

# **Breed genetic and heterosis effects on variability of growth and efficiency traits in beef cattle**

by

**Georgette Mareé Pyoos**

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University of the Free State  
Bloemfontein

External Supervisor: Dr M.D. MacNeil

Internal Supervisor: Prof F.W.C. Naser

Co-supervisor: Prof M.M. Scholtz

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## List of abbreviations

<b>Abbreviation</b>	
ADG	Average daily gain
AF	Afrikaner
AN	Angus
ARC-AP	Agricultural Research Council – Animal Production
BN	Bonsmara
DFI	Daily feed intake
FCR	Feed conversion ratio
GxE	Genotype by environment interaction
IPW	In-Pen-Weigh-Point
NG	Nguni
PBW	Partial body weight
RFI	Residual feed intake
SE	Standard error
SM	Simmentaler
THI	Temperature humidity index

## DECLARATION

I, Georgette Mareé Pyoos, declare that this thesis submitted for the fulfilment for the degree: Doctor of Philosophy, Animal Science at the University of the Free State titled “Breed genetic and heterosis effects on variability of growth and efficiency traits in beef cattle” is my own work. I furthermore declare that this thesis has not been submitted before for any other degree or examination at any other university. I also declare that all sources I have used or quoted have been indicated and acknowledged by complete references.



Signed \_\_\_\_\_

Georgette Mareé Pyoos

15 March 2024

Date

Student number: 2017147766

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## ABSTRACT

The first goal of this investigation was to characterize breed genetic effects for indigenous and exotic breeds of beef cattle under South African conditions. A second goal was to characterize within animal daily variation in partial body weight and feed intake during the postweaning period. It is intended that these characterizations will lead to better choices among breed resources, particularly for emerging farmers. Thus, a crossbreeding trial was conducted in South Africa, Northern Cape, over a period of eight years from 2015 until 2022. Afrikaner, Bonsmara and Nguni dams were mated with Afrikaner, Bonsmara, Nguni, Angus, and Simmentaler sires. Data were collected according to the National Beef Recording and Improvement Scheme in South Africa. There were 212, 324, 303, 179 and 234 calves sired by Afrikaner, Nguni, Bonsmara, Angus and Simmentaler sires, respectively. There were 182, 633 and 437 calves produced by Afrikaner, Nguni and Bonsmara cows, respectively. Birth and 205-day weights were analyzed including effects of year, sex, age of dam, the genetic expectation for breed group, and the interactions of year with the breed direct and maternal effects and individual heterosis. The probability levels (P-values) for the interaction of the genetic effects and year indicate plasticity with respect to the inter-year environment. Plasticity is defined as deviations in an individual's phenotype in reaction to environmental fluctuations. The P-values for birth weight interactions of Afrikaner, Angus, Nguni and Simmentaler direct effects with year were 0.06, 0.09, 0.01, and  $< 0.01$ , respectively. The corresponding P-values for 205-day weight were 0.69, 0.03, 0.15, and 0.10. Thus, birth weight appeared to be more plastic, i.e., more sensitive to the variation among years, than was 205-day weight. The temperature-humidity index during the study period varied between 78.5 and 81.6. Previous studies indicate that heat stress is induced if temperature humidity index  $\geq 72$  and thus the preweaning environment was very harsh. After weaning, the male calves were transported from Vaalharts to Irene in groups of 25-28 according to their weight. Upon arrival, the animals were given a 2-week adaptation period and were then allocated to pens in the GrowSafe system according to their body weight. This system of allocation resulted in the partial confounding of breed groups, contemporary groups, and the days on feed. The data were analysed with linear models that included the categorical effects of test group and breed group and the continuous effect of days on test. Breed group effects on daily feed intake and partial body weight were not detected ( $P > 0.05$ ). As expected, the animals ate more and became heavier as the test progressed ( $P < 0.05$ ). The breed groups differed in their growth rate as evidenced by the significant interaction between the breed group effect and the linear effect of days on test for partial body weight. However, the rate at which animals increased their daily feed intake was invariant to their genotype. In partitioning the interaction of breed group with days on test into

single degree of freedom effects, only the effect of individual heterosis on partial body weight ( $0.99 \pm 0.35$  kg/day) was significant ( $P < 0.01$ ).

