Residual feed intake as selection tool in South African Bonsmara cattle

by

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Declaration

I hereby declare that this thesis, submitted for the MSc (Agric) Animal Science: Animal Breeding and Genetics degree at the University of Pretoria, is my own work, and has not previously been submitted by me for a degree at any other University

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Abstract

The largest expense in the beef industry is feed costs and decreasing feed intake without decreasing growth performance and avoiding an increase in mature weight, will decrease cost and thereby increase profits. Feed efficiency is therefore an important trait in the beef cattle industry. The Bonsmara breed was used as it is currently the breed with the highest participation in Phase C testing and has feed intake records. The most widely used measure of feed efficiency is feed conversion ratio (FCR), which is highly correlated with growth (ADG= -0.66 ± 0.04) and mature size (length = 0.58 ± 0.06; height= 0.41 ±0.06) and may increase the maintenance cost of the herd. Residual feed intake (RFI) is a linear trait and is the difference between actual feed intake and predicted feed intake required for the observed rate of gain and body weight. It has favourable genetic correlations with mature size (length = 0.01 ± 0.07; height = -0.05 ± 0.07) and feed intake (0.79 ± 0.03). The purpose of this study was to determine RFI's association with traits of economic importance the effect on ranking of bulls when selecting for RFI instead of FCR or Kleiber ratio (KR). Data from centralised growth tests were analysed and found a h^2 estimate for RFI of 0.27 ± 0.02, and genetic correlations of 0.65 ± 0.04 with FCR, 0.12 ± with KR, -0.08 ± 0.04 with scrotal circumference (SC), -0.01 ± 0.09 with weaning weight (WW) and 0.02 ± 0.07 with metabolic mid-weight (MMW). Spearman correlations were calculated and showed a difference in ranking of EBV's for RFI and FCR (0.60), RFI and KR (0.18), and FCR and KR (-0.54). In this study, small contemporary groups posed a problem in the reliability of RFI. The genetic variation of RFI justifies its inclusion in a selection programme for the Bonsmara breed in South Africa, however, small contemporary groups, the possibly more favourable results that may be obtained through a selection index, and some concerns over the lack of association with growth rate requires further investigation before applying RFI selection in the industry.

List of abbreviations

ACC	Acetyl-CoA carboxylase
ADG	Average Daily Gain
ARC	Agricultural Research Council
ATPase	Adenosine triphosphatase
BHB	β-hydroxybutyrate
BTA	*Bos Taurus* autosome
BW	Body weight
cntgrp	Contemporary group
CP	Crude protein
DFI	Daily feed intake
DMI	Dry matter intake
EBV	Estimated Breeding Value
FCR	Feed conversion ratio
FSH	Follicle Stimulating Hormone
GEBV	Genomic Estimated Breeding Value
GHR	Growth Hormone Receptor
h^2	Heritability
HIF	Heat increment of feeding
IGF	Insulin-like growth factor
IGFBP	Insulin-like growth factor binding proteins
IMF	Intra-muscular fat
IU	International units
K^+	Potassium
KR	Kleiber ratio
LD	Linkage disequilibrium
LE	Body length
LH	Luteinising Hormone
LHRH	Luteinising Hormone-releasing Hormone
ME	Maintenance efficiency
MEI	Metabolisable energy intake
MMW	Metabolic mid-weight
Na^+	Sodium
NEFA	Non-esterified fatty acids
NPN	Non-protein nitrogen
NRC	National Research Council

PEG	Partial efficiency of growth
QTL	Quantitative trait loci
RFI	Residual feed intake
r_g	Genetic correlation
RGR	Relative growth rate
r_p	Phenotypic correlation
RTU	Real time ultrasound
SC	Scrotal circumference
SD	Standard deviation
SH	Shoulder height
SMP	Sparse Matrix Package
SNP	Single Nucleotide Polymorphism
UCP	Uncoupling proteins
WW	Weaning weight

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Chapter 1

Introduction and Aim

1.1 Introduction

The beef cattle industry in South Africa is an important industry providing employment and food to various social classes in the country. Beef cattle production in South Africa has increased, with an increase of one million head from 1994 to 2004, to an estimated total of 14.1 million cattle in 2010. Beef producers include subsistence farmers (3 million), small-scale farmers (240 000) and commercial farmers (50 000), with the latter owning 60% of the country's cattle (Department of Agriculture, Forestry and Fishery, 2010). Developing countries, such as South Africa, has experienced (and will continue to experience) a dramatic increase in the demand for meat, not only due to an increase in population size, but also urbanisation and increase in income (Delgardo *et al.,* 1999). This creates the need in the livestock industry to devise a strategy for the application of sustainable systems and practices that will utilise available resources maximally while striving to minimise the effect on the environment (Capper *et al.,* 2008). In South Africa there are approximately 70 feedlots and 495 abattoirs, with the largest feedlot accommodating 120 000 cattle and processing 1 600 daily for both local consumption and exports. Approximately 68.61% of the land in South Africa is used for extensive grazing (Department of Agriculture, Forestry and Fishery, 2010) but the increase in human population will decrease the availability of land.

The sole purpose of beef cattle farming is not merely to produce more beef for the market, but also to produce income for the farmer and his employees. The profit of an enterprise is determined by both income and expenses. Output traits influencing profit, such as weight, reproduction and carcass traits, have received much emphasis, often neglecting the main factor influencing expenses – feed intake. Feeding costs is by far the largest expense in the beef industry, comprising about 55 to 75 % of the total costs associated with beef cattle production (Arthur *et al.,* 2001a; Basarab *et al.,* 2002), with approximately 75% of feed energy intake utilised for maintenance (Archer *et al.*, 1999). Feed efficiency is therefore an important to consider in a selection programme. Feed efficiency is an index of at least two traits, which are stereotypically intake and growth. More overall efficient cattle will have lower dry matter intakes, less manure production, less methane emissions and weights similar to that of less efficient cattle (Nkrumah *et al.*, 2006; Hegarty *et al.*, 2007).

Efficiency can be influenced by many factors, such as age, diet type, environmental temperatures, growth promotants and other management and environmental factors (NRC, 2000). These factors are environmental and temporary, while genetic improvement in feed efficiency is not. Ways to improve efficiency genetically include choice of breed, the use of crossbreeding, and selection within breeds (Herd *et al.*, 2003). In order to perform selection for feed efficiency within breeds, measures of feed efficiency are required to identify more efficient animals from the group. There are various measures of feed efficiency, of which Feed Conversion Ratio (FCR) is generally used as the efficiency measure of choice despite its strong association with growth rate (Mrode *et al.,* 1990; Bishop *et al.,* 1991, Koots *et al.*, 1994, Nkrumah *et al.,* 2004), leading to an increase in mature size, which in turn increases the maintenance cost of the breeding herd (Liu *et al.,* 2000). Residual feed intake was proposed for beef cattle by Koch *et al.* (1963) and is defined as the difference between actual feed intake and predicted feed intake required for the observed rate of gain and body weight. This trait has been shown to be independent from mature weight and average daily gain while being highly correlated to feed intake and FCR, leading to the reduction of feed intake without decreasing growth performance or increasing cow size (Archer *et al.,* 1999; Archer *et al.,* 2002; Herd *et al.,* 2003; Crews, 2005; Nkrumah *et al.,* 2007a). Another limitation using FCR is that it is a ratio trait while RFI is a linear trait. The use of ratio traits usually places more emphasis on the component with greater variation, leading to unpredictable results (Gunsett, 1984). A unit improvement in a ratio trait such as FCR does not always indicate an overall improvement in efficiency, making this information difficult to interpret (Crews, 2005).

It has also been shown that selecting for RFI could have favourable implications for the environment, which has become a factor of increasing importance. Animal production systems are of interest since it has been estimated that livestock (monogastric and ruminants) is responsible for up to 18% of global methane emissions (Steinfeld *et al.,* 2006) while methane emissions from ruminant livestock contribute approximately 12% to anthropogenic greenhouse gas emissions (Crutzen *et al.,* 1986). High methane production has implications for the environment as methane emissions contribute to greenhouse emissions. Following selection for low RFI animals, methane production and energy lost as methane has been shown to be as much as 25-28% lower in low RFI steers compared to high RFI steers, leading to approximately 16,100 L less methane per year (Nkrumah *et al.*, 2006; Hegarty *et al.,* 2007). The effect of selection for RFI on methane emission makes RFI an attractive trait.

In the commercial farmer sector in South Africa, the most popular pure breeds are Brahman, Simmentaler, Bonsmara and Nguni, with the Bonsmara and Angus being the breeds with the most herds participating in the National Beef Recording and Improvement scheme (Scholtz, 2010). The current measures of feed efficiency for Bonsmara cattle are FCR and Kleiber ratio (KR), the main advantage of KR being that feed intake (an expensive trait to measure) is not required in the calculation.

1.2 Aim of study

In South Africa, RFI is currently not used as a feed efficiency measurement in Bonsmara cattle. The purpose of this study is to determine RFI's association with various traits of economic importance and whether using EBV's for RFI instead of FCR or Kleiber ratio will change the ranking of bulls.

The investigation of RFI as a measure of feed efficiency was requested by the South African Bonsmara Breeders Society. The Bonsmara is a result of a well-documented crossbreeding programme and is now a prominant breed in South Africa with more than 100 000 registered animals. The Bonsmara breeders are also actively involved in performance testing, with an average of 95% participation (the highest participation of all South African breeds) in the National Beef Recording and Improvement scheme over the years 1999 to 2008.

Data of 39 years was provided by the Agricultural Research Institute (ARC) on request of the Bonsmara Breeders Society for this study. The following procedures were done to evaluate RFI as a possible selection criterion to improve feed efficiency:

- Calculate RFI
- Estimate genetic parameters for RFI, FCR, KR, daily feed intake (DFI), Average Daily Gain (ADG), weaning weight (WW), metabolic mid-weight (MMW), shoulder height (SH), body length (LE) and scrotal circumference (SC).
- Estimate breeding values for all traits
- Compile genetic trends from 1999 to 2009
- Compare the ranking of bulls for feed efficiency when selecting for RFI, FCR and KR respectively

Chapter 2

Literature review

2.1 Introduction

Residual feed intake, also called net feed intake, is defined as the difference between actual feed intake and predicted feed intake required for the observed rate of gain and body weight, with a low RFI value indicating a more efficient animal. Many studies have found heritability estimates varying from 0.14 to 0.58 (Koch *et al.*, 1963; Fan *et al.,* 1995; Arthur *et al.*, 2001a, 2001c; Archer *et al.*, 2002; Crews *et al.*, 2003; Schenkel *et al.*, 2004; Crowley *et al.,* 2010; Mujibi *et al.,* 2011; Berry & Crowley, 2012). Considerable variation in RFI has been found in species such as mice (Archer *et al.*, 1998), poultry (Byerly, 1941; Luiting & Urff, 1991), pigs (Foster *et al.*, 1983; Gilbert *et al.*, 2007; Hoque *et al.*, 2007) and cattle (Koch *et al.*, 1963). Genetic variation in RFI has also been reported in a range of cattle breeds in many countries including Australia (Arthur *et al.*, 2001a), Britain (Herd & Bishop, 2000), Canada (Liu *et al.*, 2000) and France (Renand *et al.*, 1998). From all the studies done on various breeds, it can be concluded that sufficient variation exists between and within both tropical and temperate breeds, holding great selection potential. The aim of this chapter was to review relevant literature on RFI and other measures of feed efficiency with specific reference to the physiology, molecular basis and genetic parameters

2.2 Measures of efficiency

Measures of feed efficiency include feed FCR also referred to as feed:gain ratio, maintenance efficiency (ME), partial efficiency of growth (PEG), Kleiber ratio (KR), relative growth rate (RGR), RFI (Archer *et al.*, 1999; Nkrumah *et al.,* 2004), residual gain (RG) and Residual intake and body weight gain (RIG) as described in table 2.1.

The main trait used to select for feed efficiency, namely FCR, has a heritability estimate of around 0.41 (Nkrumah *et al.,* 2007a). This ratio is linked to frame size since, when steers are fed to a specific weight endpoint, large framed animals have a lower FCR than small framed animals (Thonney *et al.*, 1981). Metabolic mid-weight (MMW) is correlated with ADG and RGR, which are both high in large framed animals (Nkrumah *et al.,* 2004). This could lead to negative effects in the breeding herd since increased body size will increase maintenance requirements. It has been shown that cows that are larger at maturity are associated with lower cow/calf pair efficiency (Albertini *et al.,* 2008). Since FCR is a ratio trait, an improvement in FCR will not necessarily lead to an increase in efficiency. Changes in FCR could be due to either one of the component traits of the ratio, meaning a change in FCR could either be due to an increase in growth rate or a decrease in feed intake.

Table 2.1 Examples of different measures of efficiency

Measure of efficiency	Definition	Reference
Feed conversion ratio (FCR)	The actual units of DMI required for one unit gain in body weight	Brody (1945)
Maintenance efficiency (ME)	Metabolisable energy intake (MEI) for maintenance per unit of metabolic body weight, which is body weight raised to the power 0.75	Webster *et al.* (1974)
Partial efficiency of growth (PEG)	Ratio of average daily gain per unit of feed used for growth (actual feed intake minus expected feed intake for maintenance)	Kellner (1909)
Relative growth rate (RGR)	Average daily gain divided by live weight	Fitzhugh & Taylor (1971)
Kleiber ratio (KR)	Average daily gain divided by metabolic weight, which is body weight raised to the power 0.75	Kleiber (1947)
Residual feed intake (RFI)	The difference between actual feed intake and predicted feed intake required for the observed rate of gain and body weight	Koch *et al.* (1963)
Residual gain (RG)	The difference between actual growth rate and predicted growth rate for the observed feed intake and body weight	Koch *et al.* (1963)
Residual intake and body weight gain (RIG)	Combination of RG and RFI, and is the sum of (-1 x RFI) and RG, both standardised to a variance of one	Berry & Crowley (2012)

It seems that FCR underestimates differences between animals in energetic efficiency, which may be due to the effects of growth and body weight on feed intake (Archer *et al.,* 1999; Nkrumah *et al.,* 2004). This trait is also influenced by differences in growth and maturity patterns of different animals (Kennedy *et al.,* 1993; Archer *et al.,* 1999). The variation in gain efficiency between breeds reflects the effect of maturity pattern and frame size. Smaller breeds are more efficient over a constant period of time, although larger breeds with higher rates of gain are more efficient when a constant level of gain is reached (Gregory *et al.,* 1994).

Kleiber ratio (KR) is defined as ADG divided by metabolic weight. Metabolic weight is live weight raised to the power of 0.75 and is a value describing the relationship between body surface area and volume (Kleiber, 1932). This relationship shows that larger animals use energy more efficiently per unit live weight than smaller animals and therefore an animal that weighs twice as much as another won't require twice as much energy for maintenance. An advantage of using KR for selection is that feed intake, which is expensive to measure, is not required. Selection to improve efficiency using KR or RGR may lead to desirable effects in growing animals, but may not be desirable once the animals are older and no longer growing. Using KR or RGR as a selection tool may not lead to results markedly different than when using FCR (Nkrumah *et al.,* 2004).

The feed efficiency measurement PEG is defined as the ratio of average daily gain per unit of feed used for growth (actual feed intake minus expected feed for maintenance), has a heritability of 0.56 (Nkrumah *et al.,* 2007a) and is highly correlated with RFI (-0.75), suggesting that selection for PEG should lead to similar results than when selecting for RFI (Arthur *et al.,* 2001b; Nkrumah *et al.,* 2004). The high correlation could be expected, since PEG and RFI both incorporate components of feed intake due to maintenance and growth in their calculations. However, PEG is correlated to weight traits such as ADG (0.24), metabolic weight (-0.23) as well as RGR (0.36). This means that although PEG and RFI are highly correlated, PEG may lead to an increase in growth and body size (Nkrumah *et al.,* 2004). Arthur *et al.* (2001b) found a weak correlation (0.04 ± 0.05) between PEG and growth rate.

In beef cattle, the concept of RFI was proposed by Koch *et al.* (1963), which holds the potential to overcome the disadvantages of FCR. Feed intake was adjusted for weight and gain to divide feed intake into two portions - the expected feed intake based on level of production and weight, and a "residual portion". The residual portion was found to be moderately heritable (0.28) and could be used as a tool to rank animals on feed efficiency. Compared to other measures of efficiency, RFI has been reported to be unaffected by pretest environmental variations in age, body weight and age of dam, making comparisons across environments and contemporary groups easier (Herd & Bishop, 2000). However, more recent studies have shown that factors such as season, diet, test length and stage of maturity have effects on RFI (Mujibi *et al.,* 2010; Durunna *et al.,* 2011).

A correlation above 0.90 was found between phenotypic RFI and genotypic RFI, suggesting that they can be regarded as the same trait (Nkrumah *et al.,* 2007a). Therefore the observed phenotype is a strong indication of the animal's genetic make-up for RFI (Hoque *et al.,* 2006; Nkrumah *et al.,* 2007a). In the calculation of RFI, expected feed intake is derived from linear regression of feed intake on MMW and ADG in growing calves, while in lactating and/or pregnant cows, expected feed intake will be regressed on weight and milk and/or fetal growth (Basarab *et al.,* 2007). RFI measured post-weaning and at maturity have a correlation above 0.90 (Archer *et al.,* 2002), suggesting that efficient growing animals selected at a young age will remain more efficient throughout their lives and therefore be more beneficial to more than one sector in the beef cattle industry (Crews, 2005).

The finding that RFI is independent of growth and weight traits has been criticised as unfavourable as an increase in ADG is desired (Berry & Crowley, 2012). Slow-growing animals can have a low RFI and will spend more time in feedlots, which will increase feeding costs. Koch *et al.* (1963) also proposed, and preferred, residual gain (RG), which is the difference between expected growth rate and actual growth rate for the observed feed intake and body weight. This trait is therefore associated with growth rate, but not feed intake (Berry & Crowley, 2012) and has been adopted as a measure of efficiency by the American Angus Association (MacNeil *et al.,* 2011). Selection for RG may increase growth rate without increasing feed intake, and allow animals to spend less time in feedlots. Residual feed intake and body weight gain (RIG), which is a combination of RFI and RG, has been proposed by Berry & Crowley (2012) and is the sum of (-1 x RFI) (to present RFI in such a way that a positive value is favourable) and RG, both standardised to a variance of one. Selection for this trait allows for selection of fast-growing animals that consume less feed than expected, without increasing body weight (Berry & Crowley, 2012).

Further criticising RFI, a single measure of feed efficiency combining growth, size and feed intake, does not provide additional information than obtained from the component traits (Kennedy *et al.*, 1993) and a more positive result may be obtained from a linear index of component traits (Smith, 1967; Gunsett, 1984). The decision to use RFI, RG or RIG depends on the breeding objectives of the breeder. Animals that eat less to achieve average performance will be the result of selection for RFI, high performing animals that consume average amount of feed will be the result of selection for RG, and animals with a balance of intake and performance will be a result of selection for RIG or the use of a selection index.

2.3 Genetic parameters for RFI

The extent to which efficiency can be improved using RFI depends on the presence and strength of correlations with other important traits, such as growth and weight traits, reproductive traits and meat quality traits (Herd *et al.*, 2003). It is also important to consider correlations with other measures of efficiency, such as FCR, RGR, PEG and KR to determine which would be more economically beneficial. Both FCR and RFI are moderately heritable (Van der Westhuizen *et al.*, 2004). Heritability estimates found in various studies are shown in table 2.2.

