{w}$$

where $\hat\tau_\mathrm{c}$ and $\hat\tau_\mathrm{w}$ are the log-carcass quality and log-body weights fixed effects parameter estimates. Then conditional on $\mathrm{y_w}$

$$\begin{aligned} &\mathrm{var}(\hat\mu_\mathrm{cw}) = \mathrm{var}(\hat\mu_\mathrm{c}) + \Sigma_\mathrm{cw}\Sigma_\mathrm{ww}{}^{-1}\mathrm{var}(\hat\mu_\mathrm{w})\Sigma_\mathrm{ww}{}^{-1}\Sigma_\mathrm{wc} \\ &- \Sigma_\mathrm{cw}\Sigma_\mathrm{ww}{}^{-1}\mathrm{cov}(\hat\mu_\mathrm{w}, \hat\mu_\mathrm{c}) \\ &- \mathrm{cov}(\hat\mu_\mathrm{c}, \hat\mu_\mathrm{w})\Sigma\Sigma_\mathrm{w}{}^{-1}\Sigma_\mathrm{wc} \end{aligned} \qquad \mathbf{(9.1)}$$

The (co)variance matrices can be found by noticing

$$\mathrm{var}\begin{bmatrix} \hat\tau_\mathrm{c} \\ \hat\tau_\mathrm{w} \end{bmatrix} = \sigma^2(\mathrm{X^T H^{-1} X})^{-1}$$

where X is the fixed effects design matrix for the joint analysis of log-body weights and log-carcass quality and $\sigma^2 H$ is the full variance-covariance matrix for that analysis. Notice

$$\mathrm{var}\begin{bmatrix}\hat{\mu}_{\mathrm{c}}\\ \hat{\mu}_{\mathrm{w}}\end{bmatrix}=\mathrm{var}\left(\begin{bmatrix}\mathrm{X}_{\mathrm{c}} & 0\\ 0 & \mathrm{X}_{\mathrm{w}}\end{bmatrix}\begin{bmatrix}\hat{\tau}_{\mathrm{c}}\\ \hat{\tau}_{\mathrm{w}}\end{bmatrix}\right)$$

$$=\sigma^{2}\begin{bmatrix}\mathrm{X}_{\mathrm{c}} & 0\\ 0 & \mathrm{X}_{\mathrm{w}}\end{bmatrix}\left(\mathrm{X}^{\mathrm{T}}\mathrm{H}^{-1}\mathrm{X}\right)^{-1}\begin{bmatrix}\mathrm{X}_{\mathrm{c}}^{\mathrm{T}} & 0^{\mathrm{T}}\\ 0^{\mathrm{T}} & \mathrm{X}_{\mathrm{w}}^{\mathrm{T}}\end{bmatrix}$$

The terms in **(9.1)** can be determined. Confidence intervals on the log-scale can then be determined in the standard manner using the normal approximation.

On the original scale, the confidence interval is simply the back-transformation of the confidence interval on the log-scale.

If the estimate is back-transformed, this is not the mean on the original scale, rather it is the median.

Calculation of the mean involves

$$\mathrm{e}^{\mu_{\mathrm{cw,i}}+\frac{1}{2}\sigma^{2}\mathrm{c}_{\mathrm{w,i}}}$$

A prediction interval for a new y_c given y_w can be found using the distribution

$$\mathrm{y}_{\mathrm{c}}-\hat{\mu}_{\mathrm{cw}}|\mathrm{y}_{\mathrm{w}}\sim \mathrm{N}(0,\Sigma_{\mathrm{cc}}-\Sigma_{\mathrm{cw}}\Sigma_{\mathrm{ww}}{}^{-1}\Sigma_{\mathrm{wc}}+\mathrm{var}(\hat{\mu}_{\mathrm{cw}}))$$

The interval for y_c based on this distribution can be back-transformed as above with the same interpretation.

These intervals will be wider than confidence intervals because they provide an interval for an observation rather than a mean.

There is an argument for using the confidence or prediction interval. The confidence interval for the mean performance provides “what we might expect to see based on experience”, because of years of averaging! The prediction interval reflects the variation likely to be encountered over many animals, that is variability in carcass traits. Both intervals will be presented below, but the confidence intervals reflect more the industry **expectations** in terms of variations.

9.3. Implementation of the model

With respect to the accessibility and the potential users of the model at this stage, it was decided to implement the model in the R program (2004). The model has three phases, i.e. input of data, calculation of predictions and presentation of the results.

Model input

Input to the model is in four components (Table 9.1):

1- Sex, steer (as a default) and heifer

2- Breed (default is Hereford), H = (Hereford x Hereford), S = (South Devon x Hereford), A = (Angus x Hereford), J = (Jersey x Hereford), B = (Belgian Blue x Hereford), W = (Wagyu x Hereford), L = (Limousin x Hereford)

3- Age (days)-weight (kgs) pairs (Table 9.1)

4- Slaughter age (default is 700 days for Steers and 500 days for Heifers)

Model results

The model potentially provides seven outputs (Figure 9.1) as follows:

1. Median of carcass quality traits
2. Means of carcass quality traits
3. Prediction means of carcass quality
4. Lower prediction interval of carcass quality traits (95%)
5. Upper prediction interval of carcass quality traits (95%)
6. Lower confidence interval of carcass quality traits (95%)
7. Upper confidence interval of carcass quality traits (95%)

Market values

In the current study, the economic value of slaughtered animals was determined by retail meat yield. Retail meat yield was calculated from carcass weight, fat thickness, and rib-eye area (Equation 9.2). Based on the equations developed from a bone out trail conducted in 1997 (Ewers et al., 1999). The animals were 1995-drop steers of the crossbreeding project reported herein. In this analysis, it was assumed the domestic wholesale value was \$4.00/kg of lean meat, equivalent to approximately \$1.35/kg live weight (Equation 9.3). Some export markets pay a premium for marbled meat so a premium of \$0.30/kg/% IMF on marbling over 3% IMF (Equation 9.4).

$$\textbf{Retail meat yield}\text{ (kg)} = -24.511 + 0.65774 \times (\textbf{HCWt}) - 0.59595 \times (\textbf{P8}) + 0.54763 \times (\textbf{EMA}) \quad \textbf{(9.2)}$$

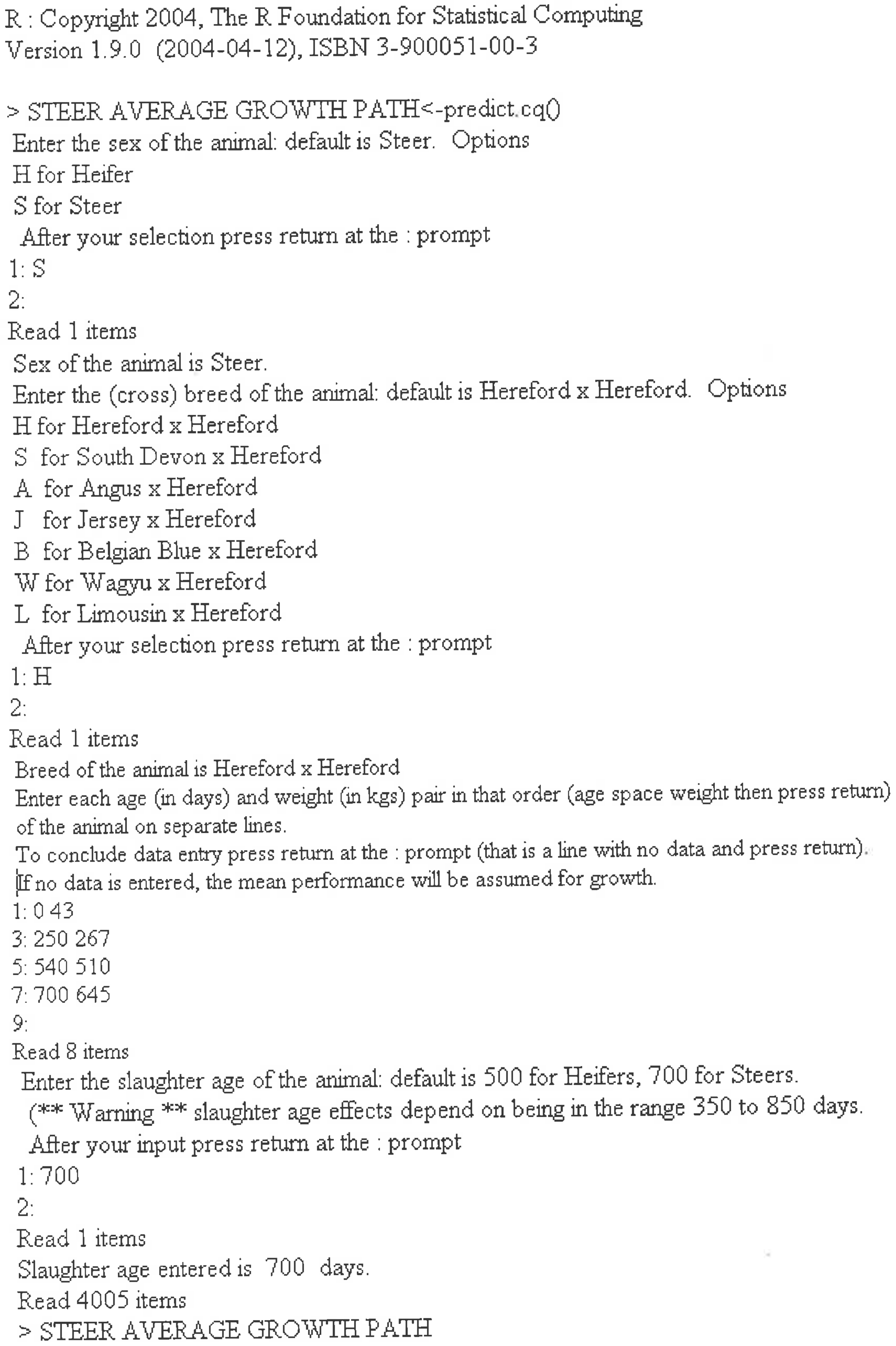
$$\textbf{Domestic value} = \$4.00 \times (\textbf{Retail meat yield}) \quad \textbf{(9.3)}$$

$$\textbf{Export value} = [4.00 + 0.30(\textbf{IMF-3})] \times (\textbf{Retail meat yield}) \quad \textbf{(9.4)}$$

Thus, based on the outputs obtained from the model (9.1), using equations 9.3 and 9.4, the following traits also could produce:

8. Economic value based on the predictions for domestic market
9. Economic value based on the predictions for export market

Table 9.1. R-programme inputs and results screen from the prediction model (example: "average scheme" of steers from experiment 9.1)



```
R : Copyright 2004, The R Foundation for Statistical Computing
Version 1.9.0  (2004-04-12), ISBN 3-900051-00-3

> STEER AVERAGE GROWTH PATH<-predict.cq()
 Enter the sex of the animal: default is Steer.  Options
 H for Heifer
 S for Steer
  After your selection press return at the : prompt
1: S
2:
Read 1 items
 Sex of the animal is Steer.
 Enter the (cross) breed of the animal: default is Hereford x Hereford.  Options
 H for Hereford x Hereford
 S  for South Devon x Hereford
 A  for Angus x Hereford
 J   for Jersey x Hereford
 B  for Belgian Blue x Hereford
 W for Wagyu x Hereford
 L  for Limousin x Hereford
  After your selection press return at the : prompt
1: H
2:
Read 1 items
 Breed of the animal is Hereford x Hereford
 Enter each age (in days) and weight (in kgs) pair in that order (age space weight then press return)
 of the animal on separate lines.
 To conclude data entry press return at the : prompt (that is a line with no data and press return).
 If no data is entered, the mean performance will be assumed for growth.
1: 0 43
3: 250 267
5: 540 510
7: 700 645
9:
Read 8 items
  Enter the slaughter age of the animal: default is 500 for Heifers, 700 for Steers.
   (** Warning ** slaughter age effects depend on being in the range 350 to 850 days.
   After your input press return at the : prompt
 1: 700
 2:
 Read 1 items
 Slaughter age entered is  700  days.
 Read 4005 items
 > STEER AVERAGE GROWTH PATH
```

```
$medians

        Hereford  South    Angus    Jersey   Belgian  Wagyu    Limousin
HCWt    329.63    348.60   347.23   287.84   355.18   299.78   343.56
P8Fat   16.31     13.21    18.99    14.47    11.16    15.34    13.58
EMA     72.00     80.50    75.74    67.72    89.38    72.58    83.46
IMF     4.91      5.03     6.10     6.14     3.94     5.68     4.15
$means
        Hereford  South    Angus    Jersey   Belgian  Wagyu    Limousin
HCWt    329.67    348.63   347.27   287.87   355.22   299.81   343.60
P8Fat   16.34     13.23    19.02    14.49    11.18    15.36    13.60
EMA     72.02     80.52    75.75    67.74    89.40    72.59    83.48
IMF     4.93      5.05     6.11     6.15     3.95     5.70     4.16
$pred.means
        Hereford  South    Angus    Jersey   Belgian  Wagyu    Limousin
HCWt    331.57    350.64   349.27   289.53   357.26   301.53   345.57
P8Fat   17.60     14.24    20.48    15.60    12.04    16.54    14.65
EMA     72.64     81.21    76.41    68.32    90.17    73.22    84.20
IMF     5.37      5.50     6.66     6.70     4.30     6.20     4.53
$lower.PI
        Hereford  South    Angus    Jersey   Belgian  Wagyu    Limousin
HCWt    265.42    280.81   279.65   231.84   286.13   241.52   276.77
P8Fat   7.48      6.07     8.71     6.64     5.13     7.05     6.24
EMA     55.20     61.74    58.08    51.94    68.55    55.67    64.01
IMF     2.12      2.18     2.64     2.66     1.70     2.46     1.80
$upper.PI
        Hereford  South    Angus    Jersey   Belgian  Wagyu    Limousin
HCWt    409.37    432.75   431.13   357.35   440.91   372.09   426.47
P8Fat   35.58     28.75    41.37    31.51    24.29    33.37    29.56
EMA     93.92     104.97   98.77    88.31    116.55   94.62    108.82

$lower.CI
        Hereford  South    Angus    Jersey   Belgian  Wagyu    Limousin
HCWt    319.42    338.83   337.01   279.58   345.32   291.73   334.11
P8Fat   14.44     11.84    16.93    12.92    10.02    13.83    12.21
EMA     69.22     77.59    72.94    65.26    86.14    70.05    80.48
IMF     4.25      4.39     5.31     5.35     3.44     4.98     3.62
$upper.CI
        Hereford  South    Angus    Jersey   Belgian  Wagyu    Limousin
HCWt    340.16    358.65   357.76   296.34   365.33   308.05   353.28
P8Fat   18.42     14.73    21.29    16.19    12.44    17.02    15.11
EMA     74.90     83.53    78.65    70.28    92.75    75.20    86.55
IMF     5.68      5.78     7.01     7.04     4.51     6.49     4.75
$wt.medians
        Hereford  South    Angus    Jersey   Belgian  Wagyu    Limousin
0       42.01     42.46    38.94    34.89    42.85    37.51    42.85
250     262.56    267.07   264.39   240.39   268.51   241.35   267.63
540     400.27    416.04   408.14   364.61   412.65   362.16   405.32
700     651.17    693.64   678.40   607.25   674.59   610.05   680.49

"attr(,""class"")"
[1]       carcasspred
>
```

9.5. Evaluation of the model

Evaluation of the model consisted of examining a dependent and independent experiment that included some "what-if" scenarios that may apply to different circumstances in beef production. The purpose of the examinations was to determine the effects of different growth rate schemes (Experiment 9.1) and independent growth path (Experiment 9.2) on subsequent weight of carcass (HCWt), fat depth (P8), eye muscle area (EMA) and intramuscular fat (IMF) and economic values for domestic and export markets. Evidence exists that when growth patterns are interrupted, animals alter composition of growth so that it is possible to alter product composition to meet given specifications. The dynamics of genetic propensity for maturation, pattern for modifying growth pattern through the use of mass can alter body mass accumulation, and tissue distribution in accumulating deferred growing systems (Dockerty et al., 1973).