Adding the binary indicator of heat stress to the linear model indicated highly significant effects on both daily feed intake ( $-9.69 \pm 1.31$  g/day) and partial body weight ( $48.2 \pm 2.1$  g/day). Animals that were heavier consumed more feed ( $37.7 \pm 4.8$  g/day;  $P < 0.01$ ) and animals that consumed more feed were heavier ( $57.1 \pm 9.3$  g/kg;  $P < 0.01$ ) as this is expected. Estimates of the serial correlations of daily feed intake and partial body weight were calculated for each animal. These correlations were transformed to z-statistics before being analysed further. Average estimates for the z-transformed serial correlation of daily feed intake and partial body weight for each animal were 0.1003 and 3.0506, respectively. The 95% confidence interval for daily feed intake was  $0.095 < z < 0.106$ ; and for partial body weight it was  $3.041 < z < 3.061$ . However, it does not appear these differences are related to the breed composition of the animals. The high degree of between-animal variation in the estimate of the serial correlation indicates animals differ markedly for feed they consume from day-to-day. In contrast, the estimates of serial correlation of partial body weights were very high and consistent across animals. Thus, there is little need to average values over days to achieve an accurate estimate of partial body weight at any specific point in time. An evaluation of postweaning feed intake that was conducted over a 36-day period would, on average, produce an accuracy of the daily feed intake mean for an individual animal of 0.80. The inter-day variance in feed intake served as a metric for the evaluation of plasticity. These data were analyzed using Friedman's test based on a non-parametric two-way analysis of variance. The breed groups differ significantly in their plasticity of feed intake. Linear functions of the breed group effects indicated that the Nguni, Simmentaler, Afrikaner, and Angus breed direct effects were more variable over time than was the Bonsmara direct effect. The estimated heterosis effect was small and not significant indicating that crossbred cattle would be no more variable over time in feed intake than their straightbred counterparts. Some commercial producers and probably all subsistence producers might choose a less plastic and more robust set of breed resources, which may perform well, regardless of the current environment. However, resource-rich commercial producers might prefer to utilize more plastic breed resources to capitalize on times when the environment is favorable and mitigate less favorable times.

Key words:

Environment, Plasticity, Crossbreeding, Beef, Cattle, Feed, Partial body weight, Serial correlation, Breed additive, Heterosis

# CHAPTER 1

## Research Objectives

The optimal use of breed resources provides a means for beef producers to address concerns about environmental variability that have recently come to the forefront (Tedeschi and Beauchemin, 2023). Unfortunately, until the work of Pyoos et al. (2020; 2022) there has not been a properly designed experiment comparing breed resources and estimating heterosis effects conducted in South Africa since the time of Els (1988). Furthermore, the indigenous breeds of South Africa have not been evaluated in studies of breed difference that have also been done internationally.

The studies reported herein follow on from previous experimentation, which evaluated crossbreeding effects on the component traits of cow efficiency in the indigenous Afrikaner, Bonsmara and Nguni breeds, which were crosses with each other in all possible combinations, as well as, with the Angus and Simmentaler used as specialized sire lines (Pyoos, 2018).

The study may supply baseline information, which can be used in the evaluation of the efficacy of the present crossbreeding systems in South Africa. It also supplied information that can be used to develop breeding objectives and to validate results of simulation studies on crossbreeding in the South African context.

During postweaning, feed intake and growth are traits of substantial interest. There are several reports in the scientific literature that use technology to capture daily feed intake and summarize its relationship with weight gain over a test period (e.g., Mononen et al., 2022; Kenny et al., 2018). Certainly, this relationship is important to the efficiency of a cattle-feeding enterprise. However, few if any of these reports have been directly concerned with the variability of feed intake from day to day over the test period.