Table 2.2 Heritability estimates for RFI found in different breeds

Breed	**Heritability**	**Reference**
Multiple breeds	0.38 ± 0.07	Schenkel *et al.* (2004)
Multiple breeds	0.45 ± 0.06	Berry & Crowley (2012)
British breeds	0.28 ± 0.11	Koch *et al.* (1963)
Angus	0.28	Fan *et al.* (1995)
Angus	0.23	Archer *et al.* (2002)
Angus and Charolais	0.39 ± 0.03	Arthur *et al.* (2001a), Arthur *et al.* (2001b)
Charolais	0.32	Arthur *et al.* (2001c)
Charolais	0.55	Crowley *et al.* (2010)
Charolais-sired	0.58 ± 0.20	Crews *et al.* (2003)
Limousin	0.23	Crowley *et al.* (2010)
Hereford	0.14	Fan *et al.* (1995)
Bonsmara	0.31	Van der Westhuizen *et al.* (2004)
Crossbreds	0.42 ± 0.15	Nkrumah *et al.* (2007a)
Crossbreds	0.29 ± 0.12	Mujibi *et al.* (2011)

2.3.1 Weight traits and feed intake

Correlations between various traits and RFI are shown in table 2.3, and correlations between various traits and FCR are shown in table 2.4. There are no significant correlations between RFI and both ADG and BW, and therefore RFI is seen as independent from production traits (Herd *et al.,* 2003). The high correlation found between RFI and feed intake means that while low and high RFI animals have the same ADG and final body weight, low RFI animals consume less feed. Cattle with high and low RFI have similar growth potential post-weaning and milk production (Arthur *et al.,* 1999, 2005). The low correlation between FCR and feed intake indicates that a decrease in FCR does not necessarily lead to a decrease in feed intake, and therefore not an overall improvement in efficiency. The negative correlation between FCR and cow size as well as ADG confirms that using FCR as a selection criterion for efficiency would lead to an increase in weight traits. In some studies, a relationship between RFI and mature weight has been found, indicating that selection for low RFI may lead to an increase in mature weight. Other studies found no significant genetic or phenotypic correlation between RFI and ADG or mature weight (Herd & Bishop, 2000; Arthur *et al.,* 2001a; Schenkel *et al.,* 2004; Nkrumah *et al.,* 2007a). It is important to note that when RFI is calculated using expected feed intake from feeding standard formulas, it is not automatically independent of production and will therefore be correlated with ADG and mature weight as indicated in studies by Fan *et al.* (1995), Arthur *et al.* (2001a) and Smith *et al.* (2010). The equations used by the National Research Council (NRC) overestimate energy requirements and can't be used to predict feed intake for the calculation of RFI. It is therefore essential to calculate RFI by modelling the actual data (Liu *et al.* 2000).

2.3.2 Reproductive traits

Several studies reported no or weak correlations between RFI and scrotal circumference (SC) in bulls (Arthur *et al.,* 2001a; Fox *et al.,* 2004; Schenkel *et al.,* 2004). There is a negative correlation between SC and age at puberty of their daughters (Koots *et al.,* 1994) and therefore selection for RFI is not expected to negatively affect age at puberty. However, puberty corresponds to the time where rate of fat deposition begins to increase relative to the rate of protein deposition (Owens *et al.,* 1993). The effect of RFI on reproduction has been scrutinised as the decreased fat composition associated with selection for low RFI may reduce the productivity of the cow-calf operation (Lancaster, 2008). Arthur *et al.* (2005) found that cows selected for low RFI calved five days later during the calving season, while Basarab *et al.* (2007) showed that dams of progeny with low RFI calved four days later during the calving season. In high and low RFI cows there were no differences in pregnancy rates, calving rates, weaning rates or the birth and weaning weights of their calves (Arthur *et al.,* 2005; Basarab *et al.,* 2007), but dams giving birth to high RFI calves had a higher twinning rate and calf death loss (Basarab *et al.,* 2007). Low RFI heifers have been shown to reach puberty 13 days later than high RFI heifers, while pregnancy and conception rates were unaffected (Schaffer *et al.,* 2010). This delay in puberty was also found in a study where low RFI heifers tended to reach puberty later than high RFI heifers (Basarab *et al.,* 2007). However, in addition to no difference in pregnancy rate, Lancaster *et al.* (2006, 2008) found no difference in the percentage of heifers cycling and age at puberty. Loyd (2009) concluded that selecting for low RFI may lead to shorter postpartum intervals since low RFI cows exhibited estrus and developed a corpus luteum earlier than high RFI cows.

Table 2.3 Genetic correlations between RFI and production, reproduction, profitability and metabolic traits

Trait	**r_g**	**Reference**
DMI	0.56	Lancaster. (2008)
	0.64	Herd & Bishop (2000), Archer *et al.* (2002)
	0.79	Arthur *et al.* (2001c)
	0.69	Smith *et al.* (2010)
	0.54	Baker *et al.* (2006)
	0.75	Nkrumah *et al.* (2004)
	0.81	Schenkel *et al.* (2004)
	0.51	Mujibi *et al.* (2011)
Mature weight	None	Arthur *et al.* (2001a)
	-0.09	Herd & Bishop (2000)
	-0.22	Archer *et al.* (2002)
Metabolic weight	-0.02	Nkrumah *et al.* (2004)
	-0.17	Berry & Crowley (2012)
Weaning weight	-0.05	Van der Westhuizen *et al.* (2004)
Shoulder height	-0.02	Van der Westhuizen *et al.* (2004)
ADG	-0.06	Arthur *et al.* (2001a)
	0.02	Archer *et al.* (2002)
	-0.09	Van der Westhuizen *et al.* (2004)
	None	Herd & Bishop (2000), Schenkel *et al.* (2004), Nkrumah *et al.* (2004), Lancaster (2008)
	-0.03	Mujibi *et al.* (2011)
	0.01	Berry & Crowley (2012)
Methane production	0.44	Nkrumah *et al.* (2006)
Heat production	0.68	Nkrumah *et al.* (2006)
Retained energy	-0.67	Nkrumah *et al.* (2006)
Maintenance energy requirement	0.42	Castro Bulle *et al.* (2007)
Post-wean profitability	-0.59	Van der Westhuizen *et al.* (2004)
SC	0.05	Van der Westhuizen *et al.* (2004)
	-0.03	Arthur *et al.* (2001a)
	0.15	Schenkel *et al.* (2004)
KR	0.15	Berry & Crowley (2012)

Table 2.4 Genetic correlations between FCR and production, reproduction, profitability and metabolic traits

Trait	r_g	Reference
Cow size	-0.29	Herd & Bishop (2000)
	-0.54	Archer *et al.* (2002)
Shoulder height	-0.24	Van der Westhuizen *et al.* (2004)
DMI	0.15	Archer *et al.* (2002)
	0.29	Smith *et al.* (2010)
	0.40	Baker *et al.* (2006)
	0.49	Nkrumah *et al.* (2004)
ADG	-0.56	Smith *et al.* (2010)
	-0.65	Baker *et al.* (2006)
	-0.63	Nkrumah *et al.* (2004)
	-0.69	Van der Westhuizen *et al.* (2004)
	-0.53	Berry & Crowley (2012)
Metabolic weight	0.07	Nkrumah *et al.* (2004)
	-0.62	Robinson & Oddy (2004)
	-0.57	Hoque *et al.* (2006)
	0.35	Berry & Crowley (2012)
Weaning weight	-0.03	Van der Westhuizen *et al.* (2004)
KR	-0.75	Berry & Crowley (2012)
RFI	0.70	Herd & Bishop (2000)
	0.85	Arthur *et al.* (2001a)
	0.57	Arthur *et al.* (2001c)
	0.69	Schenkel *et al.* (2004)
	0.62	Nkrumah *et al.* (2004)
	0.75	Van der Westhuizen *et al.* (2004)
	0.48	Berry & Crowley (2012)
Post-wean profitability	-0.92	Van der Westhuizen *et al.* (2004)
Scrotal circumference	-0.06	Van der Westhuizen *et al.* (2004)
	0.06	Schenkel *et al.* (2004)
Methane production	0.19	Nkrumah *et al.* (2006)
Heat production	0.37	Nkrumah *et al.* (2006)
Retained energy	-0.24	Nkrumah *et al.* (2006)

2.3.3 Carcass and meat quality traits

Correlations between carcass traits and FCR are shown in table 2.5, and correlations between carcass traits and RFI in table 2.6. Studies have shown that more efficient animals have less subcutaneous fat (Robinson *et al.*, 1999; McDonagh *et al.*, 2001; Herd *et al.*, 2003; Richardson *et al.*, 2004; Baker *et al.* 2006). Low RFI cattle are expected to have a leaner carcass as there are positive genetic correlations between RFI and carcass fat traits. Many studies have not found any correlation between RFI and longissimus muscle area (Basarab *et al.* 2003; Nkrumah *et al.* 2004, 2007; Brown, *et al.,* 2005). Richardson *et al.* (2004) reported a 13.2% decrease in subcutaneous fat and intra-muscular fat (IMF) in the progeny from cattle selected for low RFI. This could lead to unfavourable correlated responses in meat quality and heifer fertility traits (McDonagh *et al.* 2001; Arthur *et al.*, 2005). It appears that the relationship among RFI, fat thickness and IMF may be different in purebred or crossbred groups of cattle, as there are inconsistencies in data presented by studies (Baker *et al.*, 2006). The calculation of RFI can be adjusted for backfat thickness to minimise the reduction in backfat when selecting for lower RFI (Basarab *et al.*, 2003; Smith *et al.*, 2010). Even considering the decrease in fat, low RFI animals still meet market specifications for feedlot animals (Richardson *et al.*, 1998; Nkrumah *et al,.* 2004), produce carcasses of acceptable fat finish and deliver carcass weights similar to that of high RFI animals and should therefore be more profitable (Herd *et al.,* 2003).

Concerning quality traits, steaks from high RFI steers seem to have lower off-flavour scores and less cook loss percentage than those of low RFI steers. There is no difference in tenderness as observed by a sensory panel or measured by shear force values (Baker *et al.,* 2006). There is also no difference in loin muscle depth or growth (Kelly *et al.,* 2010).

Table 2.5 Genetic correlations between FCR and carcass traits

Trait	**r_g**	**Reference**
Backfat gain	-0.03	Nkrumah *et al.* (2004)
Ultrasound backfat	0.20	Nkrumah *et al.* (2004)
Grade fat	0.21	Nkrumah *et al.* (2004)
Lean meat yield	0.09	Nkrumah *et al.* (2004)
Yield grade	-0.18	Nkrumah *et al.* (2004)
Loin muscle area	0.24	Nkrumah *et al.* (2004)
Rib fat	-0.28	Schenkel *et al.* (2004)
Lean meat yield	0.38	Robinson & Oddy (2004)
	-0.32	Koots *et al.* (1994)

Table 2.6 Genetic correlations between RFI and carcass traits

Trait	r_g	**Reference**
12th – 13th rib fat depth	0.17	Arthur *et al.* (2001a)
Rump fat depth	0.48	Robinson & Oddy (2004)
IMF	0.06	Arthur *et al.* (2001a)
	0.22	Robinson & Oddy (2004)
	0.17	Robinson *et al.* (1999)
	None	Nkrumah *et al.* (2004), Carstens *et al.* (2008)
Subcutaneous fat	0.17	Arthur *et al.* (2001a)
	0.16	Schenkel *et al.* (2004)
Longissimus muscle area	-0.17	Schenkel *et al.* (2004)
Backfat gain	0.30	Nkrumah *et al.* (2004)
Ultrasound backfat	0.19	Nkrumah *et al.* (2004)
	0.22	Basarab *et al.* (2003), Lancaster *et al.* (2008)
Grade fat	0.25	Nkrumah *et al.* (2004)
Lean meat yield	-0.22	Nkrumah *et al.* (2004)
Yield grade	0.28	Nkrumah *et al.* (2004)
Carcass fat	0.14	Basarab *et al.* (2003)
Carcass lean	-0.21	Basarab *et al.* (2003)
Marbling score	0.22	Basarab *et al.* (2003)
	None	Nkrumah *et al.* (2004)
Empty body fat	0.26	Basarab *et al.* (2003)

2.3.4 Other efficiency traits

Correlations between other feed efficiency traits and various traits are shown in tables 2.7 and 2.8. The high correlation between RGR and KR shows that they can be considered as the same trait. This explains the low correlations between RFI and both these traits (RGR = -0.04; KR = -0.004). There is a strong association between RFI and PEG, but they cannot be considered as the same trait. Even though they are similar, PEG is not independent from weight traits.

Table 2.7 Correlations between PEG and various traits

Trait	**r_g**	**Reference**
Methane production	-0.55	Nkrumah *et al.* (2006)
Heat production	-0.50	Nkrumah *et al.* (2006)
Retained energy	0.62	Nkrumah *et al.* (2006)
DMI	-0.52	Nkrumah *et al.* (2004)
	-0.55	Lancaster (2008)
	-0.82	Arthur *et al.* (2001b)
Backfat gain	-0.30	Nkrumah *et al.* (2004)
Ultrasound backfat	-0.25	Nkrumah *et al.* (2004)
	-0.16	Lancaster *et al.* (2008)
Grade fat	-0.27	Nkrumah *et al.* (2004)
Lean meat yield	0.24	Nkrumah *et al.* (2004)
Yield grade	-0.25	Nkrumah *et al.* (2004)
ADG	0.24	Nkrumah *et al.* (2004)
	0.25	Lancaster (2008)
	0.04	Arthur *et al.* (2001b)
Metabolic weight	-0.11	Nkrumah *et al.* (2004)
MEI	-0.60	Nkrumah *et al.* (2004)
RGR	0.36	Nkrumah *et al.* (2004)
	0.60	Arthur *et al.* (2001b)
RFI	-0.75	Lancaster. (2008)
	-0.89	Nkrumah *et al.* (2004)
	-0.65	Arthur *et al.* (2001b)

Table 2.8 Correlations between various traits and RGR and KR respectively (Nkrumah *et al.,* 2004)

Trait	**RGR**	**KR**
KR	0.96	-
DMI	0.18	0.36
ADG	0.72	0.85
Metabolic weight	-0.23	-0.03
MEI	0.48	0.53
RFI	-0.04	-0.004
FCR	-0.75	-0.73

2.4 Economic impact

In the USA beef production per total inventory increased from 62kg in 1955 to 113 kg in the early 2000's (Elam & Preston, 2004). This improvement in weight gains can be attributed to the implementation of strategies such as intensive feedlot systems, nutrition, reproductive technologies, use of growth promoters and other pharmaceuticals, crossbreeding and selection programs with emphasis on output traits (Carstens *et al.,* 2008). With the increase in mature weight and weight gains, FCR appears to have decreased, although some believe that true feed efficiency and maintenance energy required by the breeding herd has not improved over the past 50 years (Archer *et al.,* 1999; Johnson *et al.,* 2003). This creates the need for a more descriptive and effective measure of feed efficiency.

The two traits influencing FCR are feed intake and growth. To increase feed efficiency, the ideal is to decrease feed intake (also decreasing costs) without decreasing growth (maintaining income). Since feed intake is highly correlated with growth traits, a single, focused selection for decreased feed intake will lead to an undesirable decrease in growth, while selection for increased growth will lead to increased feed intake (Almeida *et al.,* 2007). There are weak correlations between FCR measured post-weaning and mature cow feed intake ($r = 0.15$) and mature cow FCR ($r = 0.20$). This shows that when using FCR, efficient young calves will most likely not be efficient as mature cattle (Archer *et al.,* 2002), or that FCR is not a suitable trait to use to define and identify feed efficiency after maturity. However, this study by Archer *et al.* (2002) showed a genetic correlation of -0.22 between RFI measured post-wean and MMW of mature cow, suggesting that RFI is not independent from weight and, like FCR, may increase cow weight.

Feed efficiency improvements should increase profitability since input costs will be decreased. A 10% improvement in ADG as a result of a 7% increase in appetite has been shown to improve profitability with 18%.

The economic benefit can be seen clearly when compared to an improvement in efficiency: a 10% improvement in feed efficiency increased profitability by 43% (Fox *et al.,* 2001). A 5% increase in feed efficiency has even been shown to have an economic effect four times greater than a 5% improvement in ADG (Gibb & McAllister, 1999).

Even though RFI has an unfavourable positive correlation with carcass fatness, this effect should not decrease profitability since the carcass still meets market standards (Nkrumah *et al.,* 2004) and RFI can be adjusted to include carcass fatness traits to minimise the unfavourable responses (Crews, 2005). A study on South African Bonsmara cattle by Van der Westhuizen *et al.* (2004) has shown that selecting for RFI will not necessarily be more profitable than when selecting for FCR. This study compared the effect of selecting indirectly for post-wean profitability (M-value) using RFI and FCR. Factors taken into account to determine the M-value include slaughter weight, price per kg carcass weight, body weight at the start of the test, live weight price per kg for weaners, feed intake, feed price per kg, bank interest rate, test length and veterinary costs. They found that FCR and M-value are highly correlated (-0.92). A correlation of only –0.59 was found between RFI and M-value. From these results it was concluded that using FCR would be more profitable.

2.5 Environmental impact

It has been shown that selecting for RFI could have favourable implications for the environment, which has become a factor of increasing importance. Animal production systems are of interest since it has been estimated that livestock (monogastric and ruminants) is responsible for up to 18% of global methane emissions (Steinfeld *et al.,* 2006) while methane emissions from ruminant livestock contribute approximately 12% to anthropogenic greenhouse gas emissions (Crutzen *et al.,* 1986). High methane production has implications for the environment as methane emissions contribute to greenhouse emissions. In Canada, agriculture contributes approximately 10% to the total Canadian greenhouse gas emissions, of which 2.6% is methane (Nkrumah *et al.,* 2006). Following selection for low RFI animals, methane production and energy lost as methane has been shown to be as much as 25-28% lower in low RFI steers compared to high RFI steers, leading to approximately 16,100 L less methane per year (Nkrumah *et al.*, 2006; Hegarty *et al.,* 2007). The effect on methane emission when making use of estimated breeding values (EBV's) to select for low RFI animals has also been investigated and it was found that a 1kg/d reduction in an EBV for RFI can lead to a 13.38g/d reduction in methane emission (Hegarty *et al.,* 2007).

The earliest studies regarding the investigation of the effect of RFI on methane emissions, related RFI to methane production based on estimates derived from the relationship between RFI and dry matter intake (DMI). This led to a theoretical estimation of a 5% difference in methane production between high and low RFI animals (Herd *et al.,* 2002a; Okine *et al.,* 2003). Later, Nkrumah *et al.* (2006) showed the first experimental evidence of an association between RFI and methane production, which was followed by the study by Hegarty *et al.* (2007), showing the magnitude of methane emission associated with the use of an EBV to select for lower RFI. It has been shown that by using RFI as a selection tool in Australia, a reduction of 568,000t methane can be achieved between 2002 and 2025. It has been estimated that by 2025 enteric methane emissions from the Australian beef herd in the study will be 3.1% lower than in 2002 (Alford *et al.,* 2006).

Energy use and partitioning are related to differences in dietary energy losses (urinary, methane and fecal), heat production and energy retention (Delfino & Mathison, 1991; Basarab *et al.*, 2003). The difference in methane production in high and low RFI animals cannot be explained by the difference in feed intake alone (Machmüller & Clark, 2005). Possible reasons could be differences in metabolisability of feed and possible individual animal differences in methane production (Nkrumah *et al.,* 2006). There is a genetic link between methanogens and their hosts, meaning the presence of methonogenic bacteria in an animal is not only under dietary constraint, but also by the animal itself (Hackstein *et al.,* 1996). In humans, methane production has a heritability estimate of 0.42 (Flatz *et al.,* 1985). Methane production can also be reduced through nutritional strategies, as high grain diets that may contain vegetable fats or ionophores, will reduce energy lost through urine and methane (Van der Honing & Steg, 1990).

A reduction in manure production and nitrous oxide content can also be expected to be associated with reduced intake in low RFI animals (Okine *et al.,* 2001; Herd *et al.,* 2002a), which will decrease nitrogen pollution in soil. This decrease in nitrogen in manure will not only be due to a decrease in nitrogen/protein intake, but may also be due to a greater efficiency of utilisation of dietary nitrogen by the animal, as low RFI animals have reduced protein turnover and accrete body tissue at the same rate as high RFI animals (Richardson & Herd, 2004).

2.6 Physiology of RFI

The finding that RFI is independent from production traits (refer to section 2.7 for correlations with other traits) indicates that variation in RFI may be due to variation in basic metabolic processes (Herd & Bishop, 2000). The main physiological processes that are thought to be involved in RFI are feed intake, digestion of feed, metabolism and body composition, physical activity and thermoregulation (Herd & Arthur, 2009). Differences between steers and bulls also occur in feed intake (16% higher in steers), PEG (11% lower in steers) and RFI (13% higher in steers) (Nkrumah *et al.,* 2004). The mechanisms involved have the following contribution to variation in RFI: 9% for difference in heat increment of feed (HIF) (Standing Committee on Agriculture, 2000), 14% for differences in digestion (Richardson *et al.,* 1996), 5% for differences in body composition (Richardson *et al.,* 1999), and 5% for differences in activity (Arthur *et al.*, 2001b). The remaining proportion is thought to be contributed by factors including heat loss associated with variation in processes such as protein turnover and ion transport (Herd *et al.,* 2004).