9.5.1. Experiment 9.1.

Influence of backgrounding growth rate on carcass quality traits and market values of crossbred cattle (a dependent test)

This experiment design is based on the data collected from "The Southern Crossbreeding Project". In this project (Chapter 2), calves were weaned in summer (mid December-early January) at 250-300 days of age. Calves were grown until 12-18 month of age and then transported to a commercial feedlot for 70-90 days (heifers) and 150-180 days (steers) except the 1997 steers which, after a good pasture season in 1998, reached marketable weight without requiring grain finishing. Dry season occurred after weaning until nearly 470 days (December to June) and wet season, between approximately 470 days and 600 days (July to December) every year. Feed was of low quality and availability during late summer-autumn each year. In the feedlot, steers and heifers were fed a minimum of 60% grain (various but primarily barley) with approximately 12MJ/kgDM energy and 13% protein. This experiment included various schemes based on varying backgrounding and feedlot growth rates and keeping body weights at the 300 days constant. The design of the experiment in heifers and steers are given in Table 9.2. It was assumed that all heifers and steers slaughtered at the same age and backgrounded and finished for the same days (Figure 9.2).

Heifers. The heifer scenarios, which have been used in this example, were (Table 9.2):

1) weaning followed by no gain until slaughter (VLVL),

2) weaning followed by no gain followed by high growth (1.45 kg/d) until 362 kg live weight at the same slaughter age (VLH),

3) weaning followed by low growth rate (0.68 kg/d) followed by no gain during backgrounding period until 362 kg live weight at the end (LVL),

4) average growth path based on the predicted mean obtained from cubic sire model (Chapter 5), which resulted from low growth rate during backgrounding and feedlot periods (Ave),

5) weaning followed by the low growth rate up to slaughter (LL),

6) weaning followed by high gain in both periods until 608 kg live weight at slaughter age (HH).

Steers. The seven growth path schemes that have been used for steers were (Table 9.2):

1) no gain from birth to slaughter (NGNG),

2) weaning followed by no gain during backgrounding but very high growth rate (2.11 kg/d) during feedlot (NGVH),

3) low growth rate from weaning to slaughter (LL),

4) same as the heifers the average growth path of steers obtained from cubic sire model (Chapter 5), growth rate during the pre-weaning, backgrounding and feedlot periods were 0.86, 0.49 and 1.48 kg/d, respectively (Ave),

5) medium growth rate (0.84 kg/d) during both periods after weaning (MM),

6) high growth rate during backgrounding period but no gain during feedlot period (HNG),

7) weaning followed by high gain (1.28 kg/d) up to slaughter (HH).

Figure 9.1 depicts that at all schemes, steers were slaughtered at the same age (700 days). After entering the input for each scheme, the model provided seven outputs as illustrated in Tables 9.1 and 9.3. For added convenience, the model provided predicted of carcass traits and live weights at entered ages. Based on the predictions of the model for HCWt, P8 and IMF for seven breeds, economic values for the domestic market and export market of each scenario were computed. For simplicity, in both examples, results corresponding to purebred Hereford have been selected from the outputs.

Table 9.2. Experimental schemes for the growth rate during backgrounding and finishing periods

	Growth rate kg/day					Age (days)-body weights kg				
Heifer	Pre-weaning	Backgrounding		Feedlot		Birth	250 d	420 d	500 d	Slage
NGNG	0.90	no gain	0.00	no gain	0.00	39	246	246	246	500
NGH	0.90	no gain	0.00	high	1.45	39	246	246	362	500
LNG	0.90	low	0.68	no gain	0.00	39	246	362	362	500
Ave	0.90	low	0.54	low	0.30	39	246	338	362	500
LL	0.90	low	0.68	low	0.68	39	246	362	416	500
HH	0.90	high	1.45	high	1.45	39	246	492	608	500
Steer	Pre-weaning	Backgrounding		Feedlot		Birth	250 d	540 d	700 d	
NGNG	0.83	no gain	0.00	no gain	0.00	43	267	267	267	700
NGVH	0.83	no gain	0.00	very high	2.11	43	267	267	605	700
LL	0.83	low	0.49	low	0.49	43	267	409	488	700
Ave	0.83	low	0.49	high	1.48	43	267	409	645	700
MM	0.83	medium	0.84	medium	0.84	43	267	510	645	700
HNG	0.83	high	1.28	no gain	0.00	43	267	639	639	700
HH	0.90	high	1.28	high	1.28	43	267	639	844	700

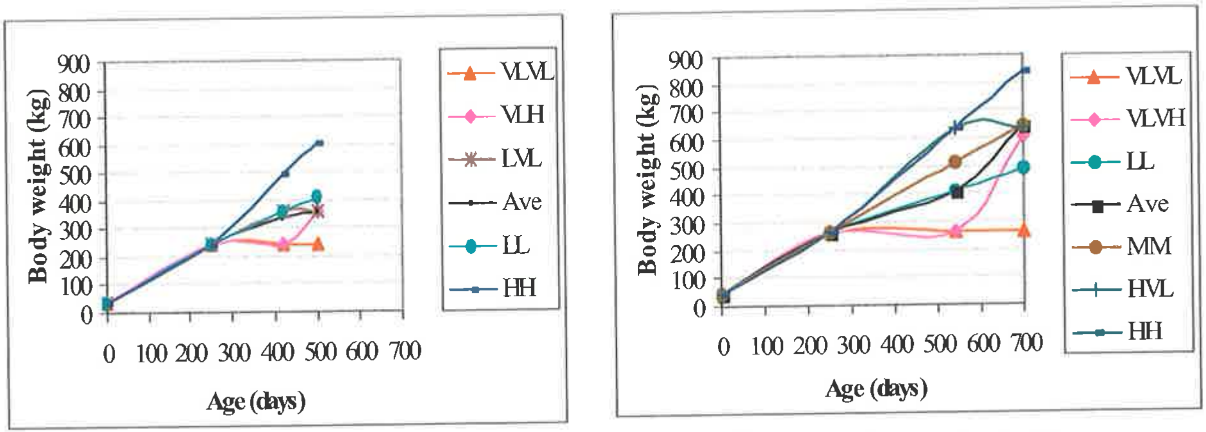


Figure 9.1. Schematic representation of growth curves of various shemes for heifers (left) and steers (right) during backgrounding and finishing periods

Results (experiment 9.1)

Predicted values of carcass quality traits for heifers and steers obtained from average growth path revealed that differences existed between breeds for all traits (Tables 9.1 and 9.3). Steers and heifers were alike with respect to breed differences in carcass traits (Table 9.1), a result that follows from not having sire breed by growth path interactions in the random effects model. Also it can be seen in Tables 9.1 and 9.3 that the median and mean values for carcass quality traits are almost similar. The Tables 9.1 and 9.3 show a 95% prediction interval produced using the original data. As a result (Tables 9.1 and 9.3), prediction intervals were wider than the corresponding confidence intervals. Based on the Ave scheme, Jersey heifers were expected to have a carcass weight in the range 147.54-235.62 kg. Note that (Table 9.3) the 95% confidence interval for the mean of the HCWt of the population was (180.01-193.12 kg) much narrower than the prediction interval, as discussed above.

All carcasses of crosses were grouped into heavy and light groups (Tables 9.1 and 9.3). Belgian Blue, Limousin, South Devon, Angus and Hereford had heavier HCWt and EMA than those of Wagyu and Jersey. Mean of carcass P8 fat was highest for Angus and lowest for Belgian Blue. Carcasses of heifers from Belgian Blue, Limousin and South Devon had less marbling (lower IMF than those of Angus, Jersey, and Wagyu). Carcasses of the Jersey and Wagyu had the lowest and Belgian Blue, Limousin and South Devon had the highest value for retail meat yield. Consequently, the same pattern was observed for the domestic and export market values (Tables 9.3). The prediction model also constructed prediction intervals and confidence limits for predicted carcass quality traits at the 95% level.

Heifers. Deviations of carcass traits of heifers obtained from different growth schemes from average growth path indicated that the carcass fat traits were the most sensitive to growth variation (Figure 9.2). At the slaughter, heifers that were backgrounded with no gain were 17% (NGNG) and 4% (NGH) lighter than those backgrounded with low growth rate (AVE) (Table 9.3, Figure 9.2). Those backgrounded and finished with high growth rate (HH) achieved 74% and 80% more P8 fat and IMF than for the average growth path when they gained 608 kg at slaughter. Increasing growth rate at 1.45 kg/d during backgrounding and feedlot periods resulted in increasing up to 30% and 50% in domestic and export carcass values, respectively (Figure 9.3). It seems that there were no significant differences between effects of both schemes LNG and average growth path in terms of carcass quality traits and the market values (Figure 9.3).

Table 9.3. Results from the prediction model for the "average growth scheme " of heifers (experiment 9.1)

	Jersey	Wagyu	Angus	Hereford	Sth Dev	Limousin	Bel Blue
Median of carcass quality traits							
HCWt	186.45	194.19	224.86	213.47	225.73	222.49	230.57
P8	10.11	10.73	13.26	11.4	9.22	9.49	7.79
EMA	68.34	73.24	76.37	72.61	81.16	84.16	90.12
IMF	3.85	3.57	3.81	3.07	3.15	2.59	2.46
Mean of carcass quality traits							
HCWt	186.48	194.22	224.89	213.51	225.77	222.52	230.03
P8	10.14	10.75	13.3	11.43	9.25	9.51	7.81
EMA	68.37	73.26	76.4	72.63	81.19	84.18	90.15
IMF	3.86	3.57	3.82	3.08	3.15	2.6	2.47
Predicted means for carcass quality traits							
HCWt	187.73	195.52	226.4	214.94	227.28	224.01	231.58
P8	11.09	11.76	14.55	12.5	10.12	10.4	8.55
EMA	69	73.94	77.11	73.31	81.94	84.97	90.98
IMF	4.21	3.9	4.17	3.36	3.44	2.84	2.69
Lower prediction interval for carcass quality traits							
HCWt	147.54	153.7	177.92	168.87	178.64	176.09	182.03
P8	4.28	4.54	5.61	4.82	3.91	4.02	3.3
EMA	51.83	55.54	57.91	55.03	61.53	63.82	68.33
IMF	1.65	1.53	1.63	1.32	1.35	1.11	1.06
Upper prediction interval for carcass quality traits							
HCWt	235.62	245.35	284.18	269.84	285.23	281.11	290.61
P8	23.89	25.32	31.34	26.96	21.78	22.4	18.4
EMA	90.12	96.58	100.73	95.8	107.04	110.98	118.85
IMF	8.98	8.31	8.9	7.18	7.34	6.05	5.74
Lower confidence interval for carcass quality traits							
HCWt	180.01	187.74	216.94	205.69	218.06	215.05	222.29
P8	8.78	9.36	11.49	9.81	8.03	8.27	6.8
EMA	64.92	69.57	72.47	68.77	77	79.91	85.53
IMF	3.35	3.11	3.31	2.65	2.73	2.26	2.14
Upper confidence interval for carcass quality traits							
HCWt	193.12	200.86	233.06	221.54	233.67	230.18	237.98
P8	11.65	12.29	15.31	13.23	10.6	10.88	8.94
EMA	71.94	77.1	80.49	76.66	85.54	88.63	94.94
IMF	4.43	4.09	4.4	3.57	3.62	2.98	2.83
Median body weights (kg)							
Birth	32.29	34.72	36.05	38.88	39.3	39.67	39.67
250 days	224.58	225.48	247	245.28	249.5	250.03	250.85
420 days	306.54	303.85	340.7	335.24	344.35	338.47	344.34
500 days	327.96	325.26	366.41	359.94	372.44	363.58	370.6
Market Values							
Domestic market $/carcass	520	550	631	598	654	651	689
Export market $/carcass	557	577	675	604	665	635	664

Steers. Some differences were detected for the effects of various schemes on the subsequent carcass quality traits of steers though not significant (Table 9.1). In general, like heifers, carcass fat traits of steers were more affected by growth manipulations than quantity traits (Figure 9.2). Steers whose growth was limited during backgrounding and weighing were 30% less than average growth path were leaner: 15% lower P8 fat and 6% lower IMF at the end of feedlot (Figure 9.2). Carcass quality traits and economic values due to HNG scheme were higher than HH scheme though not significantly. The HNG scheme had 4% higher HCWt, 19% higher P8, 3% higher EMA and 9% higher IMF compared to the HH scheme. Therefore, it appears that backgrounding growth rate demonstrated a crucial role at the subsequent carcass quality traits particularly fat traits and consequently their economic values (Figures 9.3).

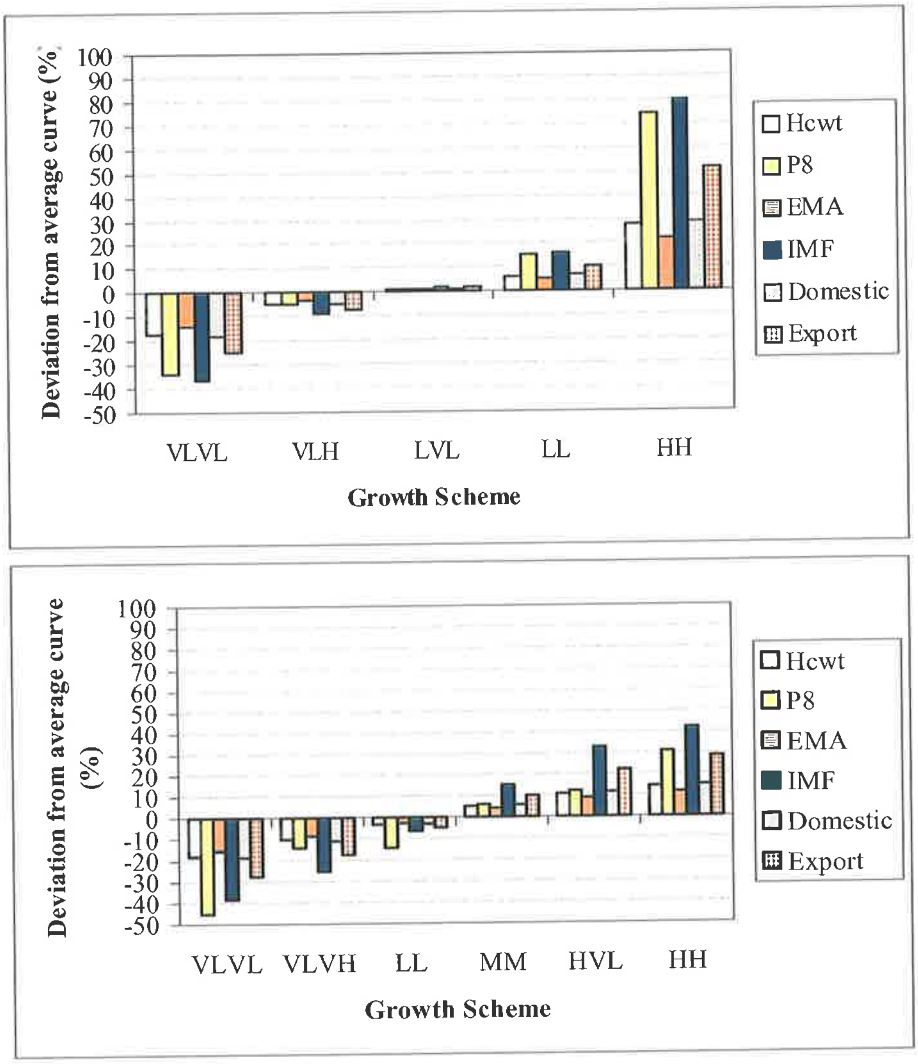
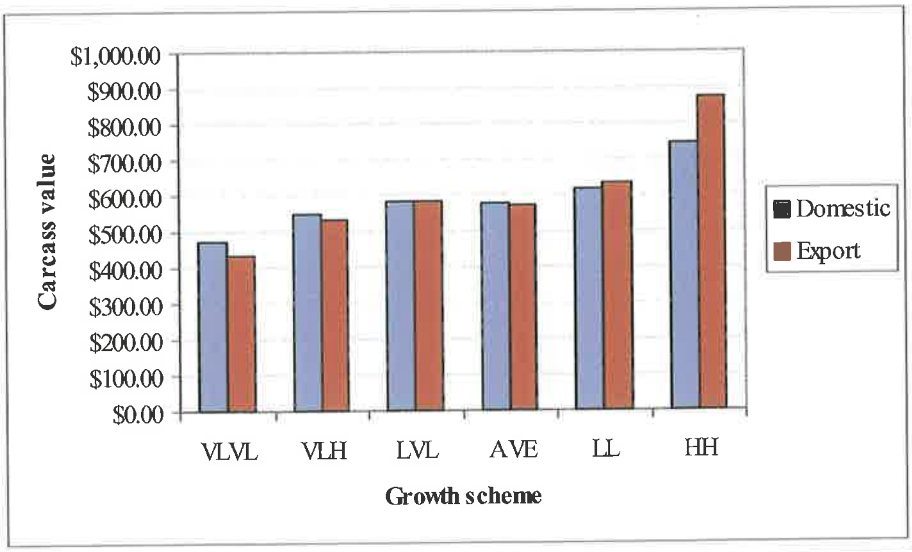


Figure 9.2. Deviations of the different schemes from the average growth path for Heifers (top) and Steers (bottom)

The following two graphs show the effect of different growth schemes on the domestic and export markets. The export market was more sensitive to growth rate modifications than the domestic market, reflecting a greater economic value for fat. The NGNG scheme had the smallest and the HH scheme, by far the largest export value. No significant differences were detected between domestic and export market when there were low and no gain during backgrounding and feedlot periods, for both heifers and steer calves. As the growth rate increased the differences between these two markets increased (Figure 9.3).