Herein, animals whose phenotype varies more from day to day are said to be more plastic (i.e., environmentally sensitive) and conversely animals whose phenotype varies less from day to day are said to be more robust (i.e., environmentally insensitive).

## **Aim**

This study aims to:

- i. Estimate the plasticity of breed genetic and heterosis effects on birth and 205-day weights of straightbred and crossbred beef calves reared at the Vaalharts Research Centre.
- ii. Estimate breed genetic and heterosis effects on daily feed intake (DFI) and partial body weight (PBW) of individual beef bulls fed at the ARC Bull Testing Centre in Irene.
- iii. Estimate effects of the average daily temperature humidity index on DFI and PBW.
- iv. Estimate the serial correlation (lagged 1 day) for DFI and PBW records of individually fed beef bulls.

## CHAPTER 2

### Literature review

#### 2.1 Introduction

Consumption of feed is essential for the maintenance of life as well as the general productive processes of agriculture. Predicted increases in the human population throughout developing countries and restricted availability of land for increased food production suggest that agricultural production needs to intensify substantially, to satisfy higher demands for food (Teferedegne et al., 2000). Hence, feed intake is a vital part in livestock production systems.

It is imperative to provide producers with information on the genetic basis for economically relevant traits and to the extent that feed costs money, feed intake is an economically relevant trait (Nielsen et al., 2013). Other measures of efficiency derived from feed intake and body weight, provide no further information beyond that compiled in the traits used in their calculation (Kennedy et al., 1993). In this study the analysis of feed intake was carried out between individual animals with simultaneous consideration of the contemporary groups in which they reside to adjust for differing environmental effects (BIF, 2010). It is possible for the contemporary groups to differ in both their mean and variance (VanVleck, 1986; Menezes et al., 2022). Within contemporary groups, the variance of feed intake may be altered because of differing environmental conditions with the genetic variance of feed intake increasing as the environment improves (Silva Neto et al., 2023). Furthermore, Silva Neto et al. (2023) showed the potential for sires to re-rank for their feed intake estimated breeding value as a function of the environmental conditions.

This re-ranking of sires for predicted genetic merit is one form of a genotype by environment interaction (GxE). Diverse genotypes of cattle that produce greater variations in adaptive and productive features allow for matching specific genotypes to the environments in which they are expected to produce (Burrow, 2012). Crossbreeding in beef cattle facilitates the use of breed complementarity and heterosis (Garrick, 2006). This technology may see greater implementation in developing countries as climatic conditions become more adverse especially in the Southern Hemisphere (Anitei, 2006; Appel, 2006; Romanini et al., 2008). Crossbreeding has also been used to counteract genotype x environmental interaction under varying environmental conditions taking advantage of heterosis that is usually higher in extreme environments (Bourdon, 1997; Scholtz et

al., 2013). In order to adapt to new or changing environmental conditions, Marai (2007) stated that animals might also change their physiology and behaviour.

This ability of a genotype to produce different phenotypes, depending on environmental conditions is defined as phenotypic plasticity (Alford et al., 2006). Essential to the way in which animals cope with environmental variation, phenotypic plasticity includes morphological, physiological, behavioural and/or phonological changes. These changes may be temporary or permanent (Rovelli et al., 2020).

As interest in sensory systems for monitoring livestock species intensifies, the study of feeding behaviours and their potential application in livestock husbandry continues to grow (Kelly et al., 2021). Enhancing production-system efficiency is vital to the consistent generation of capital and sustainability of beef production. As stated by Nielsen et al. (2013), significant results come from increasing rate of production, reducing per diem costs in terms of maintenance, as well as enhancing reproduction and minimizing losses from feeding nonproductive females. However, because variation exists between animals in utilization of feed energy further improvement is possible through appropriate consideration of feed intake. A number of studies in swine (Young and Lawrence, 1994; Quiniou et al., 2000), poultry (Meunier-Salaün and Faure, 1984; Collins and Sumpter, 2007), cattle (Ingrand, 2000), and sheep (Behrendt et al., 2021) have evaluated the feeding behaviour across time. Thus, there have been numerous studies on the role of feeding behaviour in the control of voluntary feed intake in animals (Forbes, 2007).