2.6.1 Feed intake and digestion

An increase in feed intake results in an increase in energy required for eating activity and digestion. Digestion of feed leads to heat production, which is referred to as the HIF (Herd & Arthur, 2009), and is approximately 9% of metabolisable energy intake (MEI) (Standing Committee on Agriculture, 2000). Animals with low RFI will eat less and are therefore expected to have less energy expended as HIF (Herd & Arthur, 2009). In a study on poultry, high RFI chickens had a 15% greater dry matter intake (DMI) and 21% greater heat loss (Luiting *et al.,* 1991). A greater diet-induced thermogenesis was found in high RFI cockerels (Gabarrou *et al.,* 1997). In high RFI calves with 11% greater metabolisable energy intake, a 10% greater heat loss compared to low RFI calves was reported (Basarab *et al.,* 2003). However, White (2004) reported similar heat loss between calves with high and low RFI with similar metabolisable energy intake.

After one generation of divergent selection for RFI a 6% difference in DMI was found (Richardson *et al.,* 1998) and 11% after 5 years of selection (Arthur *et al.,* 2001a). A 12-17% difference in DMI between high and low RFI steers was observed in steers fed a concentrate-based diet (Nkrumah *et al.,* 2004, 2006; Kolath *et al.,* 2006; Castro Bulle *et al.,* 2007). No significant difference in DMI was found in animals grazing forage, however, low RFI cows had a 21% numerically lower average in forage intake than high RFI cows (Meyer *et al.,* 2008). In a study with lactating cows on pasture, a small numerical difference in forage intake was found, accompanied with a 15% increase in calf BW/cow DMI between low and high RFI cows (Herd *et al.,* 1998).

Digestibility of feed tends to decrease with an increase in feed intake (Standing Committee on Agriculture, 2000) and since low RFI animals have lower feed intakes, digestibility of feed will be higher. However, intake alone does not account for all the variation in digestibility as there is also evidence showing genetic variation in total tract digestion of feed (Richardson & Herd, 2004). Favourable negative correlations have been found between RFI and dry matter digestibility, for example r = -0.33 (Nkrumah *et al.,* 2006) and r = -0.32 (Brown, 2005), meaning more efficient animals will have higher dry matter digestibilities. In a study feeding a pelleted ration with a DM digestibility of 68%, low and high RFI cattle differed in their ability to digest dry matter by approximately 1%. This difference was responsible for 14% of the difference in intake between high and low RFI groups (Richardson *et al.,* 1996). Steer progeny from parents selected for low RFI have been reported to have shown a tendency to have higher dry matter digestibilities (Oddy & Herd, 2004).

It has been suggested that high RFI lines have decreased starch digestion (Channon *et al.,* 2004). It is, however, unknown whether this is simply an effect of intake alone. No differences were found in forage digestibility for cows (Herd *et al.,* 1998) or stocker steers (Herd *et al.,* 2002b) grazing pasture. Efficiency may be affected differently by forages than by concentrate-based diets (Meyer *et al.,* 2008) although it has been shown that cattle would be ranked similarly for RFI measured on roughage versus grain diets (Crews *et al.,* 2003). Caution should be taken when assigning differences in digestion as a major factor causing variation in RFI due to difficulties in accurately measuring small differences in digestibility. Studies on monogastric animals indicate that digestibility is not an important factor (pigs: de Haer *et al.*, 1993; chickens: Luiting *et al.*, 1994; mice: Bunger *et al.*, 1998).

Selection based on RFI measured post-weaning on high quality pelleted rations fed ad-libitum does not show an accompanied inferior growth performance by cows and their calves on pasture (Herd *et al.*, 1998; Arthur *et al.*, 1999) or by steers on pastures (Herd *et al.*, 2002b). Evidence shows animals that are selected while receiving high quality feed still shows improvement in feed efficiency on pastures (Herd *et al.*, 1998, 2002b). Measuring feed intake of animals on pastures can be very complex and therefore more indirect means of intake measurements are used. These methods provide reasonable estimates of intake at each sampling and additional sampling periods are required to improve accuracy (Casler *et al.,* 1998; Curtis *et al.,* 2008), but this is labour intensive.

2.6.2 Activity and thermoregulation

Activity in this sense includes activity involved in feeding, ruminating and locomotion (Herd *et al.,* 2004). Changes in physical activity will influence total energy expenditure and feed efficiency (Susenbeth *et al.,* 1998). In chickens, activity has been identified as a major factor as it explains up to 80% of the genetic difference in RFI between high and low RFI lines (Braastad & Katle, 1989; Katle, 1991; Luiting *et al.*, 1991). In cattle, a phenotypic correlation of 0.32 was found between RFI and daily pedometer count, which when used as measurement, showed that about 10% of variation in RFI could be attributed to activity (Richardson *et al.*, 1999). In mice selected according to heat loss, low efficient (high-heat-loss) mice showed an increase in activity by twice as much as high efficient (low-heat-loss) mice. This activity difference accounted for 10.5% of the difference in feed intake (Mousel, 1998).

Animals that are more feed efficient typically take part in less daily feeding activities. More efficient steers eat fewer times per day and have less variability in DFI than less efficient steers, even when receiving different types of diets. However, the difference in daily eating periods in high and low RFI steers was found to be higher when fed a traditional diet containing roughage compared to a no-roughage diet (Golden *et al.,* 2008). Differences in feeding behaviour between high and low RFI animals have been estimated to have a moderate heritability, with lower RFI animals having meals of shorter duration, eating less frequently and at a slower rate (Robinson & Oddy, 2004). In cattle it has been undetermined whether there is a relationship between RFI and rate of respiration, which is an important method of thermoregulation (Herd & Arthur, 2009). In chickens it has been reported that low RFI lines have smaller nude body areas and are less active, thereby reducing energy lost as heat (Luiting *et al.*, 1994).

2.6.3 Body composition and metabolism

Studies have shown that low RFI cattle have less whole-body chemical fat and more whole-body chemical protein than high RFI cattle (Richardson *et al.*, 2001). Differences in body fat have also been observed in pigs, where low RFI pigs were found to have less backfat (Gilbert *et al.*, 2007). Differences in empty body fat can have a contribution of 4% to the variation in DFI (Basarab *et al.*, 2003). The increase in lean content in low RFI animals could be explained by the fact that protein turnover leads to a higher variation in efficiency of lean muscle than in fat (Herd *et al.*, 2004). Efficiency and ADG are influenced by the rate of water, protein and fat deposition since fat is more energy dense than protein or water (Ferrell & Jenkins, 1998). The maintenance of protein requires more energy than maintenance of fat due to protein turnover. Protein turnover has been estimated to contribute approximately 20% to the total inter-animal variation in basal energy expenditure (Carstens *et al.*, 2008). It is interesting to note that contrary to reports in mammals, low RFI lines in chickens have been found to have more body fat than high RFI lines (Luiting *et al.*, 1991; Trixier-Boichard *et al.*, 2002). Many physiological factors contribute to body composition, such as age and stage of maturity, which is important to take into consideration when interpreting research results concerning the association between body composition and RFI (Herd & Arthur, 2009).

Selection for improved efficiency is associated with a change in the rate of protein degradation and has been observed in many species. In a study selecting chickens for lean growth, or increased efficiency of feed to gain, a decrease in the rates of fractional protein degradation was observed (Pym, 1990). These findings are supported by a later study with chickens, in which it was found that differences in net efficiency of protein utilisation were associated with differences in fractional protein degradation rate (Tomas *et al.,* 1991).

About 90% of cellular energy is produced by the mitochondria, which are numerous and form as much as 10% of the body weight of many animals (Ojano-Dirain *et al.*, 2007), making mitochondrial function a potential candidate for the cause of variation in RFI. It has been estimated that mitochondrial proton leak and Na^+/K^+ Adenosine triphosphatase (ATPase) each contribute approximately 20% to inter-animal variation in basal energy expenditure (Carstens *et al.,* 2008). No differences were found in mitochondrial function in a study on beef steers, however, low RFI steers had a higher rate of mitochondrial respiration while the flux of electrons through the electron transport chain was impaired in high RFI animals (Kolath *et al.,* 2006).

Another factor affecting energy balance is the mass of visceral organs since an increase in mass is associated with an increase in maintenance energy requirements. Visceral tissues account for 6-10% of live weight, but 40-50% of whole body oxygen consumption in sheep (Burrin *et al.,* 1990) while the liver and gastrointestinal tract each accounts for 20% of whole-body oxygen consumption (McBride & Kelly, 1990). Concerning weight of the liver and gastrointestinal tract in cattle, studies have been conflicting. It has been reported that stomach and intestine, and liver are heavier in high RFI cattle (Basarab *et al.,* 2003), that internal organ and gastrointestinal weights are similar in high and low RFI cattle (Richardson *et al.,* 2001; White, 2004), and liver weights are similar between low and high RFI calves but gastrointestinal tract weight is higher in high RFI calves (Ribeiro *et al.,* 2007). Processes contributing the most to energy expenditure in the liver and gastrointestinal tract include ion pumping (liver = 16-55%; gastrointestinal tract = 28-60%) and protein synthesis (liver = 15-24%; gastrointestinal tract = 20-23%) (McBride & Kelly, 1990).

The metabolites discussed in this section have been investigated in an attempt to identify physiological indicators to be used as an indirect selection method. These metabolites are associated with body composition, metabolism, appetite, growth and stress. The main metabolites are Insulin-like Growth Factor-I (IGF-I), leptin, uncoupling proteins (UCP), urea, creatine, calpastatin, insulin, glucose, corticostreroids, non-esterified fatty acids (NEFA) and β-hydroxybutyrate (BHB).

2.6.3.1 Insulin-like Growth Factor-I (IGF-I)

A hormone involved in the regulation of growth and cellular metabolism, namely IGF-I, has been shown to be associated with increased feed efficiency (Bishop *et al.*, 1989; Stick *et al.*, 1998) as it affects glucose and amino acid metabolism and accretion (Jones & Clemmons, 1995). This hormone is produced in the liver, fat and muscle tissue, responds to growth hormone and circulates in plasma bound to one of six binding proteins (Jones & Clemmons, 1995; Hossner *et al.*, 1997). It has been shown to be associated with carcass fatness, live and carcass weight, RFI, ADG (Johnston *et al.*, 2001), body size, milk production and feed conversion efficiency (Davis *et al.*, 1995). The plasma concentration of IGF-I has a heritability of 0.4 (Moore *et al.*, 2005). Conflicting results regarding genetic correlations with RFI have been reported, with some studies showing a significant correlation (Moore *et al.*, 2005; Kahi & Hirrooka, 2007), while others report no correlation (Lancaster *et al.*, 2008).

The correlations reported between RFI and post-weaning plasma IGF-I concentrations differ between diets and breeds. In *Bos taurus* breeds fed a roughage diet, correlations of 0.18 (Brown, 2005), 0.39 (Johnston *et al.,* 2002) and 0.57 (Moore *et al.,* 2005) were found. In grain-based diets a correlation of –0.12 was found in implanted Brahman cattle (Wolcott *et al.*, 2006) and –0.80 in non-adapted tropical steers (Wolcott *et al.,* 2006). The relationship between RFI and plasma IGF-I concentrations was reported to become increasingly negative with age in a study by Brown (2005) and also in Brahman steers in a study by Wolcott *et al.* (2006), but decreasingly negative in tropical composite breeds (Wolcott *et al.,* 2006).

The relationship between IGF-I and feed efficiency, performance and carcass composition is complex and not yet fully understood. From the above information IGF-I concentrations seem to possibly be influenced by diet, stage of maturity at time of testing, time relative to weaning, breed and implant regimen. This questions the use of IGF-I as a reliable physiological indicator (Lancaster *et al.* 2008). In pigs, selection against IGF-I plasma concentrations has improved feed efficiency while reducing carcass fatness (Luxford *et al.*, 1998; Hermesch *et al.*, 2001). The use of IGF-I concentration as a selection tool in pigs has been patented and registered as WO9635127, AU694025, NZ306348 and EP0830607 by Owens and others in 1996 (Herd *et al.,* 2003). The patent also includes the use of IGF-II and Insulin-like Growth Factor Binding Protein-3 (IGFBP-3) and serves as a method to select animals that would produce offspring with above average carcass quality, feed conversion efficiency, growth rate, reproduction and below average feed intake.

Conflicting results found in studies may be due to IGF-I binding proteins (IGFBP) influencing the actions or concentrations of plasma IGF-I in different ways at various stages of growth. IGFBP act as carrier proteins and its functions include regulating efflux of IGF-I from the vascular space, increasing the half-life of IGF-I, allowing tissue and cellular specificity for IGF-I actions, and directly modulating the interaction of IGF-I with its receptor (Hossner *et al.,* 1997). Reports have shown that IGFBP-2 has a negative phenotypic correlation with body weight (Pagan *et al.,* 2003) and a positive correlation with growth rate (Connor *et al.,* 2000) but no correlation with backfat or loin muscle area (Lancaster, 2008). Therefore IGFBP-2 may be a candidate protein to consider as a physiological indicator for RFI in conjunction with IGF-1 (Lancaster, 2008). IGFBP-3 was found not to be associated with body weight or ultrasound measures of backfat or loin muscle area (Pagan *et al.,* 2003).

In beef cattle, the best economical use of IGF-I as an indirect selection tool is to use as a screening test to identify those animals to be placed in a RFI test station (Wood *et al.*, 2002, 2004). This will reduce the number of animals tested in testing stations and thereby save in costs.

2.6.3.2 Leptin

Leptin is associated with increased fatness in cattle as its plasma concentration is related to the extent of body lipid depots (Ji *et al.*, 1997; Chillard *et al.*, 1998; Minton *et al.,* 1998). It functions as a regulator of body weight, feed intake, energy expenditure (Houseknecht *et al.*, 1998), reproduction (Garcia *et al.*, 2002) and the immune system (Lord *et al.*, 1998). Leptin is primarily synthesised and secreted by white adipose tissue. Increased leptin concentrations lead to a decrease in feed intake and fatty acid esterification, and an increase in oxygen consumption, activity, body temperature, uncoupling protein-2 (UCP-2) expression in pancreatic islets and fat, and UCP-3 expression in skeletal muscle (Hossner, 2005). Leptin also stimulates glucose transport and glycogen synthesis in C_2C_{12} cells, and stimulates lipolysis by suppressing the expression of adipocyte Acetyl-CoA carboxylase (ACC), which is an enzyme required for lipogenesis. Leptin also induces the release of Luteinising hormone (LH), Follicle-stimulating hormone (FSH) and Luteinising hormone-releasing hormone (LHRH) and thereby influences age at sexual maturity, reproductive system maturation and mating. Leptin may even play an important role in placental-uterine-fetal growth and development (Hossner, 2005).

Leptin has been shown to have a phenotypic correlation of 0.31 with RFI (Richardson *et al.*, 2004) but there have been conflicting results among studies. Brown *et al.* (2004) found no relationship between systemic leptin concentrations with intake, performance and feed efficiency traits. On a molecular level, a Single Nucleotide Polymorphism (SNP) in the promoter region of bovine leptin gene has been shown to be associated with growth rate, feed intake and body fat, but not with measures of feed efficiency (Nkrumah *et al.,* 2005a).

2.6.3.3 Uncoupling proteins (UCP's)

There are five uncoupling proteins (UCP1, UCP2, UCP3, UCP4 and UCP5) and they are involved in the regulation of energy expenditure, with UCP1, UCP2 and UCP3 appearing to have an influence on RFI. UCP1 is found in brown adipocytes, providing a mechanism for non-shivering thermogenesis in newborns (Sell *et al.,* 2004) and therefore not important in later stages of life. The mechanism of non-shivering thermogenesis involves the movement of protons down the gradient to create heat for the maintaining body temperature (Carstens, 1998; Erlanson-Albertsson, 2003).

The proteins UCP2 and UCP3 are respectively 56% and 57% homologous to UCP1 in terms of their amino acid sequence (Erlanson-Albertsson, 2003) with UCP2 expressed in all tissues while UCP3 is expressed in muscle (Jezek *et al.,* 1998). Evidence shows that UCP2 and UCP3 are possibly involved in proton leak (Erlanson-Albertsson, 2003) and unlike UCP1 these two can move unbound protons into the mitochondria (Ricquier, 2005). Uncoupling proteins regulate the coupling of the electron transport system of the mitochondria with Adenosine triphosphate (ATP) generation and hydrolysis. The rate at which proton leakage across the mitochondria occur may be responsible for up to 50% of energy expenditure in muscle and 30% of standard metabolic rate. Part of the action of UCP's is through the cycling of protonated fatty acids (Rolfe & Brand, 1997).

2.6.3.4 Urea and creatine

Urea synthesis contributes 7.1% to oxygen consumption in the liver (McBride & Kelly, 1990) and is negatively related to protein content in bulls (Robinson *et al.*, 1992), lean growth (Clarke *et al.*, 1996) and positively related to RFI in steers (Richardson *et al.*, 2004). However, Kelly *et al.* (2010) found no relationship between RFI and systemic urea concentrations. There is a positive correlation between blood urea, FCR and DMI, which is consistent with the positive association between urea and nitrogen intake (Walsh *et al.*, 2008; Clarke *et al.*, 2009).

Creatine is positively associated with muscle mass in sheep (Cameron, 1992; Clarke *et al.*, 1996), and negatively associated with fat depth in sheep (Clarke *et al.*, 1996) and RFI (Richardson *et al.*, 2004). A positive correlation between RFI and plasma creatine:urea ratio was found, indicating that less efficient bulls have a higher turnover of creatine phosphate in muscle (Tatham *et al.,* 2000). In Angus steers, no correlations were found between RFI and urinary 3-methylhistidine, creatine or 3-methylhistidine:creatine ratio, which are measures of skeletal muscle protein turnover (Richardson *et al.* 2004).

2.6.3.5 Calpastatin

Calpastatin is a specific inhibitor of the calcium activated protease calpain system involved in protein degradation. Calpains are calcium-dependent proteolytic enzymes that degrade specific muscle proteins, such as titin, desmin and troponin T, and certain cytoplasmic enzymes, such as most protein kinases and phosphatases. They are also important in muscle tenderisation post-mortem (Hossner, 2005). Calpastatin concentration has been reported to differ between high and low RFI animals. Higher levels of calpastatin will decrease protein breakdown and thereby increase efficiency of energy use in muscle (McDonagh *et al.*, 2001). The results suggest that protein turnover could be significantly decreased in low RFI calves. There are conflicting reports on whether a relationship between calpastatin activity in loin muscle and RFI exists. McDonagh *et al.* (2001) reported a 13% greater calpastatin activity in high RFI steers, while Kelly *et al.* (2010) detected none.

2.6.3.6 Insulin and glucose

Insulin maintains sufficient cellular energy supply by maintaining a constant concentration of serum glucose through the regulation of the uptake of glucose. Insulin also stimulates glycogen, protein and triglycerol deposition, and amino acid transport while inhibiting protein degradation (Hossner, 2005). Greater insulin levels have been reported in high RFI cattle (Richardson *et al.*, 2004; Brown, 2005). This has been attributed to increased fat deposition in less efficient animals, as insulin stimulates lipogenesis. Kelly *et al.* (2010) found no association between RFI and plasma insulin concentrations.

In sheep selected for growth rate, muscles are more sensitive to insulin in animals with high growth rates. The sensitivity of insulin response to feed intake also differed, with fast growing sheep showing an increase in insulin concentration after consumption of food (Oddy, 1993a). The uptake in muscle of glucose and amino acids showed more responsiveness to insulin in the sheep with high growth rates, indicating an increase in efficiency of energy use and protein gain (Oddy, 1993b). Glucose is an essential component of normal cellular growth and metabolism (Hossner, 2005). Glucose concentrations measured at weaning are not correlated with performance or efficiency traits (Richardson *et al.*, 2004; Kelly *et al.* 2010). The glucose:insulin ratio is an indication of glucose metabolism and has no association with RFI (Kolath *et al.*, 2006; Kelly *et al.*, 2010). However, glucose:insulin has been shown to be negatively correlated with FCR and tends to be correlated with DMI. This indicates that FCR and RFI are different traits (Kelly *et al.*, 2010).

2.6.3.7 Other

In beef steers, Richardson *et al.* (2004) found an association between RFI and plasma cortisol and several red and white blood cell variables, suggesting that high RFI animals are more susceptible to stress. Corticosteroids are not beneficial for growth as they reduce protein synthesis and stimulate protein degradation by mobilising amino acids for gluconeogenesis under conditions of stress (Hossner, 2005). Nonesterified fatty acids (NEFA) are products of body fat mobilisation and appear in greater concentrations in low RFI animals. Negative correlations with NEFA and FCR have been found (Kelly *et al.,* 2010) with Richardson *et al.* (2004) reporting a 27% increase in plasma triglyceride concentrations in low RFI animals. Positive correlations between RFI and systemic concentrations of BHB have been reported (0.55 by Richardson *et al.*, 2004, 0.37 by Kelly *et al.*, 2010). Other correlations with BHB include that with DMI ($r = 0.34$) and FCR ($r = 0.25$) (Kelly *et al.*, 2010).