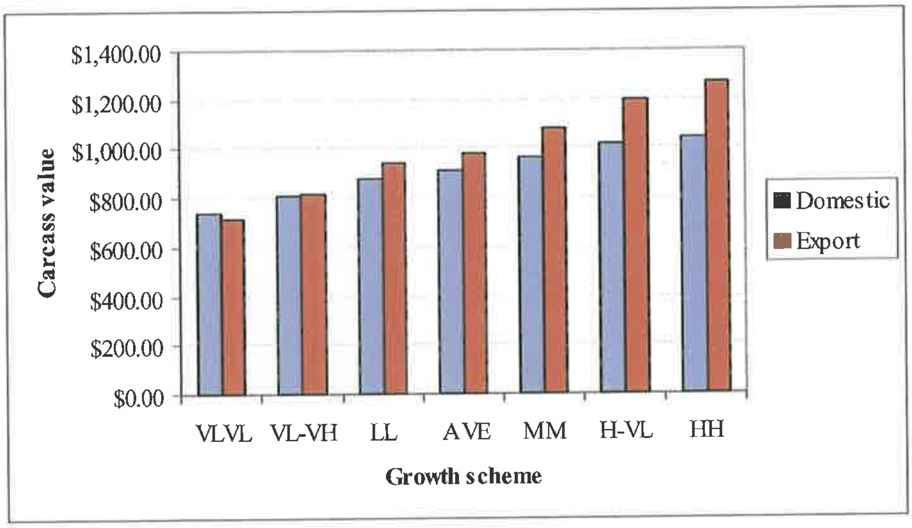


Figure 9.3. Comparsons among carcass values obtained from different growth schemes for heifers (top) and steers (bottom)

Generally, predicted median carcass quality traits of heifers and steers in this study revealed that differences existed between breeds for all traits but the ranking of the breeds within each sex were the same. With respect to breed comparisons, all schemes, followed the same pattern of quantity and fat traits for both heifers and steers.

9.5.2. Experiment 9.2.

Application of the model to another data set

The aim of this modelling study was to construct a tool to predict carcass quality traits in growing cattle under various management conditions. This aim implies that the model has to be tested against various data sets. This is critical to the success and credibility of any model. Data were collected from "The development of multi-breed EBV's in beef cattle" project, where Hereford and Angus dams were mated to Angus, Hereford, Limousin and South Devon bulls (Graham et al., 2002). Briefly, the project was designed to examine the difference between the bases used to calculate EBVs for each breed, the ranking of bulls in each breed, according to their multi-breed EBVs and to measure differences in fertility, maternal traits and reproductive performance of crossbred and pure bred cattle. However, it should be noted that this data set was not completely independent, due to rearing the steers at the same property with the same cows as the original study. The cattle were slaughtered at two final carcass weights, heavy domestic and Japanese market.

Results (experiment 9.2)

The estimated body weights from birth to slaughter resulted from the growth model and the growth path obtained from the multibreed data set are displayed in Figure 9.4. Fairly similar patterns occur for both data sets, body weights of all breeds increase over pre-weaning period, hold fairy steady after weaning, and then increased again toward the end of follow-up period. However, predicted body weights (current model) exhibited not a good enough fit at the mean level and slightly overestimation at the edge of the trajectory (Figure 9.4), probably as a function of using polynomial modelling. These issues will lead to the bias at the genetic level.

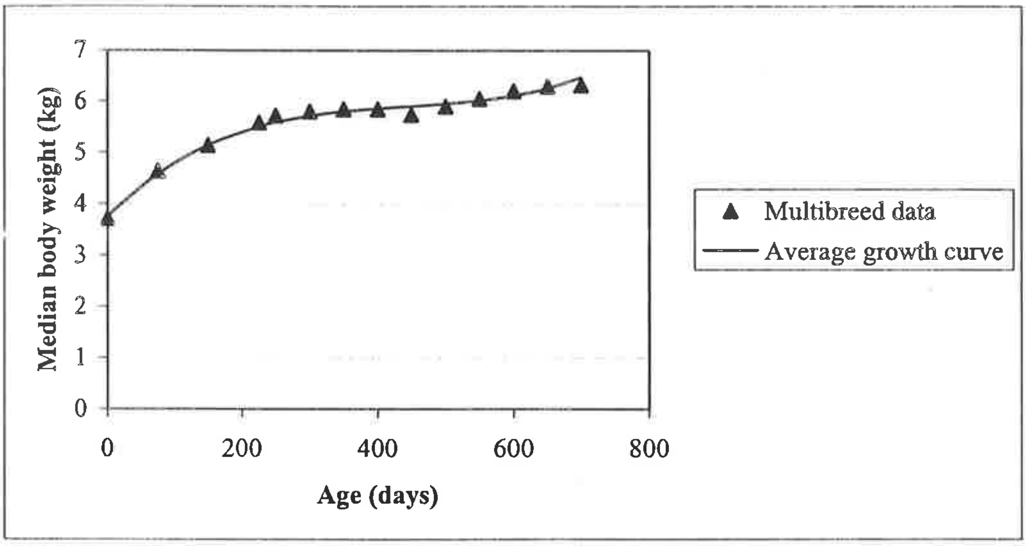


Figure 9.4. Actual growth path from the multibreed data set and predicted growth path derived from the cubic growth model

As Table 9.4 demonstrates, it seems that there were the same breed differences in growth pattern of four crossbreeds in multibreed data set.

Table 9.4. Summary statistics of the body weights and carcass quality traits from the multi-breed data set (Experiment 9.2).

	Angus		Hereford		South Devon		Limousin	
Age (days)	Mean	S.D[b]	Mean	S.D[b]	Mean	S.D[b]	Mean	S.D[b]
Birth	39.21	6.37	39.72	194.95	44.07	6.43	41.76	6.57
300	337.41	28.82	323.00	201.08	336.50	30.93	313.40	32.70
500	374.14	29.07	360.40	197.79	376.38	29.56	353.00	34.29
700	568.67	36.49	538.50	199.61	559.69	31.05	538.16	33.73
Slaughter age	693.24	12.55	704.56	203.35	695.63	13.86	701.68	13.81
	Mean	S.E[c]	Mean	S.E	Mean	S.E[c]	Mean	S.E
HCWt	310.14	3.35	294.51	3.55	306.05	3.24	302.82	3.55
P8	15.93	0.73	16.76	0.77	12.167	0.706	12.92	0.77
EMA	68.82	1.17	64.00	1.24	70.37	1.13	74.38	1.27
IMF	4.33	0.22	4.40	0.24	3.92	0.21	3.68	0.24
	Median	SD[d]	Median	SD	Median	SD	Median	SD
HCWt	309.20	16.21	295.20	19.81	308.50	17.41	302.82	15.82
P8	16.50	4.27	17.00	3.82	11.50	3.25	12.92	3.72
EMA	69.50	7.15	64.00	6.88	70.00	4.83	73.50	5.90
IMF	4.86	1.29	4.86	1.11	3.20	1.34	3.68	0.75
No.[a]	29		25		30		25	

[a] number of observations, [b] standard deviation, [c] standard error of mean, [d] standard deviation

Predicted mean, wider prediction interval than confidence interval as well as domestic and export values for HCWt, P8, EMA and IMF corresponding to each crossbreed from the data are shown in Table 9.5. South Devon and Angus sires produced progeny with heavier HCWt. The predicted mean of P8 fat depth for the progeny from Angus and Hereford sires were 17.96 and 16.44 mm (Table 9.5). The Limousin sires produced progeny that had significantly larger EMA than the other three genotypes. IMF was calculated from the equation

$$\textbf{IMF} = 1.66\ (\textbf{marble score}) + 3.2\ (R^2 = 0.99) \qquad \textbf{(9.6)}$$

developed by Kruk et al. (2002). The Angus sired progeny had significantly more marbling with mean predicted score of 0.94 and the Limousin sired progeny had the least (Graham et al., 2002), IMF had the same value in all four breeds (Figure 9.5). In general, as in experiment 1, for all carcass quality traits, the prediction interval was wider than confidence interval. For instance, the prediction interval of HCWt of Hereford ranged from 254.96 to 393.25, indicating wider range than confidence interval (306.82 to 326.76) (Table 9.4).

Evaluation of the current model involved comparing predicted values of carcass traits to its actual values, to determine how closely predicted outcomes agree with actual outcomes. The predicted outcomes derived from the predictive model, after all the unknown model parameters have been estimated from the all available age-weight data points for each breed of steers. The sires used in the data set were Hereford, Angus, South Devon and Limousin. The difference between predicted and actual values can be thought of as elements of variation unexplained by the fitted model or as a bias.

Table 9.5. Predicted mean and confidence intervals for the carcass quality traits and carcass values of steers obtained from the prediction model

	Angus	Hereford	South Devon	Limousin
Predicted means for carcass quality traits				
HCWt	335.45	318.51	336.72	331.90
P8	17.96	15.44	12.48	12.84
EMA	72.27	68.71	76.79	79.63
IMF	5.49	4.42	4.52	3.73
Lower confidence interval for carcass quality traits				
HCWt	323.67	306.84	325.38	320.88
P8	14.84	12.67	10.38	10.70
EMA	68.98	65.48	73.36	76.11
IMF	4.37	3.50	3.61	2.98
Upper confidence interval for carcass quality traits				
HCWt	343.61	326.76	344.41	339.30
P8	18.67	16.16	12.91	13.25
EMA	74.39	70.84	78.98	81.85
IMF	5.78	4.68	4.76	3.91
Market Values				
Domestic market $/carcass	904.44	904.44	964.85	956.99
Export market $/carcass	972.27	972.27	1,037.22	1,028.77

Therefore, overestimation of carcass values occurs where subtraction resulted in a positive value, and underestimation occurred where the result was negative. In addition confidence interval calculated from the actual data can be thought of as the set of true but unknown differences that are statistically compatible with the observed difference. For comparitive purposes, the differences between predicted and actual values of steers across sire breeds are shown in Figure 9.5.

Deviations of predicted from actual values for HCWt, P8 and EMA ranged from 3-13% (Figure 9.5) and in all cases they were inside the range of confidence intervals, indicating that the model fitted the test data (multi-trait data set) properly.

Table 9.6 shows model performance of the joint model based on the individual records from the multi-breed project. It is clear that model accuracy decreases as the prediction interval increases. As shown in Table 9.6 and Figure 9.6 there are wide prediction intervals for all three traits, particularly for fat traits. The performance of the model seems to be better for HCWt and EMA than P8 fat.

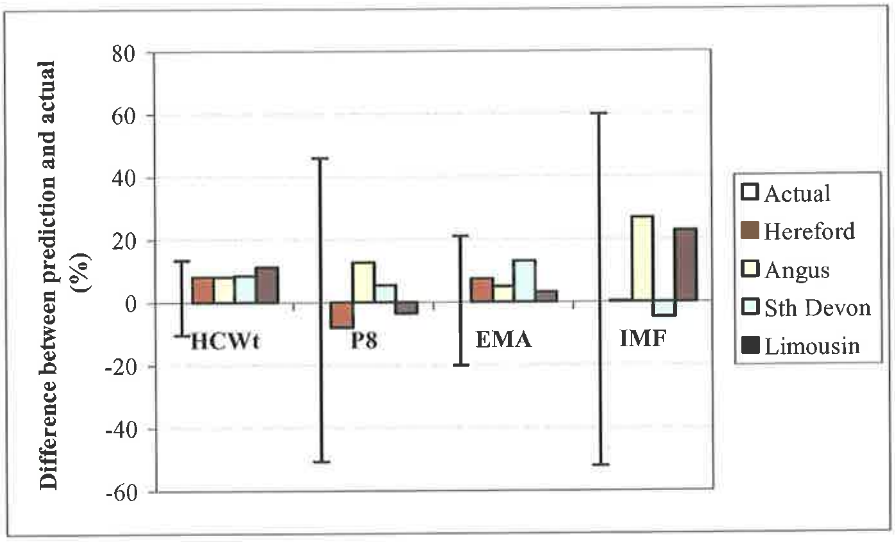


Figure 9.5. Comparison between actual mean and predicted means (Experiment 9.2)

Table 9.6. Predicted values and prediction intervals for the carcass quality traits of steers obtained from the prediction model

	Values		Prediction interval	
Calf tested	Actual	Prediction	Lower	Upper
		HCWt (kg)		
1	285	337	269	418
2	297	345	275	418
3	306	339	270	420
4	311	347	277	430
5	325	345	276	428
		P8 (mm)		
1	18	19	8	38
2	21	13	9	38
3	14	14	6	28
4	14	8	6	29
5	21	16	9	44
		EMA (cm^2)		
1	69	64	53	89
2	73	65	55	89
3	78	68	59	101
4	80	78	61	103
5	73	70	56	95
		IMF (%)		
1	5	3	2	11
2	5	3	2	11
3	4	3	1	8
4	4	3	2	9
5	5	5	2	10