The contribution of genetic variability to differences among animals in feeding behaviour and its potential use in the selection of farm animal species are also gaining in popularity (Labroue et al., 1997; Olson et al., 2020). Numerous feeding behaviour traits are documented to be mildly heritable in various beef breeds (Robinson and Oddy, 2004; Nkrumah et al., 2007; Durunna et al., 2013; Chen et al., 2014; Olson et al., 2020).

Due to the cost and difficulty of measuring DFI by individual animals, this important economically relevant trait remains less well studied than output traits such as body weight. However, recent technological developments facilitate more in-depth study of DFI than was previously feasible. One such technology is the GrowSafe beef System (Vytelle Inc., Lenexa, Kansas, USA) that can record DFI and PBW of growing beef cattle. The GrowSafe beef System captures these data in real-time from equipment that has been installed at commercial and academic facilities internationally.

Through internet-based technology, the data is subject to quality control and stored by the industry service provider.

## **2.2 Crossbreeding in cattle production**

No single pure cattle breed outrivals in every extent that influences profitability or “is best in all environments” (Burrow, 2006). It is imperative for cattle breeders to augment economically vital traits while attempting to decrease expenditures of production in their corresponding environments. This may be accomplished by relating genetic principles of selection and crossbreeding. Selection is an admirable tool particularly with traits of moderate to greater heritability i.e. growth rates and carcass traits. However, a few vital traits associated with beef production, i.e. reproductive rate, and calf survival, are of lower heritability.

Ultimately, the successes of selection programs for these lowly heritable traits are limited, but genetic progress may be improved faster with crossbreeding. Crossbreeding is one of the primordial and most essential principles of lowering costs and augmenting productivity (Miller, 2010). Breeding indigenous cows to terminal sire lines may facilitate production of calves in the emerging sector that meet more substantial commercial feedlot requirements. In this regard, MacNeil and Matjuda (2007) developed an aggregated simulation model that is reliant on user inputs for the phenotypic characterization of the germplasm and the economic characterization of the production environment to optimize breeding objectives. Khorshidi et al. (2017) carried out a simulation study with the Afrikaner as dam and Charolais as sire, using the Vaalharts data (Theunissen et al., 2014a) and reported a 27% increase in the volume of meat produced by crossbred calves. Moreover, these calves consumed 27% less feed between weaning and harvest than straight bred Afrikaner calves.

In contrast, Pyoos et al. (2020) showed relatively small genetic effects in crossbreeding systems at the Vaalharts Research Station where Afrikaner, Bonsmara and Nguni dams were mated with Afrikaner, Bonsmara, Nguni, Angus and Simmentaler sires. In this study the pure breeding system was the least efficient, followed by a crisscross system with a +2% increase, and terminal sire systems using the Simmentaler (+4%), or Angus (+8%). Despite the relatively small magnitude of the genetic effects, the advantages of crossbreeding systems were still evident.

Dickerson (1969, 1973) generated models for breed-specific genetic effects, known as crossbreeding parameters, which describe variation among a wider variety of breed crosses. Robison et al. (1981)

and MacNeil et al. (1982) first utilised multiple regression models in to quantify these effects in analyses of crossbreeding experiments and field data, respectively. When partitioning the phenotypic values of an F<sub>1</sub> crossbred animal into its crossbreeding parameters, presuming that there are no epistatic effects (between-locus interactions) and no interactions among the effects (constraints), the model can be written as follows:

$$P_{X(AB)} = \frac{1}{2}g_A^I + \frac{1}{2}g_B^I + g_B^M + h_{AB}^I + e$$

Where:  $P_{X(AB)}$  = the phenotypic value of individual X, that is sired by breed A and out of a breed B dam;

$g_A^I$  and  $g_B^I$  = the *direct* (additive genetic) *effects* of breeds A and B, respectively;

$g_B^M$  = *maternal* additive effect of the breed B dam, which provides an environment for her offspring;

$h_{AB}^I$  = the *individual heterosis* effect which is expressed in AB crossbred progenies; and

$e$  = the temporal environmental effect to which the calf is subjected.