2.7 Genomic information for RFI selection

Genomic information can be useful as a selection tool as it may increase the rate of genetic progress. Traits that are difficult to measure, as is the case with RFI, will greatly benefit from using genetic markers as a selection tool (Dekkers, 2004). Even though the discovery of markers for RFI is important to aid in selection, studies attempting to identify QTL or major genes for beef cattle feed intake and feed efficiency have not been able to deliver practically useful results (Nkrumah *et al.,* 2005b, 2007b; Moore *et al.,* 2006; Barendse *et al.,* 2007; Sherman *et al.,* 2010; Mujibi *et al.,* 2011). The differences between breeds and populations complicate the finding of markers that can be used for all beef breeds. Different cattle breeds have become genetically separated. Certain markers are close to the causal allele and others more distant. Since breeds differ genetically, markers more distant to causal alleles may not be in LD with the allele of interest in all breeds (Rolf *et al.,* 2010).

Barendse *et al.* (2007) performed a whole-genome association study by genotyping large numbers of cattle from various breeds using MegAllele Genotyping Bovine 10K SNP panel (Hardenbol *et al.,* 2005). They found 161 SNP's that showed a significant association with RFI. The 20 most significant SNP's explained 76% of the variance for RFI. Among the significant genes

- 34 contributed to energy utilisation processes by the cell, such as apoptosis, cell progression, ion channel and flux, growth and development, transcription and translation
- Three genes were involved in appetite and homeostasis of body-mass through an involvement in pathways for leptin, insulin and serotonin, showing that control of appetite and homeostasis of body mass have minor contributions to efficient feed utilisation
- Nine genes were involved in apoptosis and protein turnover
- 11 genes were involved in extracellular matrix and tissue structure, such as genes associated with muscular and myotonic dystrophy and cell adhesion
- Six genes were either genes for ion channels or involved in ion flux
- Three genes were associated with neorotransmitter flux
- Five were involved in translation and transcription
- Ten genes were involved in growth and development, and 28 SNP were on genes with unknown function Barendse *et al.* (2007).

A summary of genes found to be associated with RFI can be found in table 2.9.

The genes *ATP1A1, UBE21* and *RPLP2* play a role in basal metabolic rate (Barendse *et al.,* 2007), which is suspected of having a large contribution to RFI (Herd & Bishop, 2000). The genes *DAG1, DMD and MBNL1* are associated with muscular and myotonic hypertrophy in humans with mutations in *DMD* affecting muscular regeneration and muscular hypertrophy (Doriguzzi *et al.,* 1993; Harper *et al.,* 2002). Some of these genes' roles may be pleiotropic. The genes affecting RFI through association with cell adhesion and extracellular matrix could indicate a compromise between RFI and tissue strength. This could explain the correlations between RFI and carcass traits (Barendse *et al.,* 2007), such as the positive genetic correlation with fatness and the negative genetic correlation with muscle area of the longissimus muscle (Robinson & Oddy, 2004).

In the growth hormone receptor (GHR) gene, an intronic SNP has shown a significant allelic substitution effect on RFI while a SNP in neuropeptide Y and ghrelin introns and GHR promoter region showed possible associations with RFI (Sherman *et al.*, 2008). A polymorphism was identified in the mitochondrial genome but found to have no association with RFI (Kolath *et al.*, 2006). Many genes thought to play a role in feed efficiency through their functions in physiological regulation of feed intake, growth and energy partitioning have been investigated over the years, but the success rate has been low. This illustrates the complex challenges in predicting candidate genes at a genome-wide level (Moore *et al.*, 2009).

Table 2.9 Summary of genes found to be associated with RFI in the study by Barendse *et al.,* 2007

Gene	Role
UBE2I	Associated with the targeting of proteins for degradation, and possibly involved in blocking cell cycle progression in eukaryotes
ATP1A1	Pump maintaining Na^+/K^+ gradient on plasma membranes
FGF2	Associated with various growth processes
RPLP2	Part of 60S ribosome subunit and involved in protein elongation
KRT32	Associated with hair and nail/hoof growth
NEOROD1	Binds to insulin promoter
PDE3B	Component of *PI3K-PDE3B-cAMP* pathway, needed in leptin signaling
MPDZ	Possible protein-protein interactions with serotonin *5-HT-2C* receptor's C-terminal domain
DAG1	Associated with muscular and myotonic dystrophy
DMD	Associated with muscular and myotonic dystrophy
MBNL1	Associated with muscular and myotonic dystrophy
LAMA2	Laminin gene
LAMG1	Laminin gene
KRT1-23	Marker of terminal differentiation in epithelia
EDG1	Cell adhesion
FAT3	Cell adhesion
GPIAP1	Cell adhesion
SDK1	Cell adhesion
SPA17	Cell adhesion

It is essential that potential markers to use for selection show a consistent association with the gene and phenotype. The same genotype must lead to the same change in phenotype in all population groups. This is dependent on the linkage disequilibrium (LD) between the marker SNP and the causative SNP. Estimates of LD are low when highly diverse groups of animals are used, such as different breeds (Barendse *et al.,* 2007). The consequences of this low LD is that many of the quantitative trait loci (QTL) for RFI will be missed due to between-breed variation. However, it can still be used to find many potential markers with greater accuracy than by using only a single breed or a small number of sires within a breed (Barendse *et al.,* 2007).

Nkrumah *et al.* (2007b) used an autosomal genome scan to identify putative QTL for feedlot growth rate, DFI and feed efficiency of beef cattle. Putative QTL influencing RFI were found on chromosomes 1, 5, 7, 8, 12, 16, 17 and 26. The most significant QTL for RFI were found on *Bos Taurus* autosome (BTA) 5. Some of these QTL were in similar positions as those found to be associated with DMI, FCR and ADG. The study used a relatively small number of progeny per half-sib family and therefore the QTL effects may be overestimated.

Genomic information can be incorporated into a selection program by using genomic estimated breeding values (GEBV). The accuracy of GEBV's for feed efficiency in beef cattle has been shown to be too low to be applied successfully. In a study by Mujibi *et al.* (2011) where the accuracy of GEBV's for ADG, DMI and RFI was investigated, very low values were found (0.22 – 0.48). One factor responsible for the difficulty in applying marker assisted selection is the inconsistency of results obtained from different populations and breeds (Moore, 2011).

It has been suggested that an EBV for RFI should be presented as an EBV for feed intake adjusted for growth, instead of an EBV for efficiency as this concept is easier to interpret by breeders. The EBV and its component traits should be used in an economic selection index to optimise selection decisions based on all available information (Herd *et al.*, 2003). It is important to set up uniform guidelines for the collection of data to measure RFI and to generate EBV's and other selection tools, such as markers. This will aid in identifying superior animals with greater accuracy (Carstens *et al.,* 2008).

2.8 Conclusion

The feed efficiency measurement, RFI, is a linear trait which will decrease feed intake, methane emission and manure production without influencing growth, weight or size of the animal, unlike FCR, which is a ratio trait and associated with growth, weight and size. The response using RFI is desirable as the decrease in feed intake will decrease cost of the enterprise and its independence of mature weight and size will avoid the production of large cows with higher maintenance requirements. There is an unfavourable correlation between RFI and carcass fatness, but this should not result in a profit loss as carcasses will still meet market specifications. The independence of RFI with growth has been criticised as unfavourable as small slow-growing animals can have superior RFI measurements, which will result in animals that spend more time in feedlots with an overall higher feed intake. A South African study has found that selection using FCR will be more profitable than RFI. These concerns require further research into the economic impact of RFI and possible solutions to these problems. Metabolic processes explain a large proportion of variation in RFI and various metabolites have been researched to identify a physiological indicator for indirect selection. The metabolite IGF-I has been accepted in the pork industry, but is not yet regarded as a reliable indicator in beef cattle. A combination of genetic markers found, explain a large proportion of variation in RFI, but no major gene has been identified. The correlation between RFI and methane emission has made it a trait of great interest as increasing pressure is being placed on the livestock industry to decrease its carbon footprint.

Chapter 3
Materials and Methods

3.1 Introduction

In South Africa, beef cattle are performance tested in the National Beef Recording and Improvement scheme, which consist of different phases – Phase A1 and A2 (Reproduction and Suckling phases), Phase B (Post-wean on-farm recording), Phase C (Central Performance tests), Phase D (On-farm performance recording) and Phase E (Feedlot and Slaughter phase). Phase C, an intensive feedlot based test, is performed at several central testing stations in South Africa where body measurements, weights, feed intakes and real time ultrasound (RTU) recordings, such as sub-cutaneous fat thickness, eye muscle area and intra-muscular fat percentage, and linear classifications are recorded (Scholtz, 2010). In South Africa, commercial beef cattle are mostly kept under extensive production systems and weaner calves are sold to feedlots. Stud and commercial farmers use results from these intensive feed tests to select bulls for the selection programme in their own herds, both for replacement animals and for feedlots. Analysis of Phase C data and careful selection decisions based on this information therefore has the ability to influence overall improvement in feedlot performance of Bonsmara cattle in South Africa. The Bonsmara was the choice of breed for this study since this breed had the most tested bulls in phase C in South Africa, comprising 67% of all bulls tested from 2005 to 2009 (National Beef Recording and Improvement Scheme Annual Report 2009/2010, Agricultural Research Council (ARC)).

3.2 Materials

The data for this study was generated from growth tests performed in centralised and private stations in South Africa over a period of 39 years. Phase C data was used and included the Phases C1 (Central standardised tests at ARC testing stations), C2 (Central standardised tests at private testing centres) and C3 (Central non-standardised tests at ARC or private testing centres). The Phase C growth performance tests were performed at ARC stations in Irene (Pretoria), Vryburg, Glen (Bloemfontein), Stellenbosch, Cedara, and private testing centres – Sernick (Edenville), Viljee Crouse (Steynsrus), Marloo (Vaalpark), GW Roux (Ventersburg), Wes Kaap (Stellenbosch) and Nooitgedacht (Ermelo). The data used for this study was stored on INTERGIS, which is a database for South African data recording, and obtained from the ARC with the approval of the Bonsmara Breeders Society. The data consisted of 154 067 Bonsmara cattle of which 19 059 Bonsmara bulls were tested in Phase C between 1971 and 2010.

The Bonsmara is shown in figure 3.1 and is a result of a well-documented crossbreeding programme and consists of 5/8 Afrikaner and 3/8 exotic (Milk Shorthorn, Hereford) (Bonsma, 1980). The breed is also used in other African countries, such as Namibia, Uganda and Zambia, as well as (non-African) countries such as Argentina, Australia, Columbia, Paraguay, Uruguay and the United States of America. The Bonsmara breeders are also actively involved in performance testing, with an average of 95% participation in the National Beef Recording and Improvement scheme for the period between 1999 and 2008 (Scholtz, 2010).

Figure 3.1 A Bonsmara bull

The feed efficiency traits investigated in this study were RFI, FCR and KR. Other traits of importance included in this study are:

- Daily Feed Intake (DFI), which is economically relevant as the cost of feed is a major expense in the beef industry. It is also required in the calculation of RFI and FCR.

- Average Daily Gain (ADG) as a measure of growth performance. This trait is also required in the calculation of RFI, FCR and KR.
- Weaning weight (WW) as a weight trait. It is of economic importance as the price of weaner calves is determined by weight.
- Metabolic mid-weight (MMW) as a weight trait and component in the calculation of RFI and KR.
- Shoulder height (SH) and body length (LE) as frame size traits
- Scrotal circumference (SC) as a reproductive trait, which is the only reproductive trait measured on bulls.

3.2.1 Phase C centralised testing

All bulls taking part in centralised testing need to meet the breed standards as set by the society. The bulls from this study complied with the Bonsmara breed standards, attached as addendum A. There was an adaptation period of 28 days. Bulls were individually fed *ad lib* with a standard, complete growth diet. The ration is mixed by various testing stations in the country and private testing stations use a pelleted ration while ARC testing stations don't, however, both must conform to specific standards, as described in table 3.1 (Leslie Bergh, ARC, Private bag X2, Irene, Pretoria, South Africa. Personal communication).

Each bull had a transponder with its pen number attached to a belt around its neck, which ensured individual feeding. Weekly intakes were determined by subtracting the weight of feed remaining in the bunk from the total weight of feed given over weekly intervals. Body weight was taken at weekly intervals after a 12 hour overnight fast. Measurements taken at the end of the test are SH, LE, skin thickness and SC. In addition, functional appearance scoring was done and the animals underwent general health procedures, such as treatment against internal and external parasites, regular spray-dips and other medical treatments when necessary. The test lengths in the provided data varied from 42 days to 141 days. The test length was 20 weeks until 1990, where after it was reduced to 16 weeks, and again to 12 weeks in 1999 (Archer & Bergh, 2000).

Table 3.1 Standard ration composition for bulls participating in Phase C testing

Nutrient	**Minimum**	**Maximum**
ME (MJ/kg DM)	11.0	-
Crude Protein (CP)	135 g/kg	150 g/kg
Non-degradable intake protein	45 g/kg	-
Urea	-	7 g/kg
Protein from non-protein nitrogen NPN (% of CP)	-	20%
Fibre	125 g/kg	-
Roughage	200 g/kg	-
Fat	30 g/kg	70 g/kg
Calcium	6 g/kg	10 g/kg
Phosphate	3 g/kg	5 g/kg
Calcium:Phosphate	1.5:1	2.5:1
Sulphur	1.5 g/kg	3 g/kg
Nitrogen:Sulphur	8:1	12:1
Potassium	5 g/kg	13 g/kg
Magnesium	2.5 g/kg	-
Vitamin A	4500 000 IU*/ton	-
Vitamin D3	250 000 IU/ton	-
Vitamin E	5000 IU/ton	-
Vitamin B1	3000 IU/ton	-
Niacin	100 000 IU/ton	-
Copper	15 g/ton	-
Magnesium	40 g/ton	-
Zinc	54 g/ton	-
Cobalt	0.5 g/ton	-
Iodine	2 g/ton	-
Iron	50 g/ton	-
Selenium	0.15 g/ton	-
Monensin-sodium	29 g/ton	-
Zinc-bacitracin	25 g/ton	-

* IU: International Units

3.2.2 Data

The software used included Visual Dbase 5.7 (1999) for data management and Enterprise Guide 4.1 of SAS 9.1.3 (2006) for all statistical purposes. The summary statistics of initial weight (weight at the start of the test period), final weight (weight at the end of the test period), ADG, SH, LE, SC, FCR, KR, total feed intake, age and dam age prior to data editing are presented in table 3.2, while the number of missing values for each trait are presented in table 3.3. The data was further summarised with the use of graphs that are presented in figures 3.2 – 3.5 and addendum B. Testing stations only implemented automatic gates for feeder bunks from 1980, and prior to this date, feed was not provided *ad lib,* therefore, all data before 1981 was excluded from this study as well as data from years 1981 and 1982 due to the small number of animals tested.

Table 3.2 Summary statistics for variables with measurements before data editing

Variable	**Mean**	**Standard dev.**	**Minimum**	**Maximum**
Initial weight (kg)	266	32.02	139	414
Final weight (kg)	434	52	232	627
ADG (g)	1638	264	625	2680
SH (mm)	1190	40	1030	1580
LE (mm)	1381	53	1040	1670
SC (mm)	341	28	200	500
FCR (kg)	6.40	0.93	3.64	13.98
KR (g)	19.08	2.53	8.5	27.7
Total feed intake (kg)	1086	288	283	2140
Age (days)	358	39.31	185	852
Dam age (days)	2209	1037	645	7365

Not all animals had measurements recorded for all traits. Initial weight, final weight, age and ADG had no missing values. Kleiber ratio had the most missing values, with 12 675 animals without measurements. Table 3.3 shows the number of records with missing values with a test length of 84 days. Weaning weight is measured in Phase A and therefore summary statistics were not compiled prior to data editing.

Table 3.3 Number of missing values for various traits with a test length of 84 days

Variable	**Missing values**
Initial weight	None
Final weight	None
Age	None
Dam age	92
Total Feed intake	162
Average Daily Gain	None
Shoulder Height	1067
Body Length	1074
Scrotal Circumference	2258
FCR	1
Kleiber ratio	12 675

The range of values for traits differ between test lengths, as can be seen in figures 3.2 – 3.5 and addendum B, showing graphs of measurements for the traits in table 3.2 prior to editing. The difference in measurements among test lengths can be explained by the difference in age, as shown in figure 3.2, apart from the decrease in total feed intake, which is explained by the decrease in test length. Animals entering Phase C testing stations after 1999 (when test length was decreased to 84 days) are younger. The variation in age over years is also more consistent from 1999.

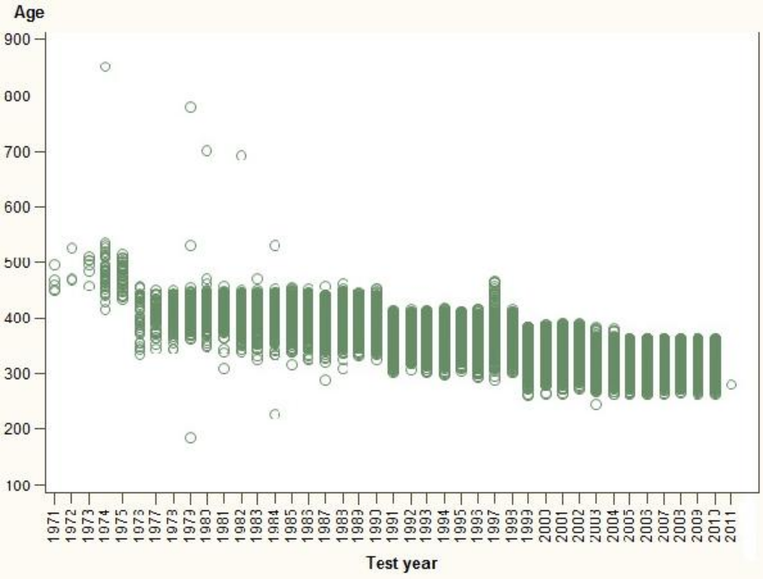

Figure 3.2 Scatter plot for age (in days) per year before data editing

The graph for ADG (figure 3.3) shows an increase in maximum measurements and variation. Figure 3.4 shows that there are more outliers for FCR during more recent years (1997 – 2010). Values were recalculated for this study.

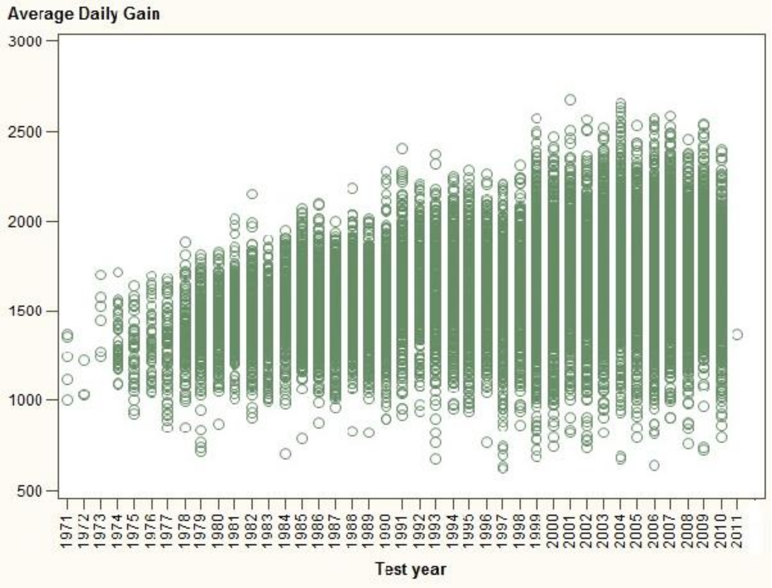

Figure 3.3 Scatter plot for ADG (in g) per year prior to data editing

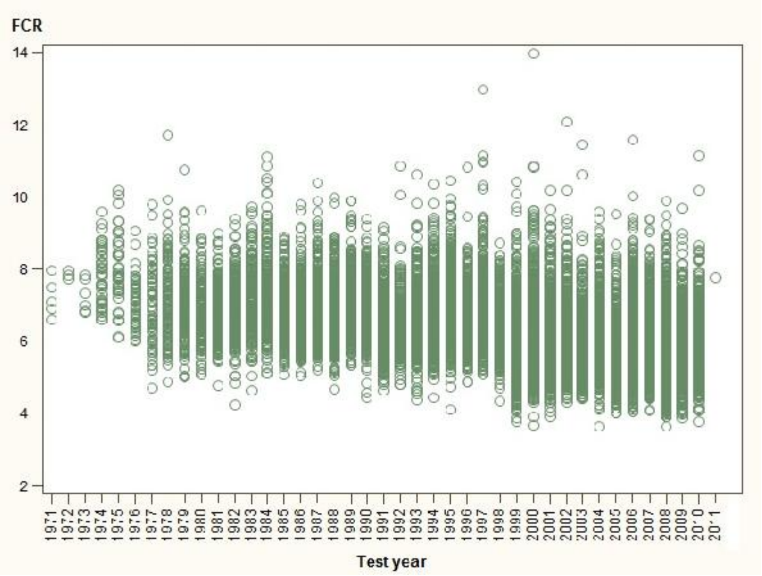

Figure 3.4. Scatter plot for FCR (in kg) per year prior to data editing

Few records were available for KR and there were no records of KR prior to 2000. Figure 3.5 shows a scatter plot for KR prior to data editing. Values were re-calculated for the animals for the purpose of this study.