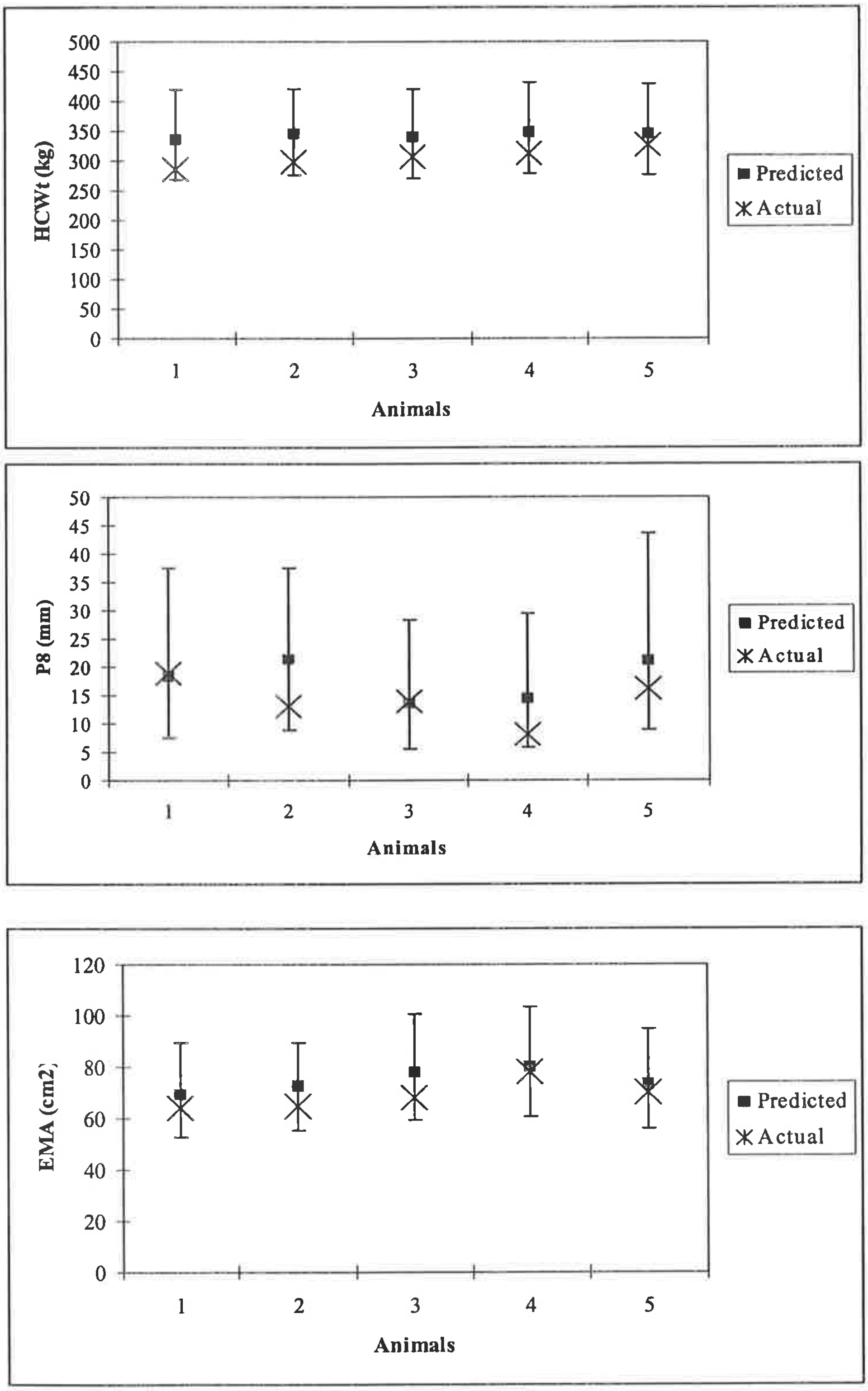


Figure 9.6. Comparison between actual value and predicted values of individual (Experiment 9.2)

9.6. Discussion

The present empirical model attempts to offer a practical solution in investigating relationships between growth and carcass traits. Empirical models (Parks, 1982; Devir et al., 1997) allow an animal's weight gain to be expressed as a relatively simple function, allowing experimental comparison of different genetics and/or feeding regimes (Thompson et al., 1985; Thompson and Barlow, 1986) and investigation of body composition (Parks, 1982; Pleasants et al., 1997). While, empirical models cannot give a real understanding of the system under study (Vetharaniam et al., 2001), such a model could be used to predict the behaviour of the system where data do not exist.

Application of the model

The current model deals with one of the greatest challenges facing growth modellers in the beef industry; how to predict carcass quality resulting from specific growth path at various stages of growth. Estimates of carcass quality over growth path help producers to predict the age required for each animal to reach a specific target body weight and market specifications. Carcass quality is influenced by many factors, including body weight, sex, breed, nutrition, health status and by interactions between these factors. Reid et al. (1971) stated that as animals grow, their carcass composition changes and their body composition is almost controlled by weight. However, there are important exceptions to this weight dependency on composition at given weights e.g., sexes differ in composition at given weights as do breeds and animals fed on widely differing planes of nutrition (Berg and Butterfield, 1976). Moreover, patterns of growth can be altered in order to manipulate slaughter age or body weight at the point of slaughter. This manipulation is also possible because cattle typically were slaughtered at weights substantially less than mature weight (Owens et al., 1995).

Hence, herein it has been attempted to predict carcass quality associated with variations in growth path.

The ability of the current model to accommodate different sexes across seven sire breeds and various post-weaning management groups at any slaughter age provides the flexibility required by producers with varying situations. The strength of the present model lies in its simplicity, which allows the user to predict body weight and carcass quality and consequently carcass value with a relatively limited number of parameters.

The outputs of the model cater for producers who wish to sell steers and heifers on within a short period of time, to the producer who wishes to target a specific market in terms of carcass quality where, for example, leanness is a major consideration (domestic market) rather than marbling (export market). Potentially, the model can be useful in answering basic questions and examining "what-if" scenarios that may apply to many different circumstances in beef production. If actual performance differs greatly from predicted performance, then it can be used to systematically evaluate why these differences are occurring. Moreover, another potential use of this model would be to incorporate it into the economic beef production model that simulates the commercial and economic decision-making process involved in the practical management of beef production. Animal nutritionists and lecturers in teaching students of meat science and encouraging them to investigate the response of the animal to a range of management and feeding planes could also use it.

Test of the model

As mentioned earlier, the goal of prediction in this chapter is to determine future value(s) of the carcass quality traits based on observed fixed effects, breed, sex and previous growth performance. We tested the model regarded as an analysis of the behavior of the model in response to various factors with the same data sets as well as against outputs of other data sets. To this end, the predicted values were computed by inputting the value(s) of the age-weight pairs of different schemes into the model. A critical part of prediction is an assessment of how much predicted values fluctuate due to the noise in the data. In the current analysis, a prediction interval for the value of carcass quality traits was computed using the fitted model. This interval gave the range of plausible values for a single future carcass quality observed at slaughter age based on the parameter estimates and the noise in the data. As a result (Tables 9.1 and 9.3), prediction intervals were always a lot wider than the corresponding confidence intervals. Referring back to the defining expression for prediction intervals (section 9.2), because the prediction interval is an interval for the value of a single new measurement from the process, the uncertainty includes the noise that is inherent in the estimates of the regression parameters and the uncertainty of the new measurement. This means that the interval for a new measurement will be wider than the confidence interval for the value of the regression function. Therefore, these intervals are called prediction intervals rather than confidence intervals because the latter are for parameters, and a new measurement is a random variable, not a parameter.

Overall, the median and mean values for carcass quality traits were similar. This occurred because as given in Chapter 2 (2.2.1), the mean of body weight was $E(\text{Body Weight}) = \exp(\mu + \sigma^2 / 2)$ and the median is $\exp(\mu)$. Because the standard error (σ) of estimation based on the log transformation is so small relative to μ then the `` $\sigma^2 / 2$" term becomes negligible and can be ignored.

For evaluation of the current model, the hypothesis was that backgrounding and growing programs could have effects on target carcass quality characteristics.

Therefore, patterns of growth during the backgrounding and feedlot altered in order to manipulate body weight at the point of slaughter. It has shown that beef cattle backgrounding and growing programs can have profound effects on subsequent feedlot performance (Drouillard et al., 1991), body composition (Loerch, 1990; Carstens et al., 1991; Knoblich et al., 1997; Choat et al., 2002) and nutrient metabolism (Thomson et al., 1982 and Fox et al., 1972). Rompalla et al. (1985) and Hersom et al. (2004) have also reported that previous nutrition that restricts cattle growth and limits body fat deposition can positively affect cattle performance in the feedlot through increased growth. It is well established that among many factors, which contribute to variation in growth performance and carcass composition in cattle, effects of previous plane of nutrition plays the major role on subsequent growth. Altering previous nutrition has also been reported to affect composition of body weight gain in the feedlot. However, there has been a large variation reported in the literature on the effect of restricted-realimentation response on body composition (Tudor and O'Rourke, 1980; Abdalla et al., 1988; Carstens et al., 1991; Sainz et al., 1995).

In experiment 1, it was assumed that calves exhibited four possible responses in consequent to experiencing various growth rates during the backgrounding period. If steers had grown as in the AVE and heifers as in the NGH schemes (Figure 9.2) the steers and heifers were able to attain the same weight for age as unrestricted counterparts. This has most recently been observed in cattle (Ryan et al., 1993; Yambayamba et al., 1996), but has been reported numerous times in sheep, pigs, and chickens (Ryan et al., 1993; Zubair and Leeson, 1994; Zubair and Leeson, 1996; Kamalzadeh et al., 1997).

Often, feed restriction at a young age and consequently slow early growth may be followed by compensatory gain later in life resulting in a similar body weight and body composition at slaughter as in unrestricted animals (Berge et al., 1991). This gain is valuable for enhanced efficiency when attempting to grow animals to particular slaughter weights.

In the NGVH scheme, steers increased their rate of gain upon feedlot, but were unable to attain the same weight for age as unrestricted animals. Apparently the growth pattern of calves backgrounded for lower growth rate was shifted toward later maturity in that they could not achieve the level of fatness as those backgrounded for faster growth rate (Figures 9.3 and 9.4). Therefore, this scheme highlighted that allowing animals to slow down in the backgrounding phase may limit potential carcass quality.

If steers had grown as in the LL scheme, then no compensation occured during feedlot, which is a less common response to nutritional restriction followed by realimentation in practice (Figure 9.2). This has been observed in various species and is usually seen when nutrient restriction has occurred at a very young age (Morgan et al., 1972; Tudor and O'Rourke, 1980).

In some cases such as NGNG scheme in heifers and steers, when nutrient restriction has been imposed during backgrounding and feedlot at a level much more severe than what might occur due to seasonal variation in a grazing system or other stresses, a reduction in mature size or permanent stunting has been observed (Taylor et al., 1981). However, the importance of such findings to this subject area is minimal since while this could occur during periods of extended drought, this type of restriction would never purposely be applied at the field level due to its obvious negative results.

The high growth rate during the feedlot period (e.g. HH scheme) had the significant influence on fat thickness and on intramuscular fat content in agreement with Robinson et al. (2001) who reported that systems of finishing (feedlot or pasture) had the significant influence on fat thickness and on intramuscular fat content. This probably occurred because the high growth rate of feedlot-finished cattle predisposes them to increase fatness (Keele et al., 1992) and even at the same growth rate, feedlot finished cattle deposit fat more that range finished cattle (Tudor and O'Rourke, 1992; Sains et al., 1995). This is likely due to reduced maintenance needs in grain fed cattle by lower visceral mass and improved efficiency of nutrients used in grain fed cattle by increasing supply of glucose precursor molecules (Oddy et al., 1997).

The variability in the body weights and gain responses that are seen within and among schemes in experiment 9.1, suggests the potential interaction of nutritional, physiological and genetic factors. So far, the four important factors which influence on those variation have been identified include the age at which the restriction is applied, the sex and genotype of the animal, the length and severity of the restriction and the quality and length of refeeding of the realimentation diet (Ryan, 1990; Zubair and Leeson, 1996). Carstens et al. (1989) reported biological mechanisms that may account for the variability in the body weights and gain due to compensatory growth include changes in feed intake, efficiency of energy and protein utilization, maintenance energy requirement, and change in composition of gain.

The types of evaluation of growth models across the literature varies from one study to another; it may consist, or be a combination, of a sensitivity and behavioral analysis of the model (Gerrits et al., 1997; Vetharaniam et al., 2001), a comparison between simulation and measurements from experiments (Oltjen and Owens, 1986;Williams et al., 1992), and a test of the developed model results against outputs of other models. It could be ideal to compare the model outputs using many different data sets. While evaluation, it is noted that the model must not be employed beyond the range of the data upon which it was developed.

Prediction issues

The joint model attempts to predict carcass quality traits from a series of body weights. The issue of error associated with the predictions obtained from the joint model has three main sources. One source is the stochastic character of the estimated model coefficients, which can be reduced only by gathering more measurements per animals distributed across the trajectory that contains more variation especially during the pre-weaning period. Besides using more frequent of body weights, it would be worth using additional growth measures along with live weights such as body measurements (height, length, girth, hip width and stifle width and etc), P8 fat depth, real time EMA. Fortunately, all these measurements are available in the data set reported herein but time limitations prevented their inclusion in this thesis.

Bias in the estimated parameters was also caused by measurement errors in the data used for model construction. It was contended that live weight often may be an unreliable indicator of empty body mass (Owens et al., 1995), due to large variations in gut fill (Stock et al., 1983), animal movement on the scales and the effects of diet switches on estimation of live weight (Tolley et al., 1988). Frequent bias in the estimation of animal weight severely limits the ability to ascribe true value to various phases of production in integrated systems. Inaccurate or biased estimates of body weight can mask effects of treatments, leading to wrong conclusions with potentially significant economic ramifications. Also, carcass weight was the crucial trait in this study.

Moreover, prediction accuracy of such a model is highly dependent on the high correlation of predictors. For example, there is a limit to the R^2 of carcass traits that can be achieved by modeling weight traits, so that even if a trait has a correlation of 0.8, it only explains 64% of the variation, leaving 36% unexplained. Furthermore, it seems that the prediction error herein comes from the large environmental variances and very small covariances between carcass traits and body weights as shown in Table 7.3 and Figure 8.2. Large prediction intervals around the individual values of P8 fat showed that the model did not perform well in the prediction of fat traits.

Considering the fact that some parameters were not able to be estimated (Table 5.6), the current model performance might have been degraded due to data structure.

Using polynomial might be caused some problem here as as outlined in chapter 5. Since the current model involves a cubic regression model, further research may necessary to develop other methods to overcome this issue. This issue will be addressed in chapter 10. As discussed earlier (Chapter 7), the size of the data set, ability of the program used, the nature of relationships between traits and number of parameter estimated could influence on the possibility of estimations.

9.7. Conclusion

The potential of the present model lies in its simplicity to give answers to 'what if' questions in order to manipulate slaughter age or body weight at the point of slaughter. The model provides a tool by which the producer can assess the impact of possible changes in future management decisions. However, the weakness lies in the lack of precision of predicted carcass traits. Results obtained from the prediction model to evaluate different growth schemes revealed that allowing animals to slow down in backgrounding phase may limit potential carcass quality.

This approach potentially is very useful if data structure issues well addressed. Still, some topics remain unsolved and need further research.

Therefore, the following activities are proposed:

- fitting management group nested within sex
- applying other independent data sets
- applying more growth measures along with live weights such as body measurements especially height and P8 fat scan
- applying functions other than polynomial, such as piecewise linear regression models and spline functions.

Chapter 10

Random regression models of growth

- Piecewise linear regression

10.1. Introduction

Various non-linear models to describe growth have been evaluated (Chapter 1). Although some of these models, yield biologically interpretable results; several difficulties are encountered in fitting non-linear growth models. Shortcomings include fixed inflection points, assumption of a monotonic increase in size from origin to asymptote and the inestimable errors in various adjustment factors, causing growth to be under or over estimated (Fitzhugh, 1976). Piecewise linear regression is another model whose use in cattle growth is very limited. Warren et al. (1980) described the method for segmented line regression, and explained it with an example using data from Hereford females.

Piecewise linear regression can be used when data sets exhibit two (or more) different linear relationships within two (or more) ranges of the same data set. Bioeconomically, there are obvious growth distinctions between pre and post-weaning growth; consequently, there has been great interest in their characteristics. Moreover, those factors connected with differences in change in the pre-weaning period may differ substantially from those that are instrumental in the post-weaning period. In addition, rates of change may have different variances pre-weaning compared to post-weaning.

The cubic model for calf growth we have used ; however, does not readily lend itself to exploring issues of this kind. Piecewise models for animal growth provide a means of dividing the growth profile into meaningful stages, and investigating key features of change in each stage. In its simplest form, this approach fits models for a two-piece trajectory rather than "smoothing" the change in a cubic function. In other words, piecewise linear growth models are attractive when focusing on the comparison of growth curves in two different periods, or investigating whether the predictors of growth change over specific periods.

The main objective of this chapter is to provide a view of the piecewise regression analysis, investigating the ability of a piecewise linear regression procedure (Hodson, 1966) to fit growth traits without the difficulties mentioned for the cubic model (Chapter 5). Thus, it was focused on the fundamental similarities and differences of the two models to address:

- Whether the piecewise model fits the data better than the cubic model at the end of growth or not?