In the case of a three-breed cross (e.g. sire breed C mated to an AB crossbred dam) the above-mentioned model can be expanded to incorporate an additional parameter, namely the maternal heterosis effect ( $h_{AB}^M$ ), due to the dam being a F<sub>1</sub> cross. The model then becomes:

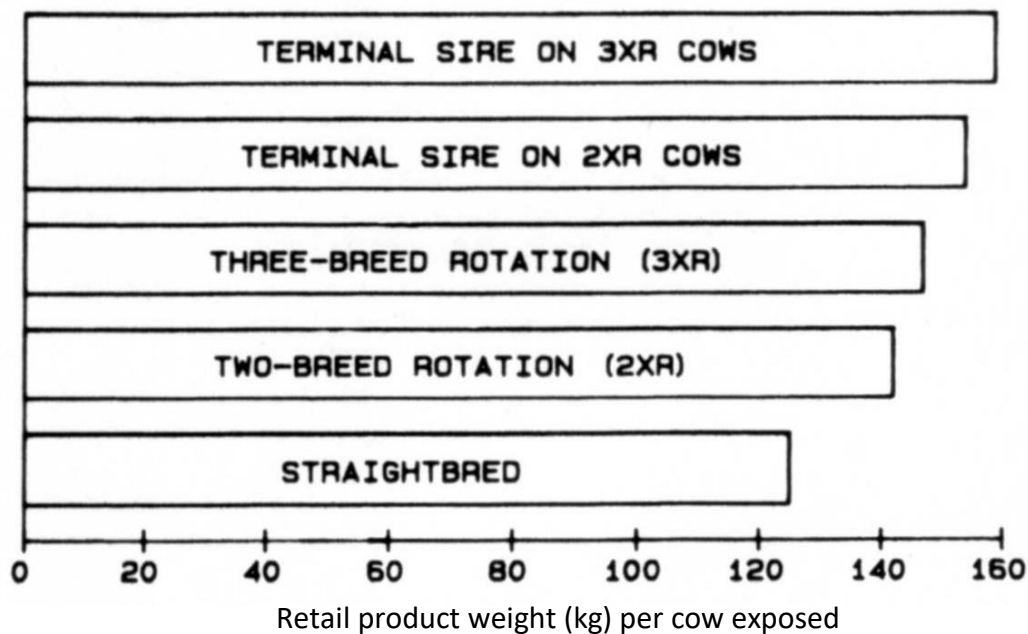
$$P_{X(C,AB)} = \underbrace{\left( \frac{1}{4}g_A^I + \frac{1}{4}g_B^I + \frac{1}{2}g_C^I \right)}_{\text{direct effects}} + \underbrace{\left( \frac{1}{2}g_A^M + \frac{1}{2}g_B^M \right)}_{\text{maternal effects}} + \underbrace{\left( \frac{1}{2}h_{AC}^I + \frac{1}{2}h_{BC}^I \right)}_{\text{individual and maternal heterosis effects}} + \underbrace{h_{AB}^M}_{\text{maternal heterosis effect}} + e$$

The objective of applying an effective crossbreeding system would be to optimize these effects (Kinghorn, 1980, 1982; MacNeil, 1988). The quantities  $g^I$  and  $g^M$  provide a suitable basis for evaluating genetic gain in crossbreeding systems between breeds A, B and C; since according to additive genetic theory, the predicted performance of such crossbreds will be proportional to breed contributions. Heterosis and complementarity also provides additional “gains” in crossbreeding and may in part offset inequalities in the additive genetic effects.