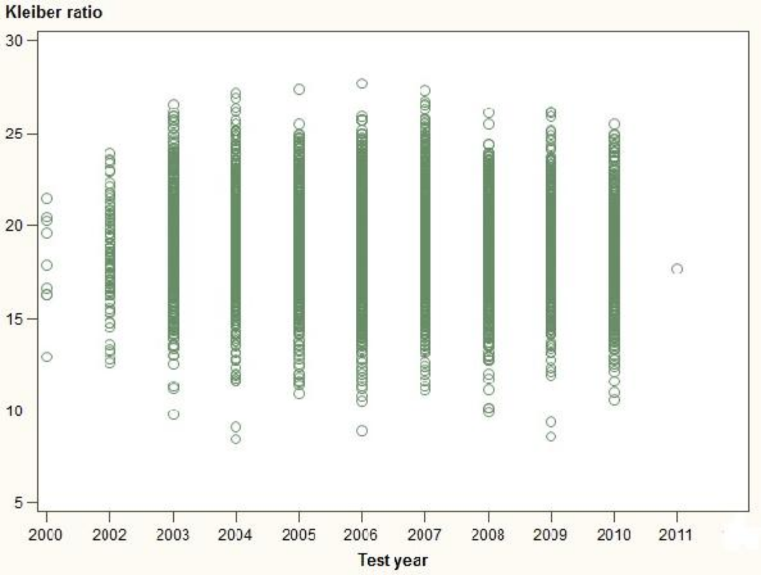

Figure 3.5 Scatter plot for KR per year prior to data editing

3.3 Methods

3.3.1 Data editing procedure

The procedures followed for data editing are shown in table 3.4. The intakes are measured weekly, and therefore intake is not expressed as a daily measurement. Weekly intakes outside three standard deviations (SD) were deleted, and the same applied for age, initial weight, ADG, SC, LE and WW. Animals had to comply with requirements for all traits to be included. Contemporary groups were made to include test year, test station, season (test number) and test phase. Small contemporary groups would lead to unreliable predictions for feed intake. All contemporary groups with less than ten records were deleted to calculate RFI more accurately within groups. Only the test length of 84 days was used since it contained the most data (5981 animals), is currently the standard test length used and the accuracy of feed intake measurements during the long test lengths is questionable. Longer test lengths could not be truncated to 84 days as traits such as SC, SH and LE are measured at the end of the test.

Table 3.4 Number of animals remaining after each step of data editing

Criteria for animal deletion	Number of records
Years before 1982 and phase D	18 333
No total feed intake (TFI)	18 171
TFI with errors, 28 day test length and incorrect test year	18 156
Weekly test intakes outside 3 SD	15 794
Test lengths 85 and 86	15 742
Ages outside 3 SD	15 722
SC, SH & LE outside 3 SD	14 351
Initial weights outside 3 SD	14 338
No weaning weights & outside 3 SD	14 004
Contemporary groups with less than 10 records	11 573
Test lengths of 140 and 112 days	5 981

Initially there were 1 146 contemporary groups and a total of 14 004 animals. Of these groups, 613 groups had less than ten animals (total of 2 431 animals) and were deleted. The remaining 533 groups had more than ten animals (total of 11 573), of which 270 groups had a test length of 84 days. After data editing, there were 3 981 animals with a test length of 112 days and 1611 animals with a test length of 140 days. Summary statistics for traits were calculated from this data using the MEANS procedure of SAS 9.1.3 (2006).

3.3.2 Calculation of RFI

To calculate RFI, MMW, ADG, actual DFI and expected DFI were required. The following formulas show how these traits were calculated:

$$\text{MMW} = ((\text{Initial weight} + \text{Final weight}) / 2)^{0.75}$$
$$\text{ADG} = (\text{Final weight} - \text{Initial weight}) / \text{Test length}$$
$$\text{DFI} = \text{Total Feed Intake} / \text{Test length}$$

Actual DFI was regressed against MMW and ADG for each contemporary group, as there were significant differences in the component traits between contemporary groups ($P < 0.05$), using the PROC REG of SAS 9.1.3 (2006) to determine expected DFI. Expected DFI was also determined per year and per station respectively and the correlations between RFI's calculated using these three expected intake values were then determined. The fitted model to calculate expected daily feed intake was:

$Y_i = \beta_0 + \beta_1 \times ADG_i + \beta_2 \times MMW_i + e_i$ (Koch *et al.,* 1963)

Where:

- Y_i is the expected DFI of animal i
- β_0 is the regression intercept
- β_1 is the partial regression coefficient of DFI on ADG of animal i
- β_2 is the partial regression coefficient of DFI on MMW
- e_i is the error

From this, RFI was calculated by subtracting expected DFI from the actual DFI (Koch *et al.*, 1963). Figure 3.6 is a graph showing how RFI was calculated from the regression line. Other measures of feed efficiency also used for this study, namely KR and FCR were calculated using the following formulas:

KR = ADG / MMW
FCR = DFI / ADG

Summary statistics, including minimum, maximum, mean and standard deviation, were calculated for these feed efficiency traits. The phenotypic Pearson correlations between RFI and FCR as well as KR were determined using the CORR procedure of SAS 9.1.3 (2006).

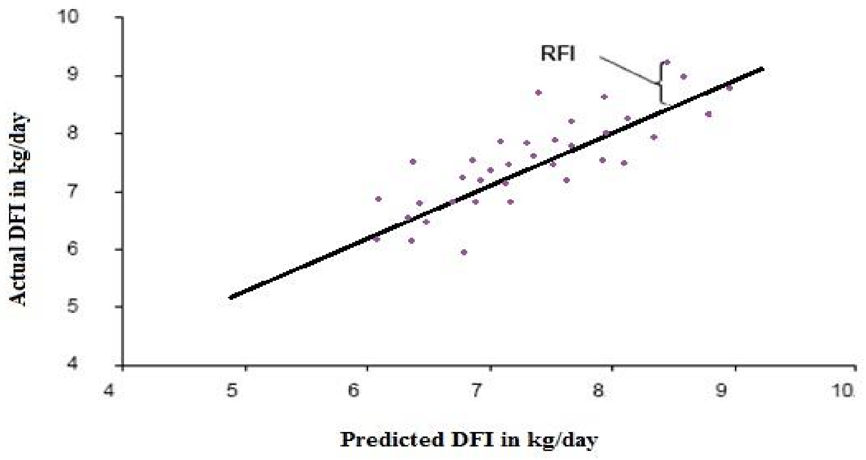

Figure 3.6 A graph illustrating the calculation of RFI as the difference between actual feed intake and predicted feed intake

3.3.3 Genetic analysis

Genetic parameters and EBV's had to be estimated for genetic analysis to determine RFI's association with other traits and whether selecting for RFI, FCR or KR will change the ranking of bulls for feed efficiency. The following steps were taken to achieve this:

Step 1: Determine fixed effects:

A stepwise forward selection model was used to identify fixed effects to be used in the calculation of estimated breeding values (EBV) with PROC GLM of SAS 9.1.3 (2006). The significance level was set at $P < 0.05$ and variables tested were:

- age
- dam age
- age^2
- dam age^2
- contemporary group (cntgrp)
- herd

Those with a significant contribution were included in the model and are shown in table 3.5.

Table 3.5 Fixed effects to be included in models for each trait

Effect	**Trait**							
	RFI	**DFI**	**ADG**	**WW**	**SH**	**LE**	**SC**	**MMW**
Age (AT linear)	X	X	X	X	X	X	X	X
Dam age (DA linear)		X	X	X	X	X	X	X
Age^2 (AT Quatratic)				X		X	X	X
Dam age^2 (DA quadratic)		X	X	X	X	X	X	X
Cntgrp (CG)		X	X	X	X	X	X	X
Herd (CG)	X	X	X	X	X	X	X	X

Step 2: Determine genetic (co)variances

Heritability estimates (h^2) and genetic correlations (r_g) between traits were determined using the following formulas:

$$h^2 = \frac{\sigma_A^2}{\sigma_P^2}$$

where:

σ^2_A = Additive genetic variance

σ^2_P = Phenotypic variance

$$r_{g(XY)} = \frac{\sigma_{Axy}}{\sqrt{\sigma^2_{A(X)}\sigma^2_{A(Y)}}}$$

where:

$\sigma_{A(XY)}$ = Additive genetic covariance between trait X and Y

$\sigma^2_{A(X)}$ = Additive genetic variance of trait X

$\sigma^2_{A(Y)}$ = Additive genetic variance of trait Y

Pedigree information covering four generations were retrieved, comprising a total of 20 398 animals, 3 851 sires and 14 520 dams. The data file consisted of the 5 981 bulls for this study and their measurements for the traits of interest. One multi-trait model including all traits was used. The fixed effects described in table 3.5 were used to determine genetic (co)variances with the use of VCE 6 (Groeneveld *et al.*, 2010). The models used were:

Model applied for the traits WW, LE, SC and MMW:

$$\mathbf{y_i = \mu + AT_i + DA_i + CG_i + H_i + A_i + e}$$

Where:

y_i = trait of animal i

μ = overall mean

AT_i = quadratic regression of age entering test of animal i

DA_i = quadratic regression of dam age of animal i

CG_i = fixed effect of contemporary group of animal i

H_i = fixed effect of herd of animal i

A_i = additive genetic effect of animal i

e = random residual error

Model applied for traits DFI, ADG, SH:

$$\mathbf{y_i = \mu + AT_i + DA_i + CG_i + H_i + A_i + e}$$

Where:

y_i = trait of animal i

μ = overall mean

AT_i = linear regression of age entering test of animal i

DA_i = quadratic regression of dam age of animal i

CG_i = fixed effect of contemporary group of animal i

H_i = fixed effect of herd of animal i

A_i = additive genetic effect of animal i

e = random residual error

Model applied for RFI:

$$\mathbf{y_i = \mu + AT_i + H_i + A_i + e}$$

Where:

y_i = RFI of animal i

μ = overall mean

AT_i = linear regression of age of animal i

H_i = fixed effect of herd of animal i

A_i = additive genetic effect of animal i

e = random residual error

Step 3: Estimate Breeding Values

The genetic (co)variances were used to determine EBV's with the use of PEST 2 (Groeneveld *et al.,* 2010). The solver of choice was the direct solution (SMP).

Step 4: Ranking of animals

The animals were ranked for RFI, FCR and KR according to their EBV's and measurements respectively and the Spearman correlations between these rankings were determined with the use of SAS 9.1.3 (2006).

Step 5: Genetic trends

Graphs were compiled to show genetic change over the period 1999 to 2009. All animals, measured or not, were included in the trends. The EBV's were standardised by dividing all EBV's with one standard deviation (square root of the additive genetic variance). The weighted average EBV's per year were calculated for each trait and plotted on a graph with standard deviation on the y-axis and year on the x-axis. The base year was set at 2000 and therefore the average EBV for 2000 was subtracted from the average EBV's of all years. The regression equation and R^2 value were determined. The resulting genetic trends were used to determine whether genetic improvement in the population has occurred.

Chapter 4
Results

4.1 Summary of data used

After the completion of data editing, summary statistics were calculated for all relevant traits. The results of feed efficiency traits are shown in table 4.1, and performance and body measure traits in table 4.2. The largest number of observations occurred in 2006 (774), followed shortly by 2007 (771), and the lowest number of observations in 2010 (238). The year 2004 had the highest mean average daily gain (ADG) (1816.35 g/d), daily feed intake (DFI) (10.8 kg), scrotal circumference (SC) (343.12 mm) and weaning weight (WW) (255.35 kg). Lower mean performance for ADG (1646.54 g/d), DFI (9.4kg) and SC were observed in 2010.

Table 4.1 Phenotypic means and standard deviations (SD) for residual feed intake (RFI), feed conversion ratio (FCR) and Kleiber ratio (KR)

		RFI		**FCR**		**KR**	
Test year	**N**	**Mean**	**SD**	**Mean**	**SD**	**Mean**	**SD**
All years	**5981**	**0.00**	**0.63**	**5.93**	**0.84**	**22.34**	**3.10**
1999	532	0.00	0.64	5.85	0.75	22.68	2.84
2000	498	0.00	0.63	6.15	0.97	22.06	3.16
2001	391	0.00	0.57	6.04	0.86	22.38	2.90
2002	506	0.00	0.53	6.02	0.82	21.88	2.84
2003	375	0.00	0.50	5.90	0.72	22.00	3.40
2004	502	0.00	0.60	6.04	0.79	22.48	3.16
2005	449	0.00	0.57	5.73	0.72	22.85	3.06
2006	774	0.00	0.68	6.09	0.85	22.41	3.22
2007	771	0.00	0.72	5.91	0.78	23.00	3.12
2008	585	0.00	0.67	5.82	0.95	22.07	3.07
2009	360	0.00	0.58	5.68	0.83	21.95	3.06
2010	238	0.00	0.64	5.76	0.77	21.32	3.12

Table 4.2 Phenotypic means and standard deviations (SD) for metabolic mid-weight (MMW), average daily gain (ADG), actual daily feed intake (DFI), shoulder height (SH), body length (LE), scrotal circumference (SC) and weaning weight (WW)

		Trait													
Test Year	**N**	**DFI (kg)**		**ADG (g)**		**MMW (kg)**		**WW (kg)**		**SH (cm)**		**LE (cm)**		**SC (cm)**	
		Mean	**SD**	**Mean**	**SD**	**Mean**	**SD**	**Mean**	**SD**	**Mean**	**SD**	**Mean**	**SD**	**Mean**	**SD**
All	**5981**	**10.2**	**1.3**	**1744**	**267.0**	**78.1**	**6.5**	**237**	**32.0**	**1168**	**29.1**	**1362**	**45.3**	**334**	**27.6**
1999	532	10.0	1.2	1728	248.3	76.2	5.9	226	28.4	1176	24.8	1366	47.5	332	27.5
2000	498	10.4	1.3	1724	254.2	78.3	6.1	233	33.4	1176	31.7	1363	53.5	332	27.4
2001	391	10.2	1.2	1718	249.2	77.0	7.0	227	32.6	1165	29.5	1351	41.8	332	27.8
2002	506	10.1	1.4	1702	272.6	78.0	6.8	236	31.2	1167	32.0	1356	46.7	337	27.4
2003	375	10.0	1.2	1724	296.9	78.4	5.9	245	27.8	1166	28.3	1369	41.1	336	25.7
2004	502	10.8	1.3	1816	282.4	80.9	6.2	255	30.2	1175	28.0	1368	47.2	343	29.1
2005	449	10.2	1.2	1798	249.9	78.9	6.7	241	32.6	1171	29.5	1365	41.0	339	27.8
2006	774	10.4	1.2	1740	279.1	77.7	6.3	235	29.7	1162	28.0	1358	44.5	332	27.0
2007	771	10.4	1.1	1781	253.9	77.6	6.2	230	33.6	1162	24.1	1360	43.3	331	26.6
2008	585	10.0	1.4	1738	253.8	79.0	7.0	239	29.3	1165	29.3	1361	45.9	333	28.7
2009	360	9.7	1.4	1731	272.6	79.0	7.6	241	31.6	1172	31.2	1370	43.6	332	28.4
2010	238	9.4	1.2	1647	255.6	77.3	5.5	243	28.2	1169	32.1	1368	35.8	331	24.3

4.2 Phenotypic correlations and genetic parameters

The (co)variances were determined and are presented in table 4.3 and 4.4. Estimates of heritability, genetic correlation and phenotypic correlation are presented in table 4.5.

Table 4.3 Additive variances (on the diagonal) and covariances (off the diagonal) for RFI, SH, LE, SC, ADG, DFI, WW, FCR, MMW and KR of Bonsmara cattle as determined with the use of VCE 6

Trait	RFI	SH	LE	SC	ADG	DFI	WW	FCR	MMW	KR
RFI	**0.11**	-0.24	0.08	-0.37	3.87	0.032	-0.03	0.07	0.02	0.04
SH		**194.33**	197.35	64.32	849.42	2.32	47.24	-1.57	19.71	5.16
LE			**335.65**	61.49	1372.59	4.34	88.59	-2.3	32.06	8.32
SC				**202.52**	327.43	0.88	36.70	-0.66	11.24	1.04
ADG					**12801.64**	38.15	331.84	-24.15	192.62	109.18
DFI						**0.25**	1.158	0.018	0.63	0.31
WW							**68.99**	-0.56	12.43	0.70
FCR								**0.11**	-0.32	-0.22
MMW									**5.20**	0.98
KR										**1.13**

Table 4.4 Residual variances (on the diagonal) and covariances (off the diagonal) for RFI, SH, LE, SC, ADG, DFI, WW, FCR, MMW and KR of Bonsmara cattle as determined with the use of VCE 6

Trait	RFI	SH	LE	SC	ADG	DFI	WW	FCR	MMW	KR
RFI	**0.30**	-0.15	-0.59	0.57	-5.21	0.28	-0.70	0.17	-0.04	-0.06
SH		**304.94**	239.88	45.99	843.25	3.58	91.52	-0.92	30.29	2.32
LE			**844.41**	140.82	1896.95	7.07	163.50	-2.60	61.15	7.27
SC				**354.06**	998.034	4.14	52.16	-1.20	24.24	6.07
ADG					**37768.68**	82.11	392.05	-85.56	288.05	404.19
DFI						**0.57**	2.28	0.04	1.33	0.69
WW							**259.09**	0.09	32.58	-4.04
FCR								**0.34**	-0.24	-1.04
MMW									**12.09**	0.33
KR										**5.15**

The highest r_p between RFI and the traits listed are with FCR (0.43) and DFI (0.48), while weak or not significant r_p were found with weight traits (including initial weight, WW and MMW), growth (ADG), size traits (SH and LE), SC and KR. There is no r_p between KR and RFI because there are no r_p between RFI and the component traits of KR, which are ADG and MMW. The r_p of 0.43 with FCR is due to the r_p of 0.48 with DFI, which is a component of FCR. According to these results the r_p between RFI and DFI is stronger than that between FCR and DFI (0.27). There are weak r_p between FCR and size traits (SH and LE) as well as SC, and non-significant r_p with WW and MMW. There are, however r_p with initial weight (0.20) and ADG (-0.62). There are r_p between KR and all growth and weight traits (initial weight, WW, MMW and ADG. It is also has a higher r_p with DFI (0.30) than FCR, but lower than with RFI. There are no r_p between KR and size traits (SH and LE), but a high r_p of -0.69 with FCR.

There is a medium heritability estimate for RFI (0.27 ± 0.02), which is similar to that of FCR (0.23 ± 0.02) and slightly higher than that of KR (0.18 ± 0.02). There are low genetic correlations between RFI and all traits, except DFI (0.79 ± 0.03) and FCR (0.65 ± 0.04). There are medium to high genetic correlations between FCR and other traits, except for low correlations with DFI (0.11 ± 0.06) and SC (-0.14 ± 0.05). The feed efficiency measurement with the highest genetic correlation to ADG, is KR (0.91 ± 0.02), which also has the strongest genetic correlation with DFI (0.57 ± 0.05).