10.2 Statistical method

The data used in this chapter is identical to that used in Chapter 5. The random regression type analyses applied to estimate (co)variance components in Chapter 5 are used in the context of a piecewise model. Again, age was scaled (from days to years) for numerical reason. However, age was not centered as was done in the cubic model.

In this study, a two-piece linear growth model was employed to obtain the estimates of (co)variance components for pre- and post-weaning periods and the correlations between them. On the log scale, a preliminary analysis showed that quadratic terms were important for the piecewise model to fit the growth data. Suppose we wish to fit a piecewise quadratic model to mean log-body weights, that is

$$\mathrm{E}(\ln(\mathrm{Bodyweight})) = \begin{cases} \beta_{01} + \beta_{11}\mathrm{Age} + \beta_{21}\mathrm{Age}^2 \ (\mathrm{Age} \le \mathrm{Age}_{\mathrm{Pre-weaning}}) & \mathbf{(10.1)} \\ \beta_{02} + \beta_{12}\mathrm{Age} + \beta_{22}\mathrm{Age}^2 \ (\mathrm{Age} \ge \mathrm{Age}_{\mathrm{Pre-weaning}}) & \mathbf{(10.2)} \end{cases}$$

These two quadratics meet at pre-weaning age; $\mathrm{Age}_{\mathrm{Pre\text{-}weaning}}$ is the pre-weaning age in **(10.1)** and **(10.2)**.

Now, when $\mathrm{Age} = \mathrm{Age}_{\mathrm{Pre\text{-}weaning}}$,

$$\beta_{01} + \beta_{11}\,\mathrm{Age}_{\mathrm{Pre\text{-}weaning}} + \beta_{21}\,(\mathrm{Age}_{\mathrm{Pre\text{-}weaning}})^2 = \beta_{02} + \beta_{12}\,\mathrm{Age}_{\mathrm{Pre\text{-}weaning}} + \beta_{22}\,(\mathrm{Age}_{\mathrm{Pre\text{-}weaning}})^2 \qquad \mathbf{(10.3)}$$

We can solve for β_{02} and hence, reduce the number of parameters. Clearly

$$\beta_{02} = \beta_{01} + \beta_{11}\,(\mathrm{Age}_{\mathrm{Pre\text{-}weaning}}) - \beta_{12}\,\mathrm{Age}_{\mathrm{Pre\text{-}weaning}} + \beta_{21}\,\mathrm{Age}^2_{\mathrm{Pre\text{-}weaning}} - \beta_{22}\,\mathrm{Age}^2_{\mathrm{Pre\text{-}weaning}}$$

Thus the model becomes

$$\mathrm{E(ln(Bodyweight))} = \begin{cases} \beta_{01} + \beta_{11}\mathrm{Age} + \beta_{21}\mathrm{Age}^2\ (\mathrm{Age} \le \mathrm{Age}_{\mathrm{Pre-weaning}}) \mathbf{(10.4)} \\ \beta_{01} + \beta_{11}\mathrm{Age}_{\mathrm{Pre-weaning}} + \beta_{12}(\mathrm{Age} - \mathrm{Age}^2{}_{\mathrm{Pre-weaning}}) + \\ \beta_{21}\mathrm{Age}^2{}_{\mathrm{Pre-weaning}} + \beta_{22}(\mathrm{Age}^2 - \mathrm{Age}^2{}_{\mathrm{Pre-weaning}})(\mathrm{Age} \ge \mathrm{Age}_{\mathrm{Pre-weaning}}) \mathbf{(10.5)} \end{cases}$$

The model requires the definition of new explanatory variables to be used in the linear model. These variables are presented in Table 10.1.

Table 10.1. Partitioning age into pre- and post-weaning ages for calculation linear and square of age

Age (days)	Pre-weaning (days)	Post-weaning (days)	(Pre-weaning age)^2	(Post-weaning age)$^{2\,b}$
0	0	0	0	0
50	50	0	2500	0
100	100	0	10000	0
150	150	0	22500	0
200	200	0	40000	0
250^a	**250**	**0**	62500	**0**
300	250	50	62500	27500
350	250	100	62500	60000
400	250	150	62500	97500
450	250	200	62500	140000
500	250	250	62500	187500
550	250	300	62500	240000
600	250	350	62500	297500
650	250	400	62500	360000
700	250	450	62500	427500

^{a} assumed weaning age, ^{b} (Post-weaning age)^2=Age^2- Age$^2_{\mathrm{weaning}}$

The same model building process discussed in Chapter 5 was used for the piecewise model. The cubic random regressions were replaced by the piecewise random regression formulation presented above using ASREML (Gilmour et al., 2000). Thus a mixed model was again fitted, namely

$$\mathbf{y} = \mathbf{X}\tau + \mathbf{Zu} + \mathbf{e} \qquad \mathbf{(10.6)}$$

Table 10.2 presents the effects included in the model, their status and the degrees of freedom or number of variance parameters included. Thus, the piecewise models (sire and animal) in this study assume that the growth curve of each individual animal follows a second-degree polynomial. The quadratic coefficient was estimated within the breed and sex effect to take into account differences in growth due to breed and sex. This model was specified as a function of five growth parameters; mean, linear and quadratic effects of pre-weaning and post-weaning growth as a covariate.

Table 10.2. Effects, their status, degree of freedom (df) and variance parameters (V.P.) for the sire and animal piecewise model

	Status	df	V.P.	V.P.
Animal			Sire model	Animal model
Breed	F	6	-	-
Sex	F	1	-	-
Sire (or Animal)	R	-	1	1
Animal	R	-	-	1
Maternal	R	-	1	1
Animal (permanent environmental)	R	-	1	1
Management	R	-	1	1
Time				
Age	F	1	-	-
Age$_{\text{Pre-weaning}}$	F	1	-	-
Age$_{\text{Post-weaning}}$	F	1	-	-
Age$^{2}_{\text{Pre-weaning}}$	F	1	-	-
Age$^{2}_{\text{Post-weaning}}$	F	1	-	-
Animal.Time	F	1	-	-
Breed.Age	F	1	-	-
Breed. Age$_{\text{Pre-weaning}}$	F	1	-	-
Breed. Age$_{\text{Post-weaning}}$	F	1	-	-
Breed. Age$^{2}_{\text{Pre-weaning}}$	F	1	-	-
Breed. Age$^{2}_{\text{Post-weaning}}$	F	1	-	-
Sex.Age	F	1	-	-
Sex. Age$_{\text{Pre-weaning}}$	F	1	-	-
Sex Age$_{\text{Post-weaning}}$	F	1	-	-
Sex. Age$^{2}_{\text{Pre-weaning}}$	F	1	-	-
Sex. Age$^{2}_{\text{Post-weaning}}$	F	1	-	-
Sire.Age	R	-	1	1
Sire. Age$_{\text{Pre-weaning}}$	R	-	1	1
Sire. Age$_{\text{Post-weaning}}$	R	-	1	1
Sire covariances	R	-	6	6
Animal.Age	R	-	-	1
Animal. Age$_{\text{Pre-weaning}}$	R	-	-	1
Animal. Age$_{\text{Post-weaning}}$	R	-	-	1
Animal covariances	R	-	-	6
Maternal.Age	R	-	1	1
Maternal. Age$_{\text{Pre-weaning}}$	R	-	1	1
Maternal. Age$_{\text{Post-weaning}}$	R	-	1	1
Maternal covariances	R	-	6	6
Management.Age	R	-	1	1
Management. Age$_{\text{Pre-weaning}}$	R	-	1	1
Management. Age$_{\text{Post-weaning}}$	R	-	1	1
Management. Age$^{2}_{\text{Pre-weaning}}$	R	-	1	1
Management. Age$^{2}_{\text{Post-weaning}}$	R	-	1	1
Management covariances	R	-	15	15
PEAge	R	-	1	1
PE.Age$_{\text{Pre-weaning}}$	R	-	1	1
PE.Age$_{\text{Post-weaning}}$	R	-	1	1
PE covariances	R	-	6	6
Residual	R	-	1	1

10.3. Results

Table 10.3 presents the log-likelihood, number of parameters, observations and fixed effects and error variances of these two models. The random effects significantly reduced the residual variation for both models (Table 10.3).

Table 10.3. Summary of the sire and animal piecewise models

	Sire	Animal
Loglikelihood (fixed+random effects)	21119.6	21084
Loglikelihood (fixed effects)	16287.6	16287.6
Number of model parameters[a]	32	22
Number of observations	11936	11936
Number of fixed effects	15	15
Error variance	0.00753	0.00749

[a] Number of variance components

Fixed effects in the model were tested using a Wald *F*-statistic obtained by dividing the Wald statistic by its degree of freedom. As it has shown, differences due to breed and sex and their interactions with second order of time were significant (Table 10.4).

Table 10.4. ASReml F Value to test the fixed effects

Fixed effects	DF	F Value
Mean	1	162682.1
Breed	**6**	**42.99**
Sex	**7**	**158.26**
Age_{pre}	1	24393.01
Age_{post}	1	3043.45
$\text{Age}^2_{\text{pre}}$	**1**	**502.3**
$\text{Age}^2_{\text{post}}$	**1**	**100.73**
$\text{Breed.Age}_{\text{pre}}$	6	1.32
$\text{Breed.Age}_{\text{post}}$	6	9.74
$\text{Breed.Age}^2_{\text{pre}}$	**6**	**1.83**
$\text{Breed.Age}^2_{\text{post}}$	**6**	**15.89**
$\text{Sex.Age}_{\text{pre}}$	7	1.32
$\text{Sex.Age}_{\text{post}}$	7	5.5
$\text{Sex.Age}^2_{\text{pre}}$	**7**	**226.38**
$\text{Sex.Age}^2_{\text{post}}$	**7**	**7.58**

Body weights of all breeds increased during the pre-weaning period, steady flat during dry season and again increase in the feedlot period (Figure 10.1).

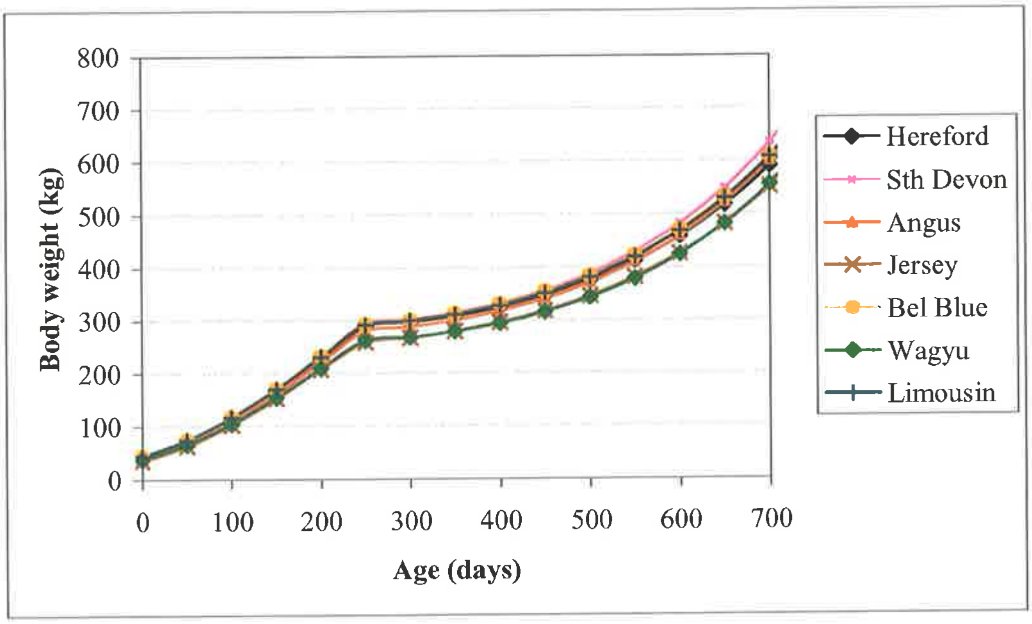


Figure 10.1. Growth curves of seven breeds obtained from the piecewise model

Figure 10.2 illustrates the percentage deviation of estimated average weight of crossbreds from purebred Herefords at various ages obtained from the piecewise model, indicating very similar pattern to the cubic model. That is South Devon, Belgian Blue and Limousin calves were consistently heavier and Jersey and Wagyu were lighter than Hereford calves, as expected. After weaning they remained steady, however, the magnitude of the percentage of deviation for Jersey became smaller than Wagyu (Figure 10.2). During pre-weaning, an interesting pattern was shown for Angus, where its percent of deviation increased dramatically, clearly lighter than the Hereford calves. Obviously, after weaning the direction of the deviation changed, so Angus calves became heavier than Hereford calves (Figure 10.2).

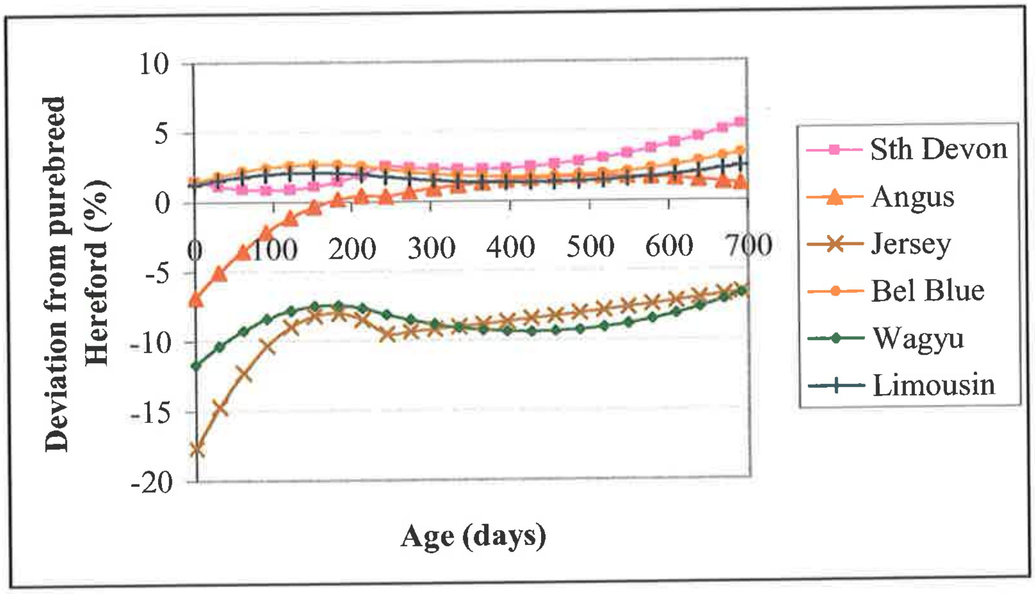


Figure 10.2. Deviation of estimated body weight of six crossbreds from purebred Hereford derived from the piecewise model

Many (32) (co)variances were able to be estimated for the sire model (Table 10.5) and 22 (co)variances for animal model. Due to small variances for the quadratic terms of sire, maternal and permanent environmental effects, their covariances with mean and linear terms were not able to be estimated (Table 10.5).