Various performance traits of crossbred animals may be predicted based on estimates of the genetic variability of the parent breeds (e.g., Theunissen, 2011; Theunissen et al., 2014a). The availability of

individual breed direct- and maternal heterosis is also of great importance. In order to supply the necessary information on heterosis, crossbreeding studies should be carried out.

The conceivable cause of most heterosis is due to the interaction of genes at individual loci from diverse breeds, concealing the effects of the ones that are inferior. Two- and three-breed rotational crosses have produced 18 and 23% increases in weaning weight per cow exposed relative to the component straightbred contemporary calves (MacNeil et al., 1988). In that study, similar advantages were maintained after weaning with straightbred calves being 9% lighter after 253 days in the feedlot, and their weights of carcass and boneless retail product being 8-9% and 6-7% lighter, respectively, than their crossbred contemporaries. Illustrated in **Figure 2.1** shows the effects of various crossbreeding systems on retail product produced per cow exposed for breeding. Additionally, the advantages of these crossbreeding systems do not include added benefit from selection within breed.



**Figure 2.1** Effects of five systems of mating on the weight of boneless retail product produced per cow exposed for breeding, taken from MacNeil et al. (1988)

Theunissen et al. (2014a,b) evaluated data from the thesis of Els (1988) for weight traits of 24 crossbred and five purebred groups of beef cattle that were raised at the Vaalharts Research Station with the objective of estimating breed additive and heterosis effects. In this study, purebred AF, Brahman, Charolais, Hereford and Simmentaler were produced. In addition, Brahman, Charolais, Hereford and Simmentaler sires produced topcross progenies from Afrikaner dams with the F<sub>1</sub> females then producing backcross and three-breed cross progenies. On average, both direct and

maternal heterosis effects were positive for all of the traits. Maternal heterosis effects for birth weight, 17-month weight, and cow weight were less than the corresponding estimates of direct heterosis. Only for weaning weight were the direct and maternal heterosis effects approximately equal.

The average effect of direct heterosis on birth weight, weaning weight, 19-month heifer weight and cow weight at partus were 1.2, 14.7, 24.9 and 19.1 kg, respectively. The predicted average weaning weights from Simmentaler x Afrikaner and Charolais x Afrikaner dams (233.3 and 230.7 kg, respectively) were greater than the predicted weaning weights from straightbred Afrikaner, Brahman x Afrikaner and Hereford x Afrikaner dams (207.4, 219.9 and 213.9 kg, respectively) (Theunissen et al., 2014a). Moreover, average direct heterosis was 17.9% for postweaning average daily gain (ADG), being the greatest in the crosses with Brahman (Theunissen et al., 2014b). The maternal heterosis effect was smaller. Both average direct and maternal heterosis effects on DFI were essentially nil.

In a more recent crossbreeding study, also conducted at Vaalharts, breed-specific genetic effects on cow efficiency and its component traits were evaluated for a three-breed diallel of Afrikaner, Bonsmara and Nguni with these breeds also joined with Angus and the Simmentaler as specialized sire lines (Pyoos et al., 2022). An undesirable impact of the hot and dry 2015/2016 summer season on the performance of all genotypes, except those sired by Afrikaner, was observed. Topcross calves from Nguni dams had lower birth weight but were similar in preweaning performance to topcross calves out of Bonsmara or Afrikaner dams.

Extensive production systems dominate cattle production in South Africa. More than 80% of all beef cattle slaughtered in the formal sector in South Africa originate from commercial feedlots. A total of 67% of feedlot animals are crossbreds, indicating that crossbreeding is playing a significant role in the commercial beef industry in South Africa. Commercial farmers mostly find formal markets for their calf crops in the large feedlot sector in South Africa (80% of cattle are finished through feedlots) (RMRD, 2010). However, only 5% of the beef cattle from subsistence farmers go through formal marketing channels. One of many reasons is that current animals from the subsistence sector do not meet the requirements of the feedlots. This market requires animals that are fast growing and efficient converters of high-quality feed and possess superior carcass attributes (RMRD, 2010).