Table 4.5 Heritabilities (on diagonal), genetic correlations (above diagonal) and phenotypic correlations (below diagonal) for RFI, SH, LE, SC, ADG, DFI, WW, FCR, MMW and KR, with standard errors, of Bonsmara cattle as determined with the use of VCE 6

Trait	RFI	SH	LE	SC	ADG	DFI	WW	FCR	MMW	KR
RFI	**0.27 ± 0.02**	-0.05 ± 0.07	0.01 ± 0.07	-0.08 ± 0.04	0.10 ± 0.07	0.79 ± 0.03	-0.01 ± 0.09	0.65 ± 0.04	0.02 ± 0.07	0.12 ± 0.07
SH	-0.01	**0.39 ± 0.03**	0.77 ± 0.03	0.32 ± 0.04	0.54 ± 0.04	0.33 ± 0.05	0.41 ± 0.06	-0.35 ± 0.06	0.62 ± 0.04	0.35 ± 0.06
LE	-0.01	0.65*	**0.28 ± 0.02**	0.23 ± 0.05	0.66 ± 0.04	0.47 ± 0.05	0.58 ± 0.06	-0.39 ± 0.06	0.77 ± 0.03	0.43 ± 0.06
SC	0.02	0.36*	0.37*	**0.36 ± 0.03**	0.20 ± 0.04	0.12 ± 0.04	0.31 ± 0.07	-0.14 ± 0.05	0.35 ± 0.05	0.07 ± 0.05
ADG	0.00	0.35*	0.39*	0.32*	**0.25 ± 0.02**	0.67 ± 0.04	0.35 ± 0.07	-0.66 ± 0.04	0.75 ± 0.03	0.91 ± 0.02
DFI	0.48*	0.39*	0.39*	0.35*	0.57*	**0.31 ± 0.03**	0.28 ± 0.08	0.11 ± 0.06	0.55 ± 0.05	0.57 ± 0.05
WW	-0.04*	0.46*	0.52*	0.36*	0.19*	0.26*	**0.21 ± 0.02**	-0.21 ± 0.08	0.66 ± 0.05	0.08 ± 0.08
FCR	0.43*	-0.05*	-0.09*	-0.05*	-0.62*	0.27*	0.03	**0.23 ± 0.02**	-0.44 ± 0.06	-0.64 ± 0.05
MMW	0.00	0.63*	0.68*	0.53*	0.44*	0.56*	0.69*	0.01	**0.30 ± 0.02**	0.40 ± 0.07
KR	0.00	0.01	0.02	0.04*	0.84*	0.30*	-0.20*	-0.69*	-0.11*	**0.18 ± 0.02**

* Significant, with significance level set at $P < 0.01$

4.3. Spearman and Pearson correlations

Three different groupings were made to calculate expected DFI to use in the calculation of RFI, namely by contemporary group, year and station. The Pearson correlation between RFI calculated by contemporary group and year was 0.67 ($P < 0.0001$), and 0.69 ($P < 0.0001$) between RFI by contemporary group and station. For all further calculations RFI calculated by contemporary group was used. Animals were ranked for each feed efficiency trait according to Estimated Breeding Values (EBV's) as well as phenotype. The Spearman correlations between these three rankings according to EBV's and phenotype respectively are shown in table 4.6, with genetic correlations above the diagonal and phenotypic correlations below the diagonal.

Table 4.6 Spearman correlations between the ranking of animals according to RFI, FCR and KR. Genetic correlations are above the diagonal and phenotypic correlations below the diagonal.

	Spearman correlations		
Trait	**RFI**	**FCR**	**KR**
RFI	-	0.60*	0.18*
FCR	0.45*	-	-0.54*
KR	-0.005	-0.69*	-

* Significant, with significance level set at $P < 0.0001$

The phenotypic Spearman correlation between KR and RFI is not significant, but there is a weak (0.18) genetic Spearman correlation between these traits, indicating that selection using these traits will deliver different results and cannot replace each other. The genetic Spearman correlation between FCR and KR are considerably stronger (0.60).

4.4 Genetic trends

Genetic trends were estimated for each trait analysed to observe genetic change in the population over the years 1999 to 2009 and are presented in figures 4.1 to 4.7. Trendlines were fitted and R^2 calculated. All the trends indicated sudden changes in EBV's for all traits in 2007, with a decrease in EBV's for all traits except FCR and SC.

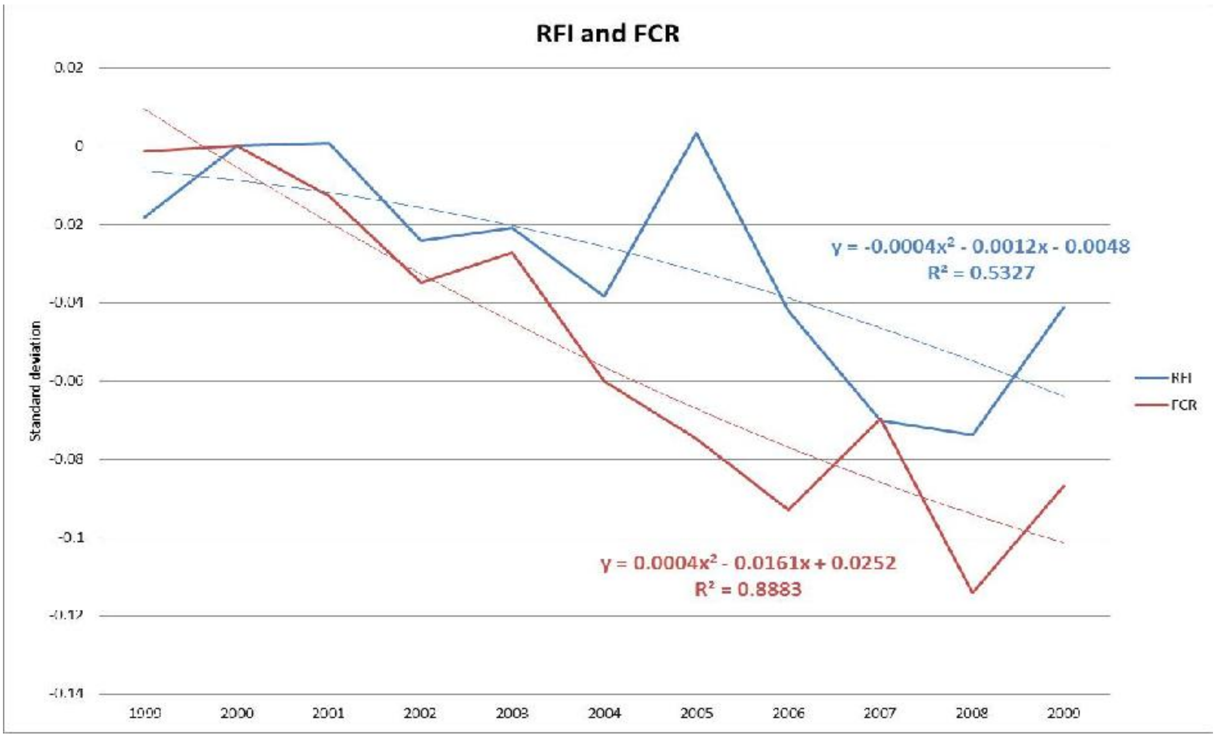

Figure 4.1 Genetic trends showing genetic change in RFI and FCR during the period 1999 to 2009, with standard deviation on the y-axis and year on x-axis. The base year is 2000 and fitted polynomial trendlines with R^2 are shown

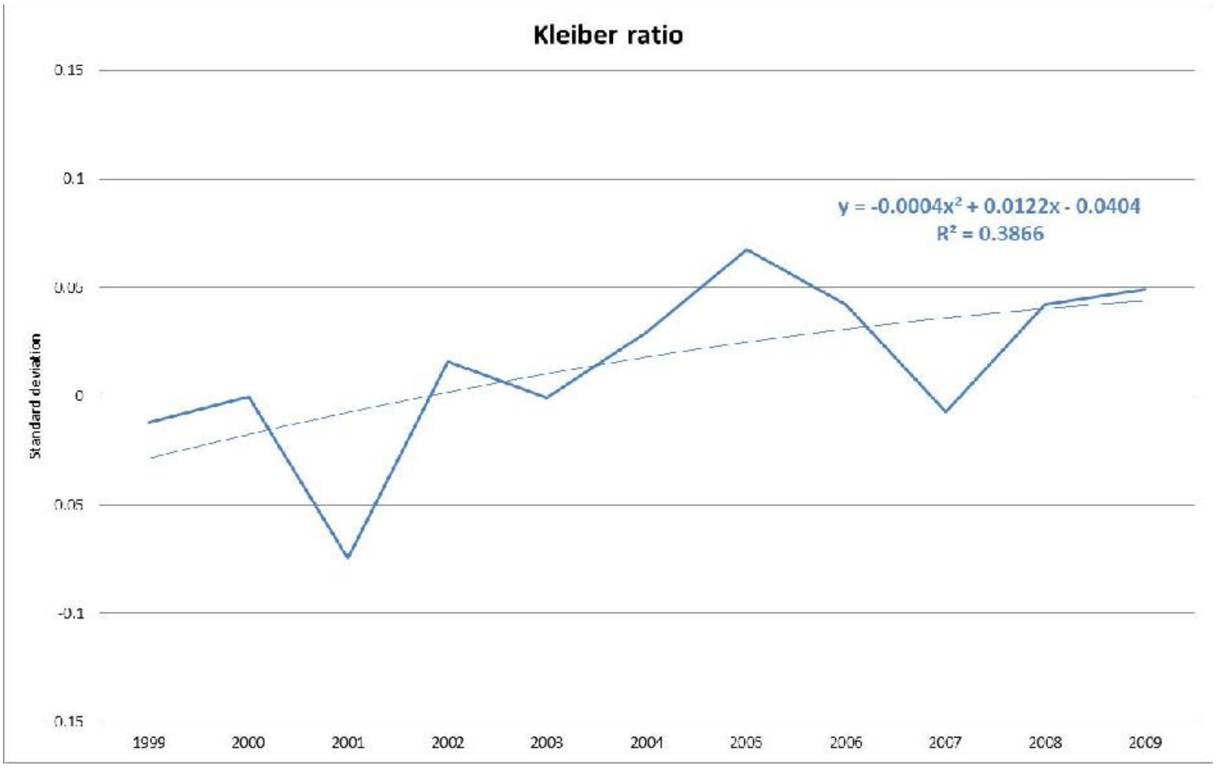

Figure 4.2 Genetic trend showing genetic change in KR during the period 1999 to 2009, with standard deviation on the y-axis and year on x-axis. The base year is 2000 and a fitted polynomial trendline with R^2 is shown

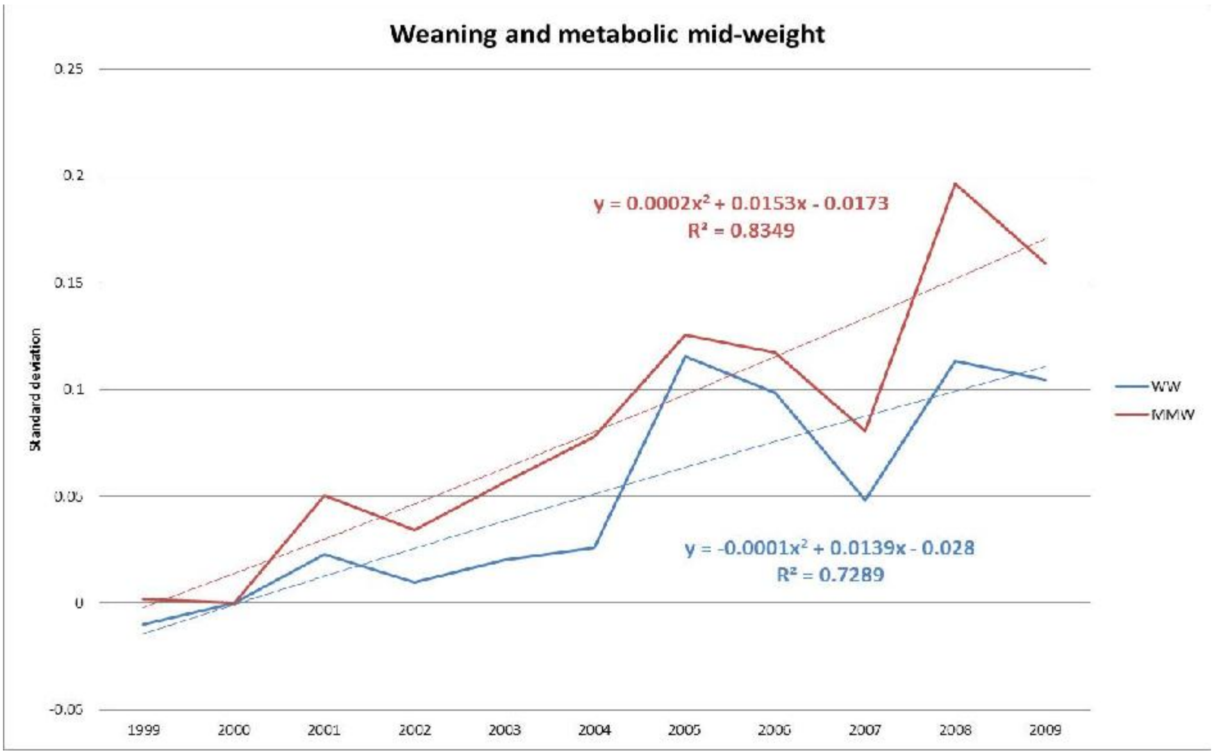

Figure 4.3 Genetic trends showing genetic change in WW and MMW during the period 1999 to 2009, with standard deviation on the y-axis and year on the x-axis. The base year is 2000 and fitted polynomial trendlines with R^2 are shown

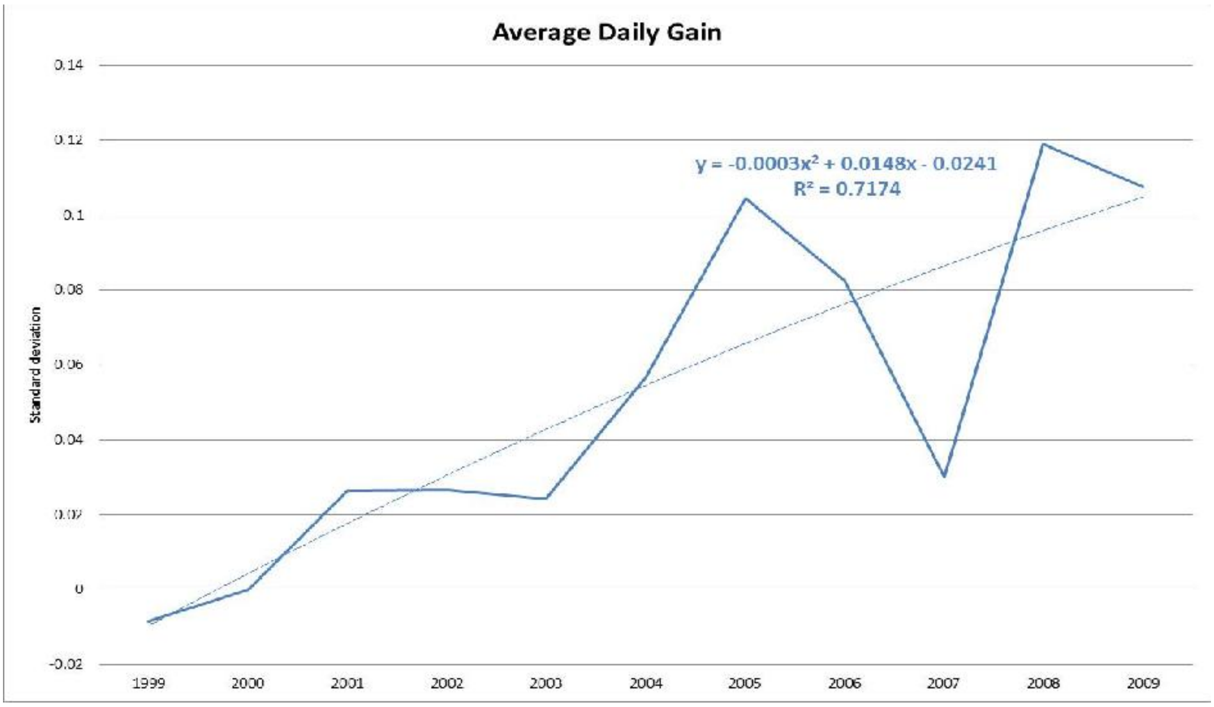

Figure 4.4 Genetic trend showing genetic change in ADG during the period 1999 to 2009, with standard deviation on the y-axis and year on x-axis. The base year is 2000 and a fitted polynomial trendline with R^2 is shown

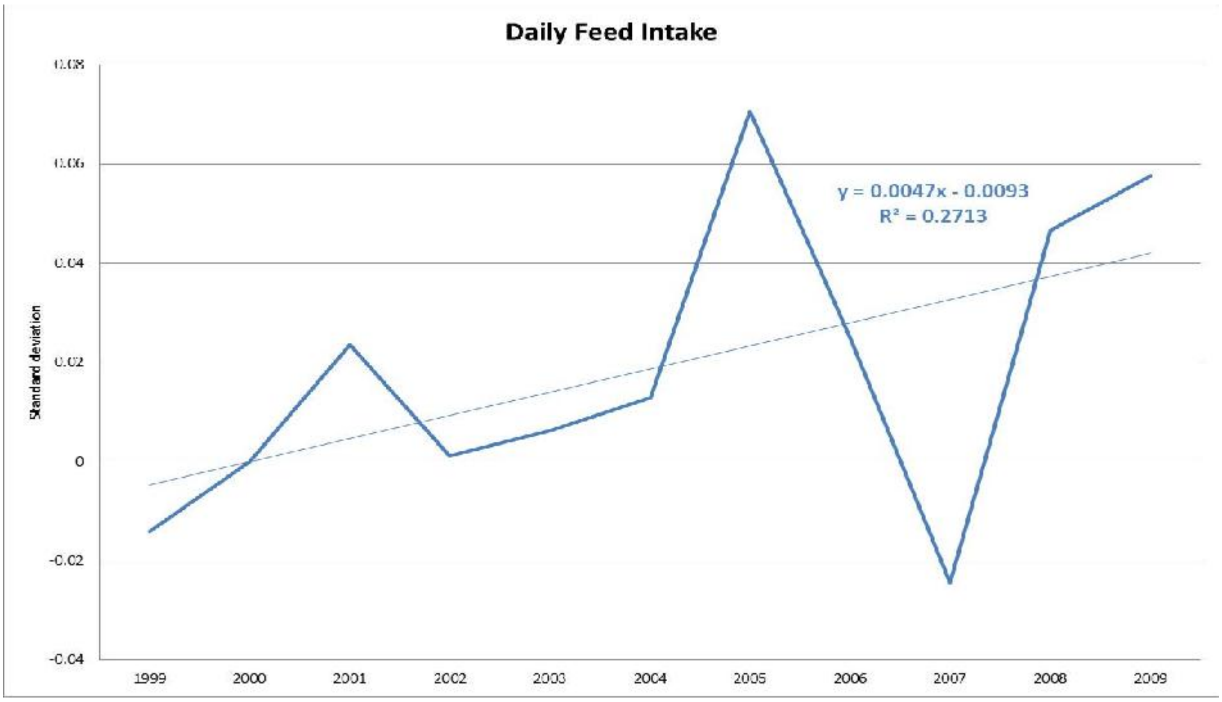

Figure 4.5 Genetic trend showing genetic change in DFI during the period 1999 to 2009, with standard deviation on the y-axis and year on the x-axis. The base year is 2000 and a fitted linear trendline with R^2 is shown