Table 10.5. Estimated Variances (on diagonal) and covariances (off diagonal) components from the sire piecewise model

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15
1. Sire.Age	✓														
2. Sire.Age$_{\text{Pre-weaning}}$	✓	✓													
3. Sire.Age$_{\text{Post-weaning}}$	✓	✓	✓												
4. Maternal.Age				✓											
5. Maternal.Age$_{\text{Pre-weaning}}$				✓	✓										
6. Maternal.Age$_{\text{Post-weaning}}$				✓	✓	✓									
7. Management.Age							✓								
8. Manag[a].Age$_{\text{Pre-weaning}}$							✓	✓							
9. Manag[a].Age$_{\text{Post-weaning}}$							✓	✓	✓						
10. Manag[a].Age$^{2}_{\text{Pre-weaning}}$							✓	✓	✓	✓					
11. Manag[a].Age$^{2}_{\text{Post-weaning}}$							✓	✓	✓	✓	✓				
12. PE[b].Age												✓			
13. PE[b].Age$_{\text{Pre-weaning}}$												✓	✓		
14. PE[b].Age$_{\text{Post-weaning}}$														✓	
15. Overall residual															✓

[a]Management, [b]Permanent environmental

10.4. Discussion:

The aim of this chapter was to compare the piecewise and cubic model. Similar growth patterns were observed for both cubic and piecewise models throughout pre-weaning and post-weaning periods (Figures 5.3 and 10.1). The percent deviation of estimated average weight of crossbreds from purebred Herefords from birth to slaughter obtained from both models indicated that, as might be expected, the South Devon, Belgian Blue and Limousin calves were consistently heavier and Angus Jersey and Wagyu were lighter than Hereford calves. Jersey and Angus demonstrated the best combination of minimum birth weight and maximum growth rate over time (Figures 5.5 and 10.2). Generally, results of relative contribution of variance components from both cubic and piecewise growth models in this study indicated that non-genetic variation accounted for the larger proportion of the total variance. Management variances were fairly high in both models, emphasising the importance of management effects.

However, some differences between piecewise and cubic model were detected. The estimated heritabilities (h^2) were low for both models due to low contribution of genetic (sire or animal) variances to the total variation of body weights.

The number of estimated parameters for the cubic model was 22 while for the piecewise model it was 32. Plotting residuals versus fitted values both models produced a distribution of points scattered about zero, and the two plots were very similar (Figure 10.3).

For both models the fit around weaning age (~200-250 days) were not very good with predominantly positive residuals. The piecewise model seems to fit the data better at the end of growth, as can be seen by the apparent trend for high fitted values for the cubic model.

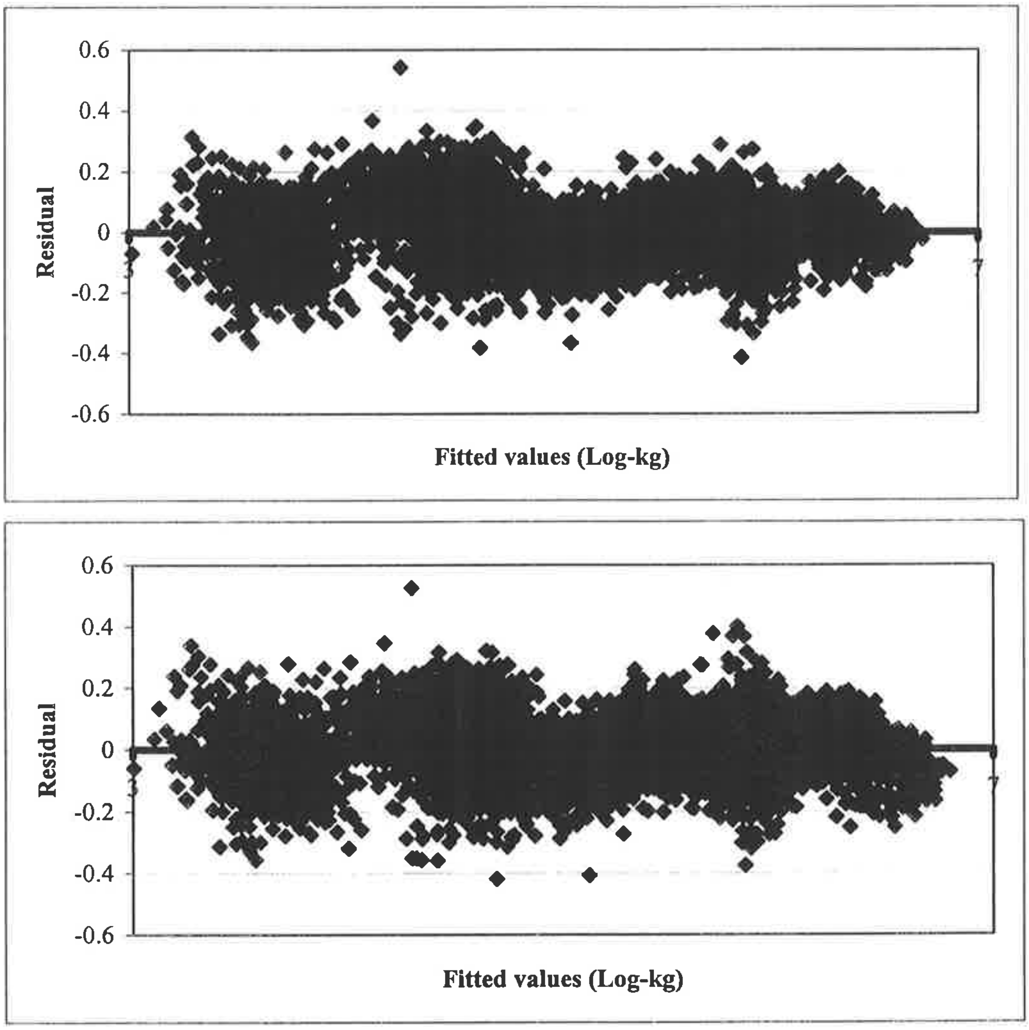


Figure 10.3. Plot of residual vs fitted values for piecewise (top) and cubic (bottom)

10.5. Conclusion

Is the piecewise model better than the cubic model?

The two models are very similar in their fit to the data; with the piecewise model being marginally better. When comparing both models, it can be seen that the piecewise model estimates more parameters than the cubic model. The log likelihood of piecewise model was greater than the cubic model. In addition, the residual variance of the piecewise model was lower than that of the cubic model. Moreover, the plots of residual versus fitted value show that a piecewise model performs better than a cubic model at the end of the trajectory for higher values on these data. Investigations into alternative models would seem to be important and perhaps modeling heifers and steers separately might be advantageous. Steers seem to have three phases of growth and a piecewise linear model of three pieces may in fact result in a better fit. However, preliminary analysis found this was poor for heifers because the middle piece (weaning-prefeedlot) had too few (sometimes zero!) weight measurements to allow accurate estimates. It may be have been useful for steer data.

Chapter 11

Concluding remarks

11.1. Introduction

This chapter deals with a brief summary of the current thesis with respect to the scientific results and industrial applications, as well as suggestions for future work. During the last few years, many studies have attempted to develop growth models to predict carcass quality traits in growing and mature cattle. There are, however, some limitations in these studies. The most important limitation is that the majorities have ignored the relationship between growth pattern and carcass traits. Addressing how continuous growth traits and carcass quality traits were correlated over time and how to predict carcass quality when the growth path is known remained an outstanding problem. Thus, the objective of this thesis was to use variation in cattle growth to develop a predictive model of carcass quality. Prediction of carcass quality over the growth path may help producers to predict the age required for individual cattle to reach a specific target body weight and market specifications.

11.2. Conclusion

The analyses of the present thesis were based on the following steps:

1. Describing variation in growth using a) principal component analysis and b) cubic random regression model c) piecewise random regression model (evaluating the application of the piecewise linear regression as an alternative model to overcome artifacts associated with polynomial models for describing growth variation)
2. Describing variation in carcass quality using a) principal component analysis and b) multivariate sire and animal models
3. Joint modeling of growth and carcass quality
4. Estimating correlations between longitudinal growth traits (body weights and relative growth rate) and carcass quality traits
5. Predicting carcass quality

11.2.1. Describing variation in growth

11.2.1. a) using principal component analysis

Principal component analysis as a widely used `dimension reduction' technique seems a useful technique for studying size and shape changes over time. The first two principal components, which accounted for 85% of total variation in growth data, have been interpreted as new traits for overall size and feedlot growth. The new traits contain information from all of the body weights originally measured at different times from birth to slaughter. Applying PCA indicated that environment and management has a big impact on body size and feedlot growth, especially in heifers. Also, significant sire breed effects implied that genetic variation is important for body size and feedlot growth traits. Sire breed effects were similar for steers and heifers. Considerable breed differences existed with Wagyu and Jersey being small and Angus, Hereford, South Devon, Limousin and Belgian Blue being much heavier. However, there were no significant breed differences in growth pattern within each sire group. This might be because either the PCA is unable to detect differences or using only body weights were not sufficient to detect some differences in growth patterns of diverse breeds. So, it would be worthwhile considering a wider range of growth traits, for example body measurements such as height and P8 fat scan, length, girth, hip height, stifle and real time EMA.

The direct heritability estimates of growth traits were moderate and high for heifers and steers, respectively. The direct estimates of feedlot growth traits were higher than overall size in both steers and heifers. The direct heritability estimates of overall size were higher for steers than for heifers, probably because either genetic variation in steers was bigger than heifers or steers were more homogeneous than heifers.

However, the number of animals in the current study was not sufficient for accurate estimation of heritability.

11.2. b) random regression models of growth

Random regression analysis was employed to provide a method for analysing independent components of variation that reveal specific patterns of change over time. (Co)variance components of growth included sire, maternal, permanent environmental and temporary environmental variances across ages. The estimates of genetic variance over time generally exhibited expected trends. However, the low genetic variances and consequently low heritability estimates obtained for all growth traits indicated the need for improved and uniform animal management over years to increase the precision of parameter estimates, and showed the scope for improvement through selection in crossbred populations.

Non-genetic variation accounted for the larger proportion of the total variation. The management variation contributed to the largest proportion of non-genetic and total variation of body weights as nutrition was based on the pasture. The higher gains of calves on pasture can be due to the higher availability of nutrients for their dams, particularly at the start of the grazing season and if they had been undernourished during backgrounding as part of the post-weaning period. The decrease in the rate of growth after weaning during the dry period was primarily due to decreasing quality of pasture as the season progressed. Thus, the significance of these feed gaps for the post-weaning growth of steers and heifers was highlighted through the backgrounding period.

All seven sire breeds showed the similar growth patterns during the pre-weaning period. However, during the post-weaning period two groups of sires, heavy and small, showed different growth patterns. Jersey and Angus demonstrated the best combination of minimum birth weight and maximum growth rate over time (Figure 5.4).

Direct heritability (h^2) increased steadily with age and increased towards the end of the trajectory, in particular beyond 650 days. Commonly, models assume that the residuals are distributed normally and independent with zero mean and equal variance, but in practice a systematic pattern was observed in the residuals over the growth trajectory. Moreover, it is possible that the fit is worst for traits with the smallest variances. This remains an unresolved problem for modelling that utilises polynomials. Several strategies may be used for obtaining "better" estimates. One could be to use larger, more carefully selected data. Another strategy would be to use functions other than polynomials that are less susceptible to artifacts. Although the choice of which type of function to use might not have a large effect on the parameter estimates within the interval that data was collected, the function might be more important as soon as data are extrapolated (Kirkpatrick et al., 1990).

Maternal heritabilities were higher than direct heritabilities, indicating that growth traits were determined more by the environmental conditions than by those of the genetic characteristics of the calf. Also, maternal heritabilities were highest for birth and weaning weights, followed by yearling, implying importance of maternal effects for birth and weaning weights rather than others.

Amongst the four growth models used in the current study, the cubic sire model seemed to be the simplest and best performing (stable) model. Twenty two (co)variances were able to be estimated. Due to the low variances for sire constant and linear terms, the covariance between them could not be estimated. Results in this study should be viewed as trends rather than absolute values, and no definite "true" parameters should be expected.

Due to using random regression with a polynomial, the model is subject to overestimates at the end of the trajectory, in particular beyond 650 days. That occurred because the variances associated with ages of most missing records become erratic. Further, most models assume that the residuals are distributed normally and independent with zero mean and equal variance, but in practice a systematic pattern was observed in the residuals over the growth trajectory because the mean profile not adequetly modelled.

11.2.1. c) Piecewise random regression model

Both piecewise and cubic models appeared to be very similar in their fit to the data. In general, some evidences indicate that piecewise model may perform better fit than a cubic model in particular, at the end of the trajectory for higher values on these data.

It could be suggested more investigations on modeling heifers and steers separately. Also, because steers seem to have three phases of growth hence, a piecewise linear model of three pieces perhaps result in a better fit.

11.2.2. Describing variation in carcass quality

11.2.2. a) using principal component analysis

A large proportion of total variations in the carcass traits were explained by the two important independent components; interpreted as market suitability and muscling. PCA made it possible to identify the most important directions of variability in the carcass quality traits considered so that HCWt and fat thickness were the main determinants of market suitability, EMA indicator of the muscling and relationship between fat thickness and intramuscular fat an indication of fat distribution components.

The proportion of variation in market suitability in steers and fatness in heifers due to year varied considerably across management groups, reflecting the effect of climate, e.g. rainfall and temperature. The steers born in 1994 and 1995 had a low value in marbling, whereas the heifers' equivalent had high marbling. There tended to be high marbling for 1996-drop steers. However, the heifers born in 1996 had a tendency to be low in marbling. Because they went to feedlot at different ages and they were on feed for different time. The 1997-drop steers tend to have an average value in marbling, but the heifers born in 1997 seem to have a tendency towards high marbling.

Significant effects of breed of sire, similar for steers and heifers, indicated that genetic variation is important among breeds for market suitability and muscling components. Three categories of sire breeds detected in both steers and heifers were as follows:

- Low growth and muscling, high fatness and marbling classes containing Jersey, Wagyu and Angus.
- Moderate marbling, including Hereford and South Devon
- High growth and muscling, low fatness, and low to moderate marbling, including Belgian Blue, Limousin, South Devon and Hereford, implying low variance of fat traits associated with heavy group.

The low estimates of heritability for market suitability and fat distribution occurred, probably due to possibly either low genetic variation within breeds or less homogeneity of these components. In contrast, the moderate estimates for muscling implied that there might be more genetic variation within breeds or more homogeneity.

However, the current analysis could not condense the carcass variation into as few components as hoped. It might be because, as reported earlier, only four traits have been considered, the carcass is a very heterogeneous product and in this dataset the carcass traits were less highly correlated with each other than expected.

11.2.2. b) using multivariate models

Multi-trait mixed sire and animal models were conducted to estimate 40 (co)variance components of four economically important carcass traits. The logic behind using multivariate models was that any strategies that maximize profit need to balance genetic potential for carcass yield with adverse correlated changes in quality of the product. Therefore, realistically, it was necessary to take more than one carcass trait into consideration in the analysis of carcass quality especially, when selecting sires for genetic improvement. Comparatively, the error variance and log likelihood of both sire and animal models demonstrated improvement for sire model, hence, the sire model selected for joint analysis. Similar to body weights, non-genetic, in particular management group variation contributed to a large proportion of total carcass variation, up to 50% of total variation (Figure 6.4).

According to the results, it was concluded that strategies to increase genetic potential for HCWt, which is the greatest determinant of carcass value at a constant age end point, would increase the genetic potential for EMA but may reduce marbling and tend to slightly increase P8. A slight negative genetic relationship may exist between EMA and marbling. However, selection for improved carcass quality might be possible without sacrificing lean growth.

11.2.3. Joint modeling of growth and carcass quality

The estimates of correlations and parameters derived from the joint model were critically important for establishment of the carcass correlation curves over time as well as development of a predictive model. Because a successful prediction of the carcass quality of cattle following specific growth path depends as much on a correct estimation of (co) variances components of its genotype parameters as on a detailed description of its environment. With perseverance, 99 variance components were able to be estimated. There are some issues for not being able to estimate some parameters, e.g., the size of data set, the nature of relationships between traits, lack of variation in pre-weaning growth, limitations of the program used and number of parameters attempted.

The magnitudes of management correlations were significantly higher than genetic, maternal and permanent environmental correlations (Figure 7.1). However, the management correlations between the mean and HCWt were not able to be estimated. There were high associations between growth traits and HCWt (as expected) and P8 fat, indicating high growth will lead to heavier carcasses with more fat depth. Also, the high genetic associations of growth rate and IMF in this study implied that selection for fast growth will likely change IMF in breeding animals.

11.2.4. Estimating correlations between longitudinal growth traits (body weights and relative growth rate) and carcass quality traits

The present analysis was designed to determine if growth traits and carcass quality traits were correlated, and if so, did that correlation vary with the age of measurement? Basically, the potential for change in carcass quality traits is largely dependent on their genetic variation and correlations with growth path. Producers need to be aware of where these correlations are optimum as well as possible antagonistic relationships among traits during specific periods of growth so that they may account for them in optimising breeding goals and management practices to meet market specifications.