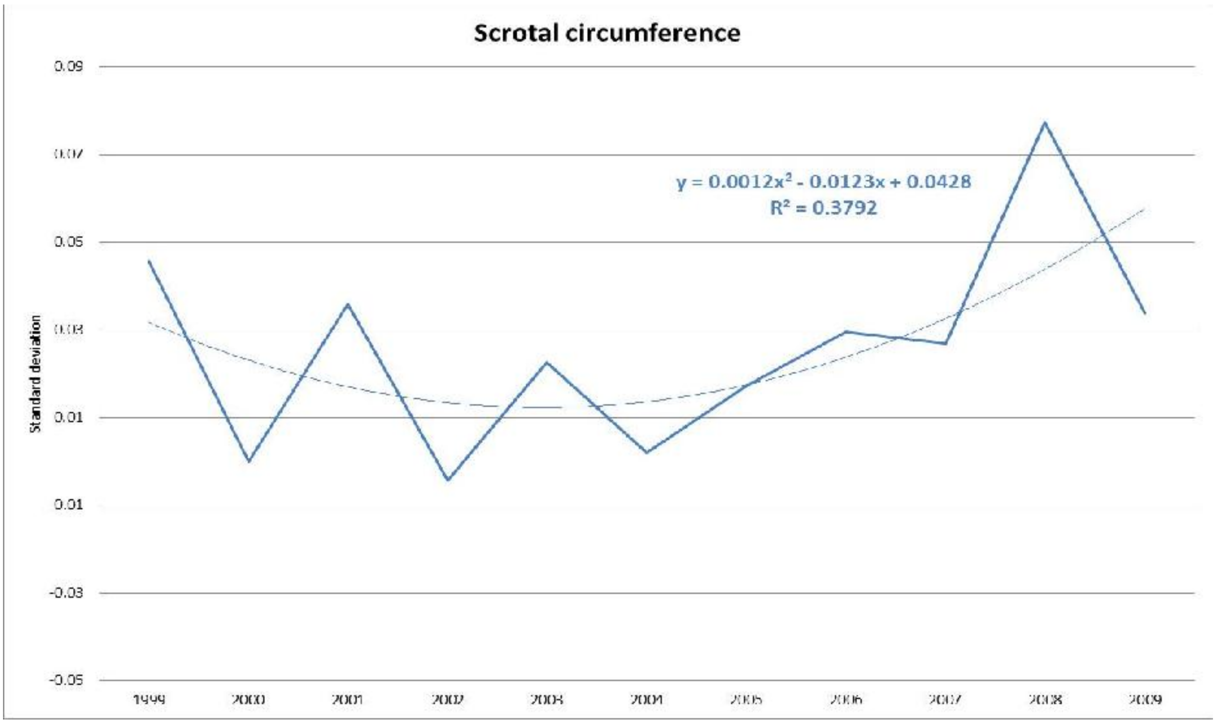

Figure 4.6 Genetic trend showing genetic change in scrotal circumference during the period 1999 to 2009, with standard deviation on the y-axis and year on the x-axis. The base year is 2000 and a fitted polynomial trendline with R^2 is shown

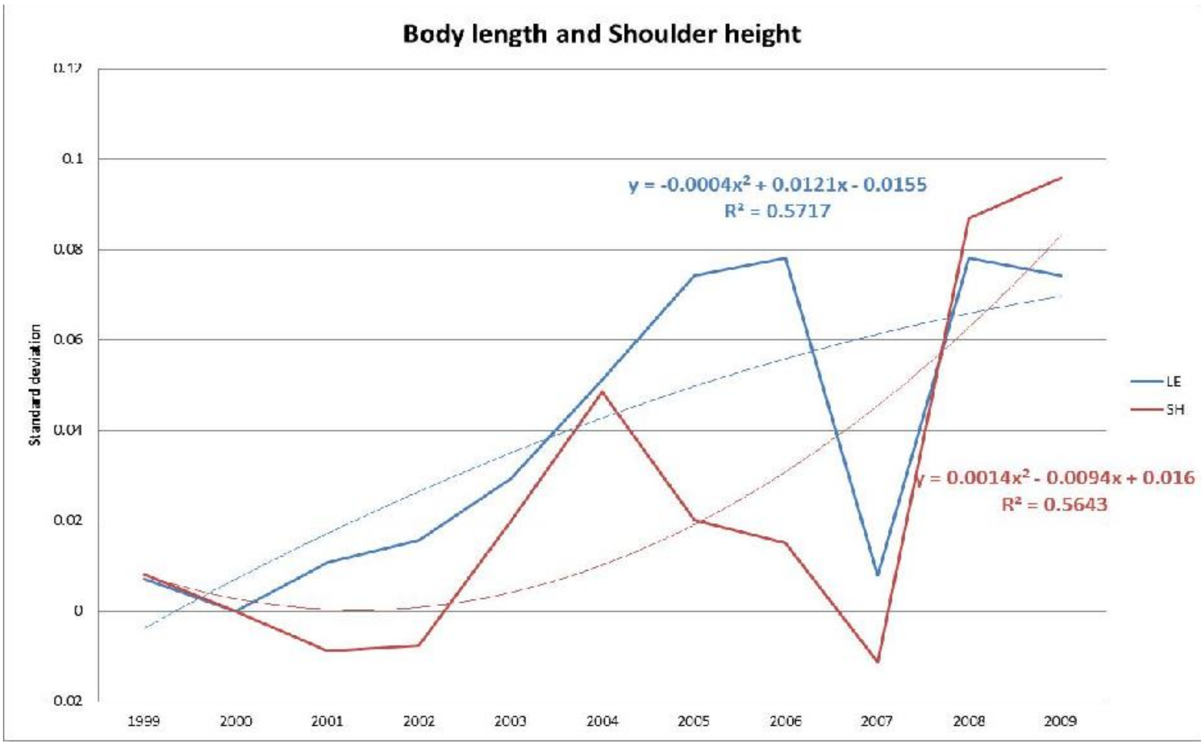

Figure 4.7 Genetic trends showing genetic change in SH and LE during the period 1999 to 2009, with standard deviation on the y-axis and year on the x-axis. The base year is 2000 and fitted polynomial trendlines with R^2 are shown

From 1999 to 2009 there was a genetic improvement of 0.02 SD in RFI, 0.09 SD in FCR, 0.06 SD in KR, 0.11 SD in WW, 0.16 SD in MMW and 0.12 SD in ADG. There is an increase in DFI of 0.07 SD, a decrease of 0.01 in SD (from 1999 to 2009, but improvement of 0.03 SD from 1999 to 2008). There is a further improvement of 0.09 SD for SH and 0.07 for LE.

Chapter 5

Discussion

There are many measures of efficiency of which Kleiber ratio (KR), feed conversion ratio (FCR) and residual feed intake (RFI) were investigated in this study. These traits were chosen above others as KR and FCR are the traits currently used by South African Bonsmara cattle breeders to select for feed efficiency. The literature reviewed indicated that the concept of RFI has received more attention since the 1990's but only in the early 2000's in South Africa. The increase in human population size, feed prices and awareness of global warming have led researchers to strive for a feed efficiency trait that would both decrease expenses and be beneficial to the environment, hence the increased interest in RFI. The aim of the study was to determine RFI's association with various traits of economic importance and whether using Estimated Breeding Values (EBV's) for RFI instead of FCR will change the ranking of bulls for feed efficiency.

Graphs compiled for traits prior to editing included data from all test lengths and therefore show the effect of age on performance. A standard age for animals to enter Phase C test stations was set when the test length was decreased to 84 days and therefore ages of animals during test length of 140 days had greater variation, while ages during the test length of 84 days had a smaller and consistent spread. The variation and values of average daily gain (ADG) have increased drastically with time as test lengths were decreased. Size traits – shoulder height (SH) and body length (LE) - were measured at the end of testing and therefore animals were smaller and weighed less after a test length of 84 days than 140 days. Final weight and size traits show that the animals were smaller and lighter after a test length of 84 days, which is due to the decrease in time spent at the feeding station.

The heritability estimate for RFI in this study was 0.27 ± 0.02, which is similar to published estimates such as 0.28 by Koch *et al.* (1963) and Fan *et al.* (1995) as well as 0.29 by Mujibi *et al.* (2011). The medium heritability indicated that there is sufficient genetic variation for RFI in South African Bonsmara cattle to improve RFI genetically by selection. This estimate is higher than the heritability for KR (0.18 ± 0.02) and similar to the heritability for FCR (0.23 ± 0.02) in this study. This suggested that the rate of genetic change when using RFI would be similar than the rate of change when using FCR, and both would be higher than the rate of genetic change when selecting for KR. The similar rate of genetic change indicated that improvement in feed efficiency will not be retarded if RFI replaces FCR as selection criterion. The choice of measure of efficiency to use therefore heavily depends on the correlations with other traits. It is of utmost importance not to apply single trait selection, but rather select for multiple traits simultaneously. This can be achieved with the use of a selection index.

Reproduction is considered to be the most important section to take into account when selecting animals and is usually largely influenced by environment, which is reflected in low heritability estimates for reproduction traits (Koots *et al.,* 1994). Any trait which could negatively affect reproductive traits should be scrutinised. The reproductive trait under investigation was scrotal circumference (SC) and showed a genetic correlation of -0.08 ± 0.04 with RFI, which differed slightly from the estimate of 0.05 found by Van der Westhuizen *et al.* (2004). The lack of association between SC and RFI suggest that age at puberty will not be affected, however, there are concerns that this is not the case, as RFI has an unfavourable correlation with fat thickness (Herd *et al.*, 2003; Richardson *et al.*, 2004), while the rate of fat deposition plays a major role in the age at puberty (Owens *et al.*, 1993). Some studies have found that RFI does not affect age at puberty (Lancaster *et al.*, 2006; Lancaster, 2008), while others have shown that age at puberty is delayed in low RFI heifers (Basarab *et al.,* 2007; Schaffer *et al.* 2010). It has also been found that low RFI cows calve later in the calving season (Arhur *et al.,* 2005; Basarab *et al.,* 2007). Female reproductive traits were beyond the scope of this study and not investigated. A medium heritability of 0.36 ± 0.03 was found for SC, which indicated that selection based on SC will have a significant effect on the rate of genetic change. The results in this study indicated that selection for feed efficiency using RFI would have no negative effect on this important reproductive trait, which is favourably correlated with age at puberty (Koots *et al.,* 1994).

The genetic correlations between RFI and weight traits were low, such as 0.10 ± 0.07 with ADG, -0.01 ± 0.09 with WW and 0.02 ± 0.07 with MMW, which are similar to estimates found by previous studies. These correlations combined with the high correlation with DFI (0.79 ± 0.03) suggested that low RFI animals will consume less feed than high RFI animals but maintain similar weights and growth rate. High genetic correlations were found between FCR and weight traits, such as -0.66 ± 0.04 with ADG, -0.21 ±0.08 with WW, and -0.44 ± 0.06 with MMW. These correlations suggested that selecting for FCR will lead to an increase in growth and weight traits. While an increase in ADG is favourable, the increase in weight traits are not, as this will increase the maintenance costs of the herd. The genetic correlations found by this study showed that selecting for feed efficiency using RFI will not influence growth performance yet decrease feed intake, while FCR will increase growth and weight traits.

A high genetic correlation of 0.79 ± 0.03 was found between RFI and DFI, which is similar to previously published estimates, such as 0.79 by Arthur *et al.* (2001c), 0.75 by Nkrumah *et al.* (2004) and 0.81 by Schenkel *et al.* (2004). A considerably lower genetic correlation of 0.11 ± 0.06 was found between FCR and DFI, which is lower than other published estimates ranging from 0.29 – 0.49 (Nkrumah *et al.,* 2004; Baker *et al.,* 2006; Smith *et al.,* 2010). The change in feed intake can therefore be expected to be higher when using RFI instead of FCR as a selection tool. The component traits of FCR are ADG and DFI, and therefore change in FCR is more likely to be due to a change in ADG, to which it is highly correlated, than a change in DFI. The low genetic correlations with SH (-0.05 ± 0.07), which is similar to the estimate of -0.02 found by Van der Westhuizen *et al.* (2004), and LE (0.01 ± 0.07) indicated that selecting for low RFI would not lead to an increase in mature size. Unlike RFI, selection for FCR would lead to an increase in mature size due to its genetic correlation with SH (-0.35 ± 0.06), which corresponds with the correlation of -0.24 by Van der Westhuizen *et al.* (2004) and LE (-0.39 ± 0.06). The correlations between FCR and weight and size traits may seem favourable when selling weaner calves to feedlots, but can be counteracted with the increase in maintenance costs of the breeding herd.

A weak genetic correlation of 0.12 ± 0.07 between KR and RFI, and a high correlation of -0.64 ± 0.05 between KR and FCR were found. The association between KR and RFI differ from the -0.004 found by Nkrumah *et al.* (2004), but is also low, and likewise the association between KR and FCR differs from the estimate of -0.73, but is also high. This showed that selecting for KR would lead to similar results as when selecting for FCR, while results will differ greatly from those obtained when using RFI. The correlation between RFI and FCR was found to be 0.65 ± 0.04, which is similar to previously published estimates ranging from 0.57 to 0.85 (Arthur *et al.,* 2001a, 2001c; Nkrumah *et al.,* 2004; Van der Westhuizen *et al.,* 2004). Even though RFI is highly correlated to FCR, using RFI as a selection tool may deliver more desirable results due to its low correlations with growth, weight and size traits and higher correlation with DFI. Improved efficiency when selecting for low RFI will therefore be due to a decrease in feed intake without a reduction in growth performance. In the case of FCR, improvement could be due to either increased growth, which is more likely, or reduced feed intake.

Age and herd contributed significantly to variation of RFI in this study. This contradicts the findings of Herd & Bishop (2000) that RFI is unaffected by pretest environmental variations, including age. However, this supports the findings of Mujibi *et al.* (2010) and Durunna *et al.* (2011) that RFI is affected by environmental factors, including stage of maturity. Defining contemporary groups to be used in practice for the calculation of RFI can be problematic since small groups will decrease the reliability of the regression used to calculate expected feed intake. Prior to data editing, 613 groups out of 1 146 consisted of less than ten animals, with an average of 3.97 animals per group. In South Africa, 67% of all bulls tested in Phase C, are Bonsmara bulls. Other breeds can be expected to have even more contemporary groups with less than ten animals. In practice, groups with less than five animals would most likely not deliver useful results. In this study RFI was calculated in three different ways – per contemporary group (including test year, test station, test number and test phase), per year and per station – and compared. The Pearson correlations between RFI calculated per contemporary group with RFI calculated per year and station were found to be 0.67 and 0.69 respectively. This shows that these results differ too greatly to replace RFI calculated by contemporary group. A possible solution is to calculate RFI on one regression including all the animals in the dataset, and including contemporary group in the model for EBV estimation. Another approach that was taken by MacNeil *et al.* (2011) is to analyse DFI, ADG and MMW and use these EBV's to predict genetic RFI.

The genetic trends showed that both RFI improved genetically by 0.02 SD and FCR by 0.09 SD in the Bonsmara breed over the last decade. This can be expected since FCR has been selected for and its high correlation with RFI indirectly led to the improvement in RFI. The genetic correlation between KR and FCR is of equal strength as that between RFI and FCR, but the genetic improvement in KR (0.06 SD) is more than that of RFI. Improvements in WW (0.11 SD), MMW (0.16 SD) and ADG (0.12 SD) were observed, which can be expected since weight traits have been the basis of selection applied. There is a genetic improvement of 0.03 SD in SC from 1999 to 2008, but a sudden decrease in improvement in 2009. There has been an increase in DFI (0.07 SD) and is possibly due to its strong association with all size, weight and efficiency traits, except for the low correlation of 0.11 with FCR found in this study. An increase in mature size has occurred, as indicated by the genetic improvement for SH (0.09 SD) and LE (0.07 SD). This could be due to selection and genetic correlations with FCR and weight traits, all of which have improved. All trends showed a sudden change in 2007, which has the second largest population size and no remarkable differences in measurements. The cause is unclear but possible reasons can be a sudden increase in the number of breeders using EBV's, an increase in the use of specific bulls, or merely by chance.

Animals were ranked according to EBV's for RFI, FCR and KR. The Spearman correlations were 0.60 between RFI and FCR, 0.18 between RFI and KR, and -0.54 between FCR and KR. Animals were also ranked according to their phenotype for these three traits and the Spearman correlations were 0.45 between RFI and FCR, -0.69 between FCR and KR, and no significant correlation between KR and RFI. The genetic and phenotypic Spearman correlations between these rankings showed that the efficiency rankings of bulls differed and selection for these traits will deliver different results. The main reason for the use of KR is that it does not require feed intake in its calculation, however, KR is also a ratio trait, which creates the same problem encountered with FCR where results are unpredictable and emphasis is placed on the component trait with the greater variation (Gunsett, 1984). Testing animals in Phase C is costly and therefore KR seems to be an attractive solution to farmers, specifically for other breeds in South Africa with low participation in Phase C testing. The difference between these traits questions their effect on true feed efficiency.

One of the main disadvantages of FCR is that it will increase mature size and thereby the cost of the breeding herd. Large animals are considered to be less efficient. However, there are debates whether keeping smaller cows is truly more profitable than keeping larger cows. A ratio to best describe overall efficiency in beef cattle is total costs to total animal product produced from cows and their calves over a period of time (Dickerson, 1970). Due to the segmentation of the beef industry, improvement of economic efficiency in one segment does not necessarily lead to an improvement in another (Notter, 2002). Smaller cows are regarded as more efficient in the cowherd since they have a high rate of reproduction, require less energy for maintenance and are able to utilise available energy more efficiently (Dickerson, 1970), however, larger animals are often preferred in feedlots (Schroeder *et al.,* 1998). An increase in mature size may or may not be economically beneficial, depending on the cost and availability of feed (Kelley, 2002). Larger cows with high growth and milk production have high maintenance requirements. When less feed is available, these cows will have decreased reproductive performance and will therefore be less efficient than smaller cows that will still be able to meet their energy requirements for both maintenance and reproduction. However, when more feed is available, larger cows are more efficient since they can meet energy requirements for maintenance, reproduction and milk production, allowing them to wean heavier calves. Smaller cows may not have the genetic potential for high milk production and will therefore accumulate fat themselves and still wean lighter calves (Jenkins & Ferrell, 1994).

It is interesting to note that even though larger animals consume more feed, the percentage increase in feed requirement is less than the percentage increase in weight (Kleiber, 1932; Johnson *et al.,* 2010). Although RFI will increase the feed efficiency of animals without increasing the mature size, the financial gain in decreased feed intake should be compared to the financial gain in increased weight to determine whether smaller animals truly are more economically efficient (Johnson *et al.,* 2010). A study by Van der Westhuizen *et al.* (2004) led to increased doubts whether using RFI would by more profitable than using FCR as their study found that post-wean profitability has a correlation of -0.92 with FCR but only -0.59 with RFI. As discussed previously, small contemporary groups will decrease the reliability of the calculated expected feed intake. The use of a selection index including all the traits of interest could deliver similar results as those obtained when using RFI and may be a better option for the end user (Van der Werf, 2004; Berry & Crowley, 2012).

Another study has stated that RFI's independence of growth rate may affect its acceptance by farmers as an increase in ADG is favourable and it is possible that small, slow growing animals will have a low RFI. However, when animals were compared and the breeds ranked according to efficiency measured by both RFI and FCR, the large breeds (Charolais and Limousin) ranked higher than the smaller breeds (Hereford and Angus) (Berry & Crowley, 2012). This, along with the lack of a correlation with ADG and weight traits found by many studies, seem to show that RFI would not necessarily lead to the selection of small, slow-growing animals. The inclusion of ADG or other size traits in a selection index could avoid the selection of small, uneconomical animals.

Berry & Crowley (2012) recently published an article in which they proposed another measure of efficiency called "Residual Intake and weight Gain (RIG)", which combines RFI and another new measure called Residual Gain (RG). Residual gain has a medium heritability of 0.28 (Crowley *et al.,* 2010) and is the difference between actual daily gain and predicted daily gain for the level of intake and body weight. The predicted daily gain is calculated by regressing actual daily gain against MMW and DFI. The calculation on RG is then done by subtracting the expected daily gain from the actual daily gain and a positive value is favourable. This trait has been adopted by the American Angus Association and is calculated post analysis (MacNeil *et al.,* 2011). Both RFI and RG are standardised to a variance of one for the calculation of RIG, followed by multiplying RFI by -1 (to account for the fact that a negative RFI is favourable) and adding RG. A positive RIG is therefore favourable and was found to have a medium heritability of 0.36 (Berry & Crowley, 2012). The goal when selecting for RIG is to breed fast-growing animals that spend less time in feedlots while consuming less feed than expected and have a minimal impact on mature weight (Crowley *et al.,* 2010; Berry & Crowley, 2012). This feed efficiency trait is of great interest and further research is needed to determine its potential.

A factor making RFI a trait of importance is its potential to decrease the carbon footprint of the beef industry. Greenhouse gases and their impact on global warming have become an issue of great concern worldwide. As the cost of feed and concerns about the environment increase, and availability of land for agricultural purposes decrease, the importance of breeding more efficient animals becomes more obvious. More efficient animals will have a smaller negative impact on the environment, which is an issue receiving more emphasis by the day, through the reduction of methane emissions and manure (Nkrumah *et al.,* 2006).

Currently the largest barrier to the adoption of RFI is the cost involved in the measurement of feed intake. The technology used is expensive, the process is labour intensive and there is a low capacity of feeding test stations (Herd *et al.*, 2003). Test periods are of long duration, with the optimum estimated period ranging between 63 to 84 days, depending on the number of days between body weight measurements (Archer *et al.*, 1997; Archer & Bergh, 2000; Wang *et al.*, 2006). It is difficult to explain RFI to farmers and it is more challenging to calculate compared to FCR since energy requirements for growth and maintenance, which are assumed in the calculation of RFI, can differ between different environments and climates (Van der Westhuizen *et al.,* 2004). The ideal solution would be to identify a genetic marker or a suite of correlated traits to use in indirect selection for RFI.