Genetic correlations between live weight with HCWt and EMA were moderate to high and positive (Table 7.3 and Figure 8.1). It seems that, selection for increased direct genetic value for pre-weaning and weaning live weights would be expected to increase HCWt, EMA and IMF (to some extent). Genetic correlations between live weight and fat traits were low. Maternal correlations between live weight and HCWt were high, indicating emphasis on dam milk or dam maternal on pre-weaning and weaning and post-weaning live weights may lead to positive correlated responses in HCWt and EMA. However, because most of the maternal correlations between weaning weight and fat traits were not large in magnitude, selection for carcass fat traits would not be expected to result in important changes in dam ability. All genetic correlations with carcass traits that were positive for direct genetic effects for pre-weaning and weaning live weights were also positive for maternal effects, except for P8, which all had small negative estimates of genetic correlations with direct effects for weaning weight. The phenotypic, genetic and maternal correlations of birth weight with HCWt, were positive and moderate to high (Figure 8.2). Birth weight had very low phenotypic and genetic correlations with P8, indicating there are very few genes that affect both traits and that there will be little correlated change in one trait as a result of selection for the other trait.

The environmental correlations between birth weight and HCWt were very low, implying that environments affecting HCWt were independent of those influencing birth weight (Table 7.3 and Figure 8.1). Likewise, the environmental estimates of correlation between weaning weight and HCWt was low, indicating independency of the environments that affect both traits.

Weaning weight and HCWt had favourable phenotypic and genetic correlations (Figure 8.2), and this may represent opportunities for increased productivity. The negative relationship between weaning weight and P8 fat depth could be related to maturing rate. Animals that are heavier at weaning may mature slower and consequently could have increased amounts of lean muscle tissue relative to external fat.

There was a moderate to high, positive genetic correlation between post-weaning growth and EMA in the present study (Figure 8.2), indicating that selection for higher growth should also lead to have more total muscle mass as reflected in the size of the EMA. The pattern of phenotypic correlations between live weight and IMF as the animal grew (Figure 8.3) were similar to a common conclusion from animal developmental studies, in that IMF is later developing than subcutaneous then intramuscular. This result indicates that during the early growth phase (about 50 kg HCWt at 50 days), IMF correlations with body weights remain low and constant, and are followed by a phase of almost linear increase as the carcass begins to fatten more rapidly (starting at ~250days). It is assumed that as mature body size is reached (~450 kg HCWt depending on breed) the increase in IMF is reduced as growth rate declines (unseen in the current report).

Management correlations between live weight and carcass traits during the pre-weaning period were positive except for IMF. The magnitude of those correlations decreased from birth to weaning, then increased dramatically during the feedlot period, where they plateaud except IMF which decreased from 500-700 days (Figure 8.1). Hence, management correlations between body weights and carcass traits were only high during post-weaning period when they were high for all carcass traits, implying major role of post-weaning growth on carcass quality traits (Figure 8.1).

The present study showed unexpectedly, the negative estimates of management correlations between relative growth rate (RGR) and carcass traits during pre-weaning period, as the variances of management during this period were very poor when the covariance between RGR and carcass traits were negative and close to zero. That means, those calves that had slower growth up to weaning produced higher values of carcass quality. Over the post-weaning period, all carcass quality traits were favourably correlated to the post-weaning RGR, implying that management has a key position in the production of fast grower animals of high carcass quality. Selection for higher RGR should also lead to heavier and fatter carcasses during this period. IMF showed positive and favourable management relationships with post-weaning period RGR, which are most frequently used in selection. Also, the current results confirm that IMF is a later developing fat depot than subcutaneous fat (Figure 8.3).

It could be concluded that producers and breeders need to consider growth, dam ability, and production efficiency in selection decisions but also carcass traits to meet demand for quality beef.

11.2.5. Predicting carcass quality

The current model deals with one of the greatest challenges facing growth modellers in beef industry; how to predict carcass quality resulting from a specific growth path measured at various stages of growth. Hence, herein, an attempt has been made to predict carcass quality associated with variation in growth path. The ability of the current model to accommodate different sexes across seven sires breeds and various post-weaning management groups at any slaughter age provides the flexibility required by producers with varying situations.

The model provides a tool by which the producer can assess the impact on quality of various production decisions. This will allow the producer to optimise marketing decisions for a particular lot of cattle, and perhaps more importantly, to predict the impact of possible changes in future management decisions. The strength of the present model lies in its simplicity, which allows the user to predict carcass quality and carcass value fairly well with a relatively limited number of parameters. The ability of the model to give answers to 'what if' questions is a very powerful one that has not previously been available to producers. Moreover, it can potentially be utilised to alter patterns of growth in order to manipulate slaughter age or body weight at the point of slaughter. Another potential use of this model in combination with other decision support software offers scope for producers and abattoirs to customise their operations to better meet their specific market specifications.

Inaccurate or biased estimates of body weight can veil effects of treatments, leading to wrong conclusions with potentially significant economic ramifications. Large prediction intervals around the mean showed that the model did not perform well in the prediction of HCWt and EMA. HCWt was the crucial trait in this study. Because of large variances of permanent environmental and very small covariances between carcass fat traits and body weights, wide confidence intervals were detected for these traits (Table 5.4).

Results obtained from the prediction model to evaluate different growth schemes revealed that differences existed between breeds for all traits but the ranking of the breeds within each sex were proportionately the same. In general, with respect to breed comparisons, all schemes followed the same pattern of quantity and fat traits for both heifers and steers. The variability in the body weights and gain responses that are seen within and among schemes, suggests the potential interaction of nutritional, physiological and genetic factors. Based on the prediction results to test different growth rate schemes, it could be concluded that allowing animals to slow down in backgrounding phase might limit potential carcass quality.

11.3. Proposal for future work

The present research deals with one of the greatest challenges facing growth modellers in beef industry and resulted in increased knowledge on how to predict carcass quality resulting from a specific growth path at various stages of growth. The general conclusion is that the empirical model offered a more practical solution in studying relationships between growth, carcass traits and investigating the effects of alternative management decisions. This approach potentially is very useful if data structure issues are well addressed. Still, some topics remain unsolved and need further research either from scientific or industrial point of view. Therefore, the following activities are proposed:

- The performance of the model could be improved by applying other independent data sets that contain more variation in pre-weaning growth.
- To ensure that evaluation of body weights by RRM is optimal, it is suggested applying another type of functions other than polynomials, such as structured ante-dependence models and spline functions.
- Another point for further research is using more growth measures along with live weights such as body measurements especially height and P8 fat scan which are commonly available, but also length, girth, hip height, stifle and real time EMA which are part of the "Southern Crossbreeding Project" data set.
- It also would be worthwhile to incorporate this model into a beef production economic model that simulates the commercial and economic decision-making process involved in the practical management of beef production. Ultimately, a total package will include the value differentials associated with both yield and quality and economic values.

***Thomas Edison** (1847-1931):*

- Results? Why, man, I have gotten lots of results! If I find 10,000 ways something won't work, I haven't failed. I am not discouraged, because every wrong attempt discarded is often a step forward....
- Just because something doesn't do what you planned it to do in the first place doesn't mean it's useless....

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Appendices

Appendices

APPENDIX 1. As file for the cubic growth sire model
APPENDIX 2. As file for the cubic growth animal model
APPENDIX 3. As file for the carcass sire model
APPENDIX 4. As file for the carcass animal model
APPENDIX 5. As file for the joint growth-carcass model
APPENDIX 6. As file for the piecewise growth sire model
APPENDIX 7. As file for the piecewise sire model
APPENDIX 8. PUBLICATIONS FROM THESIS

Conference Proceedings

Mirzaei, H. R., W. S. Pitchford, and M. P. B. Deland. 2002. Evaluation relationships among body weights of crossbred steers and heifers over time using principal component analysis. In: Proceedings of the 15th Association for the Advancement of Animal Breeding and Genetics Conference, Melbourne

Conference Abstract

Mirzaei, H. R., A.P.Verbyla, M.P.B.Deland, W.S.Pitchford. 2004. Random regression analysis of cattle growth path. In: 55th Anual Meeting of the European Association for Animal Production, Slovenia, Bled

APPENDIX 1. As file for the cubic growth sire model

```
Sire cubic model
 ID !P
 Sire 97  !A
 Dam 581  !A
 Cohort 8  !A
 POSTW 4 !I
 LYP 16 !I
 LYSP 28 !I
 Bmonth 2  !A
 Sex 2  !A
 Year  4 !I
 Breed 7  !A
 Slage
 Slage1
 Value
 wt
 agel
 ageq
 agec
 aagel
 aageq
 aagec
 al
 aq
 ac
Cubic.csv  !ALPHA !skip 1 !REPEAT
Cubic.csv     !skip 1 !MVINCLUDE !maxit 100 !EXTRA 6
 Value ~ mu Breed Sex  al aq ac,
 Breed.al Breed.aq Breed.ac Sex.al Sex.aq Sex.ac,
 !r ide(ID) ide(ID).al ide(ID).aq -ide(ID).ac Sire Sire.al -Sire.aq Dam Dam.al,
 LYP LYP.al LYP.aq LYP.ac
 0 0 4 !NODISPLAY
 ide(ID) 2
 3 0 US 0.93 -0.39 0.39 -0.14 -0.07 0.27 !GP
 0 0 0
 Sire 2
 2 0 diag 0.05 0.01 !GP
 Sire 0 0
 Dam 2
 2 0 US 0.5 0.1 0.1 !GP
 Dam 0 0
 LYP 2
 4 0 US 0.71 -0.75 1.4 -0.92 1.4 2.4 0.23 -0.48 -0.12 1!GP
 LYP 0 ID
 Predict Sex !SED !logn
 Predict Breed  !SED !logn
```

APPENDIX 2. As file for the cubic growth animal model

```
Animal cubic model
 ID !P
 Sire 97  !A
 Dam 581  !A
 Cohort 8  !A
 POSTW 4 !I
 LYP 16 !I
 LYSP 28 !I
 Bmonth 2  !A
 Sex 2  !A
 Year  4 !I
 Breed 7  !A
 Slage
 Slage1
 Value
 wt
 agel
 ageq
 agec
 aagel
 aageq
 aagec
 al
 aq
 ac
Cubic.csv  !ALPHA !skip 1 !REPEAT
Cubic.csv    !skip 1 !MVINCLUDE !maxit 100 !EXTRA 6
Value ~ mu Breed Sex al aq ac,
 Breed.al Breed.aq Breed.ac Sex.al Sex.aq Sex.ac,
 !r ide(ID) -ide(ID).aagel -ide(ID).aq -ide(ID).ac ID ID.aagel Dam Dam.aagel,
 LYP LYP.aagel LYP.aageq LYP.aagec
 0 0 3 !NODISPLAY
 ID 2
 2 0 US 0.83 -0.38 0.23 !GP
 ID 0 AINV
 Dam 2
 2 0 US 0.97 -0.38 0.16 !GP
 Dam 0 ID
 LYP 2
 4 0 US 0.52 0.34 3.63 0.1 0.1 7.2 0.1 0.1 0.1 1!GP
 LYP 0 ID
 Predict Breed Sex !SED !logn
 Predict Sex !SED !logn
 Predict Breed  !SED !logn
 ide(ID) 2
 3 0 US 0.93 -0.39 0.39 -0.14 -0.07 0.27 !GP
 0 0 0
```

APPENDIX 3. As file for the carcass sire model

Carcass sire model

```
  ID !P
  Sire 97  !A
  Dam 581  !A
  Cohort 8  !A
  POSTW 4 !I
  LYP 16 !I
  LYSP 28 !I
  Bmonth 2  !A
  Sex 2  !A
  Year  4 !I
  Breed 7  !A
  Slage
  Slage1
  hcwt
  pfat
  ema
  imf
 CARCASS.csv  !ALPHA !skip 1 !REPEAT
 CARCASS.csv    !skip 1 !MVINCLUDE !maxit 100 !EXTRA 6
 hcwt pfat ema imf ~ Trait Tr.Breed Tr.Sex Tr.Sex.Slage
 !r Tr.Sire Tr.LYP Tr.Dam
 1 2 3
 0
 Trait 0 US 0.008 0.008 0.111 0.005 0.002 0.0147 0.003 0.009 -0.0007 0.09 !GP
 Tr.Sire 2
 Trait 0 US 0.0009 -0.0005 0.01 0.0006 -0.001  0.0008 -0.00007 0.002 -0.0007
 0.0058!GP
 Sire
 Tr.LYP 2
 Trait 0 US 0.004 0.01 0.05 0.0049 0.01 0.0066 0.02 0.017 0.017 0.14 !GP
 LYP
 Tr.Dam 2
 Trait 0 US 0.001 0.001 0.003 0.0007 0.0003 0.001 0.0003 -0.001 -0.0005 0.005 !GP
 Dam

Predict Breed sex
```

APPENDIX 4. As file for the carcass animal model

Animal carcass model

```
  ID !P
  Sire 97  !A
  Dam 581  !A
  Cohort 8  !A
  POSTW 4 !I
  LYP 16 !I
  LYSP 28 !I
  Bmonth 2  !A
  Sex 2  !A
  Year  4 !I
  Breed 7  !A
  Slage
  Slage1
  hcwt
  pfat
  ema
  imf
 CARCASS.csv  !ALPHA !skip 1 !REPEAT
 CARCASS.csv    !skip 1 !MVINCLUDE !maxit 100 !EXTRA 6
 hcwt pfat ema imf ~ Trait Tr.Breed Tr.Sex Tr.Sex.Slage
 !r Tr.ID Tr.LYP Tr.Dam
1 2 2
 0
Trait 0 US 0.008 0.0094 0.111 0.0039 0.0015 0.0134 0.001 0.001 0.001 0.111 !GP
Tr.ID 2
Trait 0 US 0.0043 0.0057 0.036 0.0028 -0.0026  0.0035 0.001 0.001 0.001 0.02 !GP
ID
Tr.LYP 2
Trait 0 US 0.004 0.01 0.05 0.0049 0.01 0.0066 0.02 0.017 0.017 0.14 !GP
LYP
Tr.Dam 2
Trait 0 US 0.001 0.001 0.003 0.0007 0.0003 0.001 0.0003 -0.001 -0.0005 0.005 !GP
Dam
Predict Breed sex
Predict Breed sex
```