Although many studies have determined that a combination of genetic markers explains a large portion of the genetic variation in RFI, no major gene affecting RFI has been found (Moore *et al.*, 2009). The main barriers preventing full adoption of the use of markers are that the genetic interaction of genes affecting RFI on other traits is not fully understood and the number of animals with high accuracy estimates of RFI remains small (Moore *et al.*, 2009). Physiological indicators have also been researched and the use of IGF-I plasma concentrations as an indirect selection tool has been demonstrated (Davis & Simmen, 2006), however, at present there is increasing doubt whether IGF-I is a reliable indicator (Moore *et al.*, 2009).

This study has shown that selection for RFI will decrease DFI without increasing growth, weight or size, while selection for FCR will lead to an increase in growth, weight and size. The heritability estimate for RFI is medium and indicates sufficient genetic variation to justify selection, which is currently not applied in South African Bonsmara cattle. The small contemporary groups present a problem for the calculation of RFI and there are concerns about RFI's effect on profitability and its lack of association with growth rate. It is possible that the use of a selection index including traits of importance could deliver better results than when selecting for RFI. Further research is required, particularly on the concept of RIG, which could have the potential to select for fast growing animals that consume less feed than expected.

Conclusion

The purpose of this study was to determine RFI's association with various traits of economic importance and whether using EBV's for RFI instead of FCR or Kleiber ratio will change the ranking of bulls. The heritability estimate of 0.27 for RFI showed sufficient genetic variation for selection. The genetic correlations found by this study correspond with other studies. This indicates that RFI will not increase mature size and will decrease feed intake without decreasing growth performance or scrotal circumference. The decrease in feed intake will decrease expenses and the lack of association with ADG and mature weight should avoid a decrease in the income received. The lack of RFI's association with ADG has been criticised and is regarded by some as detrimental to the performance of animals in feedlots.

In this study a challenge was faced when calculating RFI since the small size of the contemporary groups will decrease the reliability of the expected feed intake as determined by the regression. It was overcome by excluding these groups, but this challenge is considerably larger in practice. It has also been claimed that selection using RFI will lead to the selection of slow-growing animals, thereby increasing the duration of time spent in feedlots. An alternative trait, Residual intake and body weight gain (RIG) has been proposed by other researchers and deserves further research. The purpose of this trait is to breed fast-growing animals that consume less feed than expected without affecting mature size.

Selection for FCR may increase the cost of maintaining the breeding herd due to a correlated increase in mature size. FCR is also a ratio trait, which makes it difficult to interpret since an improvement in FCR could be due to either an increase in growth or a decrease in feed intake. There are doubts whether an increase in mature size is truly undesirable, especially in areas with abundant grazing or less expensive feed sources. Farmers in these areas might prefer to use FCR and breed larger cattle. There is a high correlation between RFI and FCR, but not strong enough to be considered as the same trait. Results obtained when selecting for these two traits will differ, which can be seen from the difference in the ranking of bulls according to their genotype and phenotype. The use of a selection index to include the traits of importance for different systems could be a better solution than selecting for RFI.

The effect of the selection of RFI on the environment makes it an important trait to consider as increasing pressure is being placed on the livestock industry to reduce its carbon footprint. It has been estimated that livestock is responsible for up to 18% of global methane emissions. Selecting for RFI has the potential to decrease methane emissions by up to 28%. This advantage has made RFI an attractive trait to apply in the industry.

In conclusion, sufficient genetic variation in RFI and its independence of weight and size trait makes it feasible to include in a selection program for South African Bonsmara cattle. However, other studies show contradicting findings about the profitability of RFI and there are doubts whether larger animals are truly undesirable. Small contemporary groups presented a problem is this study as they decrease the reliability of an RFI estimate. Further research is required to find solutions for these challenges and investigate other possible measures of feed efficiency.

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Addendum A: Breed standards

These standards are obtained through the Bonsmara Society on the website www.bonsmara.co.za

1. Reproduction

1.1 A heifer must calve before or at the age of 39 months for the first time;

1.2 A calving interval may not exceed 26 months (790 days);

1.3 The minimum number of calves a cow must produce by a certain age is noted in table 1:

Table 1 Minimum number of calves a cow must produce by a certain age

Age of dam	Min. No. Calves	Max. ICP (Days)
3 years 3 months	1	-
5 years 3 months	2	790
6 years 3 months	3	578
8 years 3 months	4	628
9 years 3 months	5	563
11 years 3 months	6	596
12 years 3 months	7	558
14 years 3 months	8	582
15 years 3 months	9	555
17 years 3 months	10	575

1.4 A cow must rear at least two of any three consecutive calves (up to weaning age).

2. Milk production

2.1 A cow may wean not more than two calves with an index below 90. Once a cow has weaned three (3) calves with an index below 90 she will be culled.

3. Growth

3.1 General

The entire remaining group must be inspected together. Indices will be required for the purpose of inspection.

Note: The wean index is compulsory for all groups and for individual animals unless a valid reason is given.

In such cases the year and 18 month indices must be presented.

3.2 Heifers

a. Minimum wean index of 90

b. Minimum 12 month index of 90

c. Minimum 18 month index of 90

- In cases where heifers are inspected before the age of 18 months the wean and 12 month indices will suffice.
- In cases where the animal could not be weighed at the age of 12 months, the wean and 18 month indices will be acceptable.

3.3 Bulls

3.3.1 Bulls phase B

a. Minimum weight of 375 kg at time of inspection.

b. Minimum wean index of 90

c. Minimum 12 month index of 90

d. Minimum 18 month index of 90

Note: The scrotum circumference of phase B bulls is not officially measured. The inspector may measure the scrotum circumference and use the standards below as guidelines. (A Breeder may measure bull scrotums at 18 months of age and send measurements together with 18 month old weights to the ARC.)

Minimum scrotal circumference:
Weight 375 to 399 kg - 29 cm
400 to 449 kg - 30 cm
450 to 499 kg - 31 cm
500 to 549 kg - 32 cm
550 kg and over - 34 cm

3.3.2 Bulls phases C1, C2, C3, D1, D2 and D3

a. Minimum wean index of 90

b. Minimum ADG index of 90

c. Minimum feed conversion ratio index of 90 (Phase C only)

d. Scrotum circumference

Weight 425 kg - Minimum scrotum 305 mm.

3.3.3 All rejected bulls from Phases B, C & D as well as bulls not submitted for inspection, must be castrated or slaughtered immediately.

4. Visual appraisal

4.1 The emphasis is on the functional appearance of the animal. The inspector will determine whether the defect warrants culling the animal. Animals with congenital defects must be culled.

Refer to the attached Codes for Rejection reasons.

4.2 Type and colour

4.2.1 Basic animals

A variety of crossbred animals phenotypically representative of a Bonsmara-type will be acceptable. Different shades of red with minimum white, is acceptable.

4.2.2 Appendix and herd book proper animals

Animals must be red and neatly dehorned. White will be acceptable on the underline only.

5. Bulls for artificial insemination (AI)

The Society will control the practice of AI in Bonsmara herds in accordance with the Livestock Improvement Act of 1998 as amended.

5.1 Procedures for application

5.1.1 Bulls licensed for purpose of AI

Nominated bulls, with acceptable genetic potential will be researched by a committee appointed by the Council in respect of:

- Own performance
- Ancestral performance
- General appearance
- Progeny performance where applicable

5.1.2 Evaluation procedure for AI Bulls

Step 1: Breeder Identification of potential AI bull

- Application for registration to office

Step 2: Office Collates necessary information

- Information forwarded to Technical Work Group Chairman

Step 3: Office Appointment of Selectors

- Furnish Selector with necessary performance data and breeding values

Step 4: Selector Visual inspection of bull on the farm

- Discuss differences/recommendations with breeder.

Step 5: Office Advise breeder if process may continue.

Step 6: Breeder AI Centre/Vet/Technician compiles reproduction report.

Step 7: Centre Reproduction report is forwarded to office.

Step 8: Office Technical Committee evaluate result of report.

Step 9: Office Approval as AI bull by Committee.

Step 10: Office Approval is confirmed with AI Centre.

Step 11: Centre Bull may then be tapped.

5.2 Progeny

The Breed Society may cancel the registration of an A I bull if the performance of the progeny is not satisfactory.

6. Embryo transfer (ET)

The Breed Society will control embryo transfers in accordance with the Livestock Improvement Act of 1998 as amended.

6.1 Procedure for application

6.1.1 Apply in writing to the Breed Society, submitting ID numbers of the prospective donor cows.

6.1.2 Donor cows

Must conform to Minimum Breed Standards.

Cows must have a visual point greater than seven out of nine to be donors and above average performance data and BLUP.

6.1.3 Recipient cows

Permanent identification is compulsory as well as complete records of cows and their foster calves.

Bonsmara-type cows are preferred. Pure dairy breeds and crosses between dairy breeds are not acceptable.

6.2 Progeny

All progeny must with the exception of wean index (guideline) comply with Minimum Breed Standards.

Breeders should endeavour to have recipient cows calve during normal calving season.

7. Exceptions

7.1 With written motivation on the inspection form animals that do not meet the requirements of Minimum Breed Standards may in exceptional cases be approved by the inspector.

7.2 Written application (appeal) to the Council where applicable.

7.3 Individual animals with a code eliminating it from index calculations may be inspected provided that the corrected weight of such an animal is satisfactory in comparison with its contemporaries.

Addendum B: Scatterplots before data editing

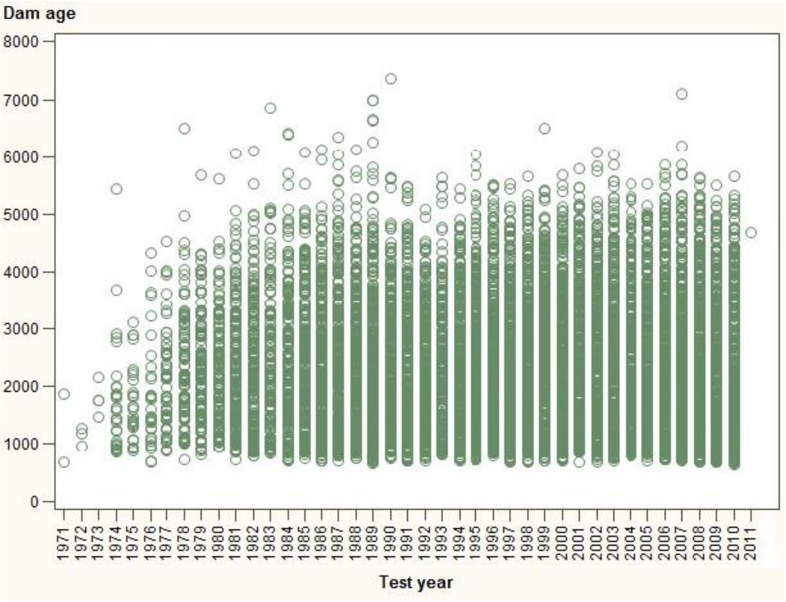

Figure 1: Scatter plot for dam age (in days) per year before data editing

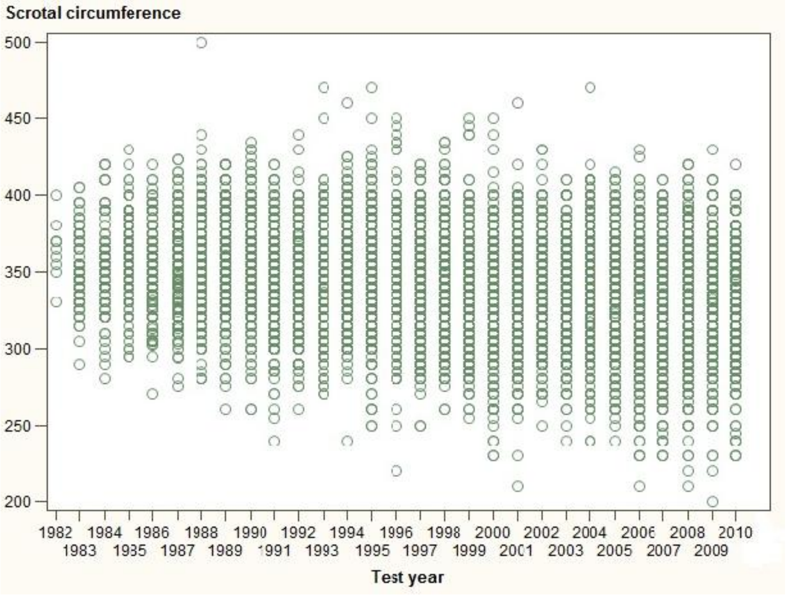

Figure 2: Scatter plot for scrotal circumference (in mm) per year before data editing

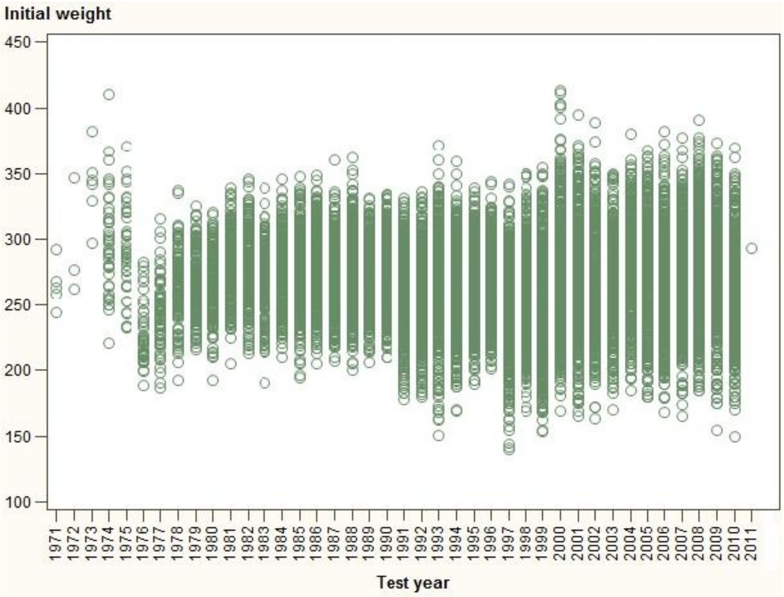

Figure 3: Scatter plot for initial weight (in kg) per year before data editing

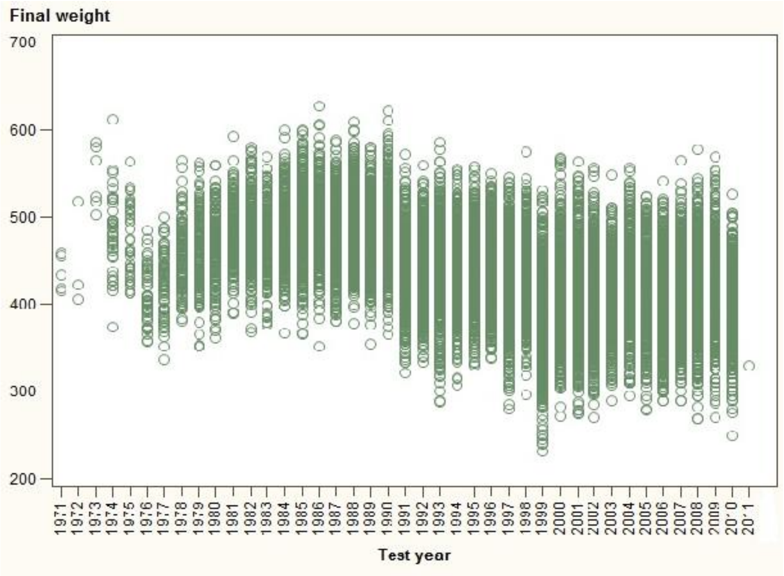

Figure 4: Scatter plot for final weight (in kg) per year before data editing

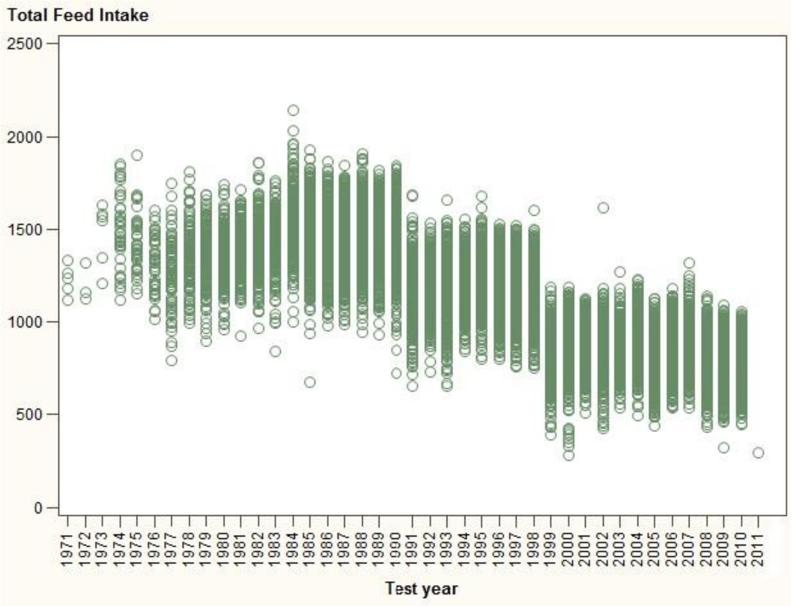

Figure 5: Scatter plot for total feed intake (in kg) per year before data editing

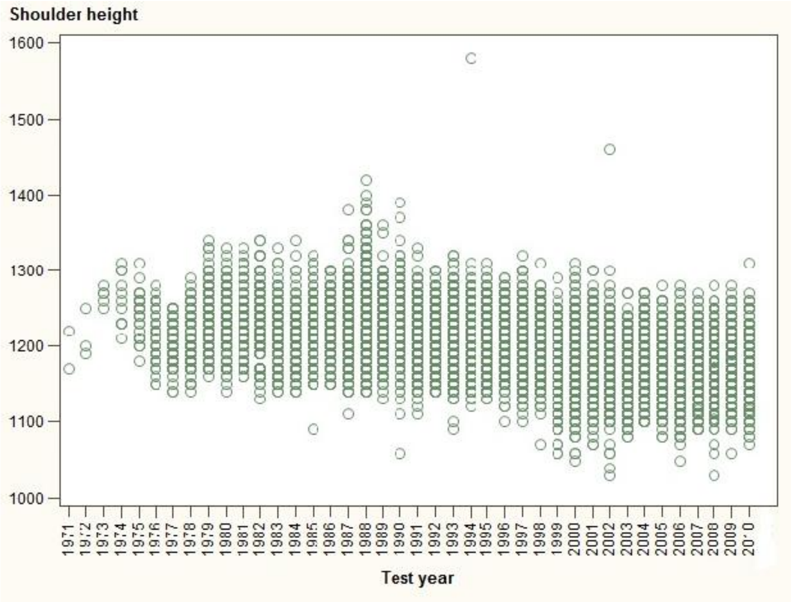

Figure 6: Scatter plot for shoulder height (in mm) per year before data editing

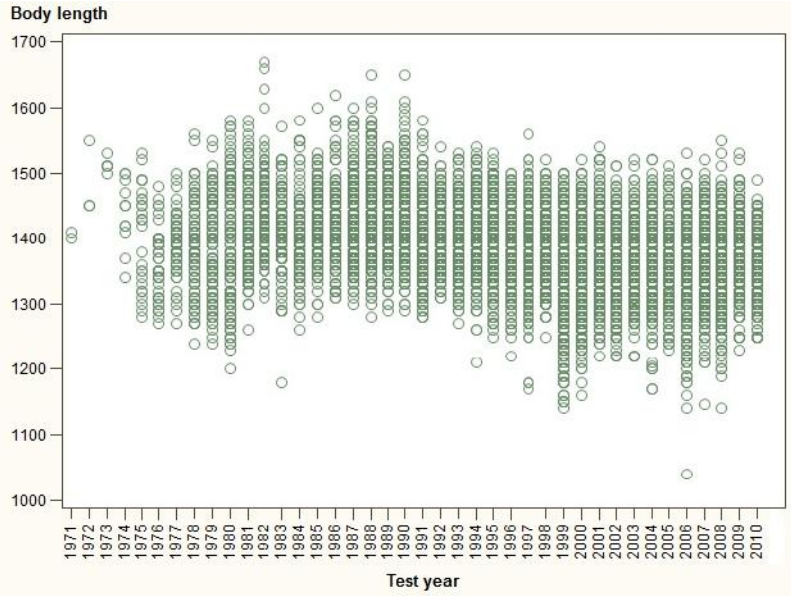

Figure 7: Scatter plot for body length (in mm) per year before data editing