APPENDIX 5. As file for the joint growth-carcass model

```
Joint GROWTH-CARCASS model
 ID !P
 Sire 97  !A
 Dam 581  !A
 Cohort 8  !A
 POSTW 4 !I
 LYP 16 !I
 LYSP 28 !I
 Bmonth 2  !A
 Sex 2  !A
 Year  4 !I
 Breed 7  !A
 Slage
 Slage1
 Value
 hamtr 5 !A # Live weight, HCWt, P8, EMA, IMF
 wt
 agel
 ageq
 agec
 aagel
 aageq
 aagec
 al
 aq
 ac
Joint.csv  !ALPHA !skip 1 !REPEAT
Joint.csv     !skip 1 !MVINCLUDE !maxit 200 !EXTRA 6
 Value ~ hamtr hamtr.Breed hamtr.Sex,
 at(hamtr,1).al at(hamtr,1).aq at(hamtr,1).ac,
 at(hamtr,1).Breed.al at(hamtr,1).Breed.aq at(hamtr,1).Breed.ac,
 at(hamtr,1).Sex.al at(hamtr,1).Sex.aq at(hamtr,1).Sex.ac,
 at(hamtr,2).Sex.Slage at(hamtr,3).Sex.Slage at(hamtr,4).Sex.Slage
 at(hamtr,5).Sex.Slage,
!r -at(hamtr,2).ide(ID) at(hamtr,3).ide(ID) at(hamtr,4).ide(ID) at(hamtr,5).ide(ID),
 at(hamtr,1).ide(ID) at(hamtr,1).ide(ID).al at(hamtr,1).ide(ID).aq,
 at(hamtr,3).Dam at(hamtr,4).Dam at(hamtr,5).Dam at(hamtr,1).Dam
 at(hamtr,1).Dam.al at(hamtr,2).Dam,
 at(hamtr,2).Sire at(hamtr,3).Sire at(hamtr,4).Sire at(hamtr,5).Sire, at(hamtr,1).Sire
 at(hamtr,1).Sire.al at(hamtr,1).Sire.aq,
 at(hamtr,3).LYP at(hamtr,4).LYP at(hamtr,5).LYP at(hamtr,2).LYP,
 at(hamtr,1).LYP at(hamtr,1).LYP.al at(hamtr,1).LYP.aq at(hamtr,1).LYP.ac
 0 0 4 !NODISPLAY
at(hamtr,3).ide(ID) 2
6 0 CORGH 0.07 0.11 -0.01 0.2 0.46 0.027 0.16 -0.06 0.034 -0.6 -0.08 -0.01 0.13 -
0.26 -0.27 13.9 0.83 11.4 0.94 0.39 0.25!GUUUUUUUUUUUUUUPPPPPP
0 0 0
at(hamtr,3).Dam 2
```

```
6 0 CORGH 0.63 -0.32 0.08 0.71 0.73 0.34 -0.36 -0.42 -0.36 -0.83 0.999 0.999 0.47
0.999 -0.65 0.86 0.3 0.50 0.65 0.15 0.27!GUUUUUUUUUUFFUFUPPPPPP
Dam
at(hamtr,2).Sire 2
6 0 CORGH 0.06 0.99 -0.28 0.24 0.27 -0.17 0.99 -0.23 0.9 -0.23 0.9 0.82 0.11 0.9 0.8
0.14 1.25 0.12 0.58 0.04 0.01!GUFUUUUFUFUFUUFFPPPPPP
Sire 0 0
at(hamtr,3).LYP 2
8 0 CORGH 0.84 0.17 0.5 0.82 0.86 0.66 0 0 0 0 -0.199 0 0.37 0 -0.71 0.70 0.66 0.44
0.72 -0.51 0.44 0.58 0.25 0.0054 0.51 0.32 -0.65 0.16 7.5 0.62 9.4 0.51 0.73 1.4 1.9
3.6!GUUUUUUZZZZUZUZUUUUUUUUUUUUUUPPPPPPPP
LYP 0 ID
```

APPENDIX 6. As file for the piecewise growth sire model

```
Sire piecewise  model
  ID !P
  Sire 97  !A
  Dam 581  !A
  Cohort 8  !A
  POSTW 4 !I
  LYP 16 !I
  LYSP 28 !I
  Bmonth 2  !A
  Sex 2  !A
  Year  4 !I
  Breed 7  !A
  Slage
  Slage1
  Value
  wt
  al1
  al4
  aq1
  aq4
Piecewise.csv  !ALPHA !skip 1 !REPEAT
Piecewise.csv     !skip 1 !MVINCLUDE !maxit 100 !EXTRA 6
Value ~ mu Breed Sex al1 al4 aq1 aq4
Breed.al1 Breed.al4 Breed.aq1 Breed.aq4 Sex.al1 Sex.al4 Sex.aq1 Sex.aq4,
!r ide(ID) ide(ID).al1 ide(ID).al4,
Sire Sire.al1 Sire.al4 Dam Dam.al1 Dam.al4,
LYP LYP.al1 LYP.al4 LYP.aq1 LYP.aq4
0 0 4 !NODISPLAY
ide(ID) 2
2 0 US 1 -0.6 0.43 !GP#0 0.1 0.1!GPPPZPP
0 0 0
Sire 2
3 0 US 0.1 -0.15 0.248 -0.005 -0.028 0.078!GP
Sire 0 0
Dam 2
3 0 US 1.2 -0.1 0.47 -0.81 -0.04 0.76!GP
Dam 0 0
LYP 2
5 0 US 0.76 1.6 8.1 -0.83 -4.49 4.99 -2.83 -11.4 5.5 17.9 -0.1 0.64 -1.9 -0.015
1.37!GP
LYP 0 ID
```

APPENDIX 7. As file for the piecewise sire model

Animal piecewise model

```
 ID !P
 Sire 97  !A
 Dam 581  !A
 Cohort 8  !A
 POSTW 4 !I
 LYP 16 !I
 LYSP 28 !I
 Bmonth 2  !A
 Sex 2  !A
 Year  4 !I
 Breed 7  !A
 Slage
 Slage1
 Value
 wt
 al1
 al4
 aq1
 aq4
Piecewise.csv  !ALPHA !skip 1 !REPEAT
Piecewise.csv    !skip 1 !MVINCLUDE !maxit 100 !EXTRA 6
Value ~ mu Breed Sex al1 al4 aq1 aq4
Breed.al1 Breed.al4 Breed.aq1 Breed.aq4 Sex.al1 Sex.al4 Sex.aq1 Sex.aq4,
!r ide(ID) ID ID.al1 ID.al4 Dam Dam.al1 Dam.al4,
LYP LYP.al1 LYP.al4 LYP.aq1 LYP.aq4
0 0 3 !NODISPLAY
ID 2
3 0 CORGH -0.86 -0.64 0.95 1.3 0.42 0.27!GUUUPPP
ID 0 AINV
Dam 2
3 0 CORGH -0.35 -0.75 -0.28 1.06 0.44 0.5 !GUUUPPP
Dam 0 0
LYP 2
3 0 CORGH 0.59 -0.52 -0.76 0.84 7.4 4.3!GUUUPPP 8.1 -0.83 -4.49 4.99 -2.83 -11.4
5.5 17.9 -0.1 0.64 -1.9 -0.015 1.37!GP
LYP 0 ID
```

APPENDIX 8. PUBLICATIONS FROM THESIS

EVALUATING RELATIONSHIPS AMONG BODY WEIGHTS OF CROSSBRED STEERS AND HEIFERS OVER TIME USING PRINCIPAL COMPONENT ANALYSIS

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[2]Struan Agricultural centre, South Australian Research and Development Institute, Naracoorte, S.A. 5271

SUMMARY

Data on 573 steers and 570 heifers calves born over a 4-year period (1994 to 1997) were obtained to describe and characterise growth of seven sire breeds raised in various management groups. The first principal component (PC1) accounted for 59% and 75% of the total variability among steers and heifers, respectively, was defined as a measure of overall size (weight at all ages). The second principal component (PC2) accounted for 20% of the total variation in steers and 10% in heifers and contrasted pre-feedlot and feedlot growth (weight at specific period). Overall size as well as feedlot growth were significantly affected by the birth years, breeds and management groups. It was concluded although principal component analysis is a useful technique for studying body size over time, that these results indicated that some differences in growth patterns of diverse breeds using only body weights could not be detected. Hence, it was suggested to consider a wider range of traits such as body measurements.
Keywords: crossbreeding, growth, principal components analysis

INTRODUCTION

Breeders have used body size characteristics to apply strategies for genetic improvement of beef cattle (Jenkins *et al.,* 1991). Body size has often been simply based on "weight for age" which has long been considered a criterion of desirability and a good practical index of efficiency in meat animals. The multivariate technique known as principal component analysis is a useful technique for studying size (Brown, 1973) and a valuable method of characterizing breeds (Destefanis *et al.,* 2000). The objectives of this study are to describe and characterise changes in growth pattern for seven sire breeds raised under various management conditions using principal component analysis. Weights at various ages are highly correlated and a large amount of the variation between animals is expected to explain by a small number of principal components. In addition, it was expected that most of the variation in weight between breeds can be observed at young ages, so breed differences in secondary principal component were not expected to be significant.

MATERIALS AND METHODS

637 Hereford cows were mated to 97 sires from seven breeds: Angus (A), Belgian Blue (B), Hereford (H), Limousin (L), South Devon (S) Jersey (J) and Wagyu (W). The data, consisted of twelve (for steers) and eight (for heifers) body weights (Wt), at successive ages, were collected from 1333 live calves born over a 4-year period (1994 to 1997) from two locations; Struan (S) and Wandillo (W) obtained from the "Southern Crossbreeding Project. Calves were growth until 12 to 18 mo of age and then transported to a commercial feedlot except the 1997 steers which, after a good pasture season in 1998, reached marketable weight without requiring grain finishing (Pitchford *et al.,* 2002).

All statistical analyses were conducted using SAS statistical software (SAS Institute Inc. 1999). Year of birth, management groups nested within birth years, birth month and breed were fitted as fixed effects and sire nested within breeds was included as a random effect. Principal components analysis (PROC PRINCOMP) was performed by the correlation matrix of the adjusted body weight at twelve successive times taken from steers and heifers of seven crossbreds. Also, a mixed model analysis (PROC MIXED) was applied to the data transformed by the coefficients of the principal components (PC scores) for both steers and heifers.

RESULTS

Table 1. The mean, standard deviation, eigenvalues and eigenvectors of the correlation matrix for body weight of steers and heifers over time for the first two principal components

	Steers				Heifers			
Body Weight	Mean(kg)	S.D ^{A}	PC1	PC2	Mean(kg)	S.D ^{A}	PC1	PC2
Birth Wt	39	6	0.26	0.04	36.6	6.2	0.29	0.16
70 days Wt	103	20	0.31	-0.22	94.4	20.9	0.36	-0.38
120 days Wt	135	26	0.33	-0.18	123	24.4	0.38	-0.23
180 days Wt	189	30	0.34	-0.09	170	28.4	0.39	-0.16
240 days Wt	281	37	0.35	-0.02	240	35.8	0.38	-0.16
280 days Wt	321	44	0.33	-0.10	286	39	0.36	-0.21
330 days Wt	307	46	0.33	-0.01	287	42	0.35	0.45
380 days Wt	351	46	0.29	-0.08	332	46.4	0.3	0.70
430 days Wt	354	47	0.33	-0.10	-	-	-	-
480 days Wt	351	53	0.20	0.46		-	-	-
530 days Wt	428	70	0.12	0.6	-	-	-	-
580 days Wt	504	73	0.15	0.56	-	-	-	-
Eigenvalues			7.11	2.26	-	-	5.98	0.82
% of total variance	-	-	59	19	-	-	75	10

^{A} Standard deviation

The first components accounted for 59% and 75% of the total variability among steers and heifers, respectively (Table 1). The projection of body weights of steers and heifers into ordination space defined by the first two principal components indicated that most of the variation in PC1 is due to the overall size (weight at all ages). All body weights at birth, pre-weaning, post-weaning and feedlot periods were positively correlated with PC1 and also with one another, however feedlot weights were not as strongly correlated as younger weights (Table 1). The second principal component (PC2) contributed about 19% and 10% of the total variation in steers and heifers and had high positive coefficients for body weights of calves at feedlot period.

Mixed model analysis of variance. Both size and feedlot growth were affected by years, breeds and management groups (Table 2). However, birth month did not have a significant influence on body weights of steers. The heritability estimates for overall size of steers and heifers were 0.36 and 0.10 respectively and for feedlot growth of steers and heifers were estimated 0.74 and 0.39, respectively.

Table 2. The probability of fixed effects, phenotypic variance and heritability of the first two principal components in steers and heifers

	Steers			Heifers		
Source of variances (Fixed effects)	Df[1]	PC1	PC2	Df	PC1	PC2
Year of birth	3	0.00	0.00	2	0.00	0.00
Management groups (cohort)	12	0.00	0.00	8	0.00	0.00
Birth months	1	0.71	0.84	1	0.00	0.08
Breed of sires	6	0.00	0.00	6	0.00	0.00
Phenotypic variance	-	3.09	0.64	-	2.80	0.19
Heritability (h^2)	-	0.36	0.71	-	0.10	0.39

[1] Degrees of freedom

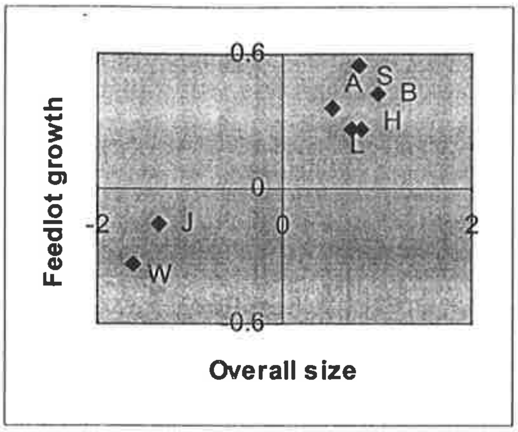

Figure 1 The breeds (see text for abbreviations) plotted against the first two principal components for body weights of Steers.

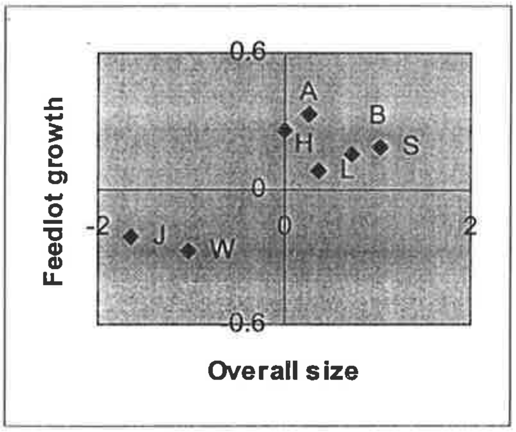

Figure 2 The breeds (see text for abbreviations) plotted against the first two principal components for body weights of heifers.

Biplot analysis of sire breed.. Figures 1 and 2 show the projection of the body weights across ages into the ordination space which used to relate the predicted means of breeds resulted from mixed model analysis of principal components to the original body weights. Offspring of sire breeds, steers or heifers, were mainly arranged in two groups: the first one including Wagyu and Jersey and the second one consisting of South Devon, Angus, Belgian Blue, Hereford and Limousin crossbreeds. Steers from Jersey and Wagyu, on the bottom-left quadrant grouped displaying both low overall size and feedlot growth. On the contrary, the second group of steers on top-right quadrant show high overall size and feedlot growth (Figure 1). Likewise, in heifers, Wagyu and Jersey projected into the bottom-left quadrant indicating low overall size and feedlot growth. However, Angus, Limousin, Belgian Blue and South Devon on top-right quadrant, were grouped with high size and feedlot growth (Figure 2).

DISCUSSION

The first two principal components (PC1 and PC2) of both steers and heifers have been used as new traits containing information from all of the body weights originally measured at different times between birth and slaughter. PC1 and PC2 were used as a basis for constructing new indices for overall size and feedlot growth of steers and heifers. In general, steers and heifers were mostly influenced by the same fixed effects. Sire breed effects were similar for steers and heifers. Considerable differences existed among steers and heifers from Wagyu and Jersey sires on the one hand and Angus, Hereford, South Devon, Limousin and Belgian Blue sires on the other. Although, principal component analysis of body weights of steers was unable to detect significant differences within each group, there were some differences within these breeds that are large in body size, as in South Devon and Angus, Hereford and Limousin and Belgian Blue and Hereford in heifers (Figure 2).

The heritability estimates were of moderate (0.36) and rather high (0.71) magnitude for overall size and feedlot growth of steers, respectively. Heritability estimates were of low (0.10) and moderate (0.39) magnitude for overall size and feedlot growth of heifers, respectively. Heritability was higher for feedlot growth than for overall size for both steers and heifers. These heritability estimates are comparable, although not consistent for heifers, with those of previous studies which reported heritability estimates of 0.47 for birth weight, 0.23 for weaning weight and 0.22 for post-weaning weight (Koots et al., 1994). However, clearly the number of animals in the current study were not sufficient for more accurate estimation of heritability

Thus, as far as the body size of diverse genotypes is concerned, the sire breed characterisation is similar for steers and heifers. While, by definition, principal components are uncorrelated, the breed means for PC1 and PC2 were correlated, so breeds with low overall growth (Jersey and Wagyu), also had low feedlot growth (Figures 1,2). It also concluded that some differences in growth patterns of diverse breeds using only body weights could not be detected. Hence, it would be worthwhile considering a wider range of traits such as body measurements.

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