In its comprehensive agricultural development program, the South African government lists the development of feedlots and market access for emerging and communal beef cattle farmers as a means to make significant contributions towards poverty alleviation and economic development in the rural areas (RMRD, 2010).

### **2.3 Genotype by environment interaction**

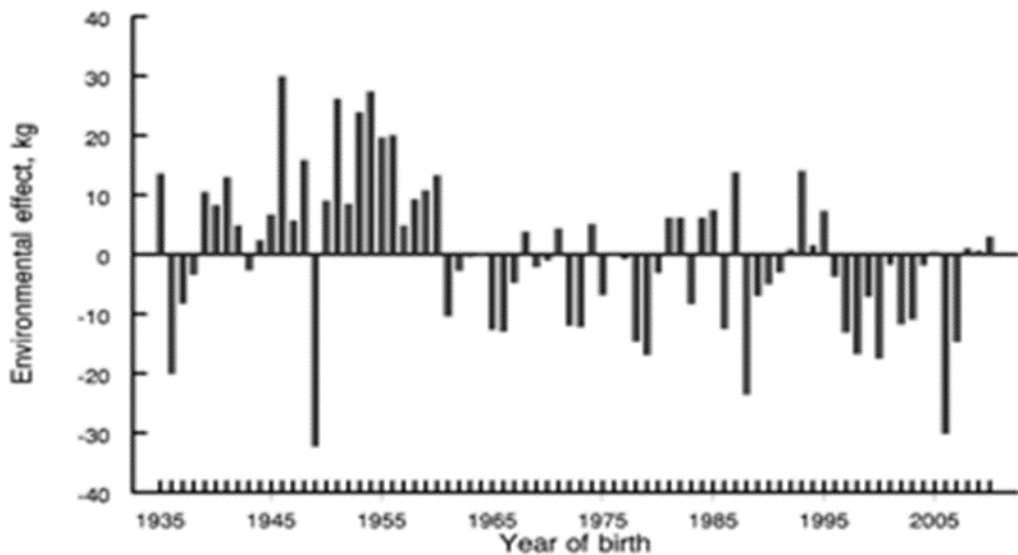
The resistance of unimproved (breed not selected based on merit) and their composites to environmental challenges make them suitable for use in harsh environments. In comparison to other livestock, sheep are moderately resilient as far as heat stress is concerned (Cloete et al., 2023). In a review on the status and utility of indigenous genetic resources, Molotsi et al. (2020) recorded tolerance to heat stress as one of the benefits of unimproved, indigenous breeds such as the Namaqua Afrikaner. Moreover, this claim was supported by results from Cloete et al. (2021), demonstrating that the respiration rate of Namaqua Afrikaners increased by 84% from cool morning temperatures of 18.9°C to hotter afternoons of 30.2°C. Breeds from temperate areas rely on higher respiration rate to maintain core temperatures. If heat stress circumstances prevail, the additional needs (such as feed intake) to offset the stress could contest with energy essential for other production purposes.

Genotype by environment interaction exists when the differences among genetic resources (e.g. breeds or sires) are a function of the environment in which they are measured. “They are important to the extent that use of the best combination of genotype and environment would permit more efficient animal production” (Dickerson, 1962). At the national level, G×E interactions occur and can be assessed by adding an interaction term to the customary quantitative genetic model (Kearney et al., 2004). For example, a random regression mixed linear model may include a reaction norm based on an environmental variable defining a factor such as climate or herd management (Fikse et al., 2003). In this way, the phenotype that results from a genetic component varies according to the local environmental circumstances (Huquet et al., 2012). Ducrocq et al. (2022) compared the modelling of G×E in genetic evaluation considering two approaches: a multiple trait model in which phenotypes that were collected in different regions were considered as separate traits and a random regression approach using long-term averages of climatic variables at the herd level in a reaction norm model. In the former approach, the estimated genetic correlation indicates the magnitude of the interaction (Falconer, 1952; Yamada, 1962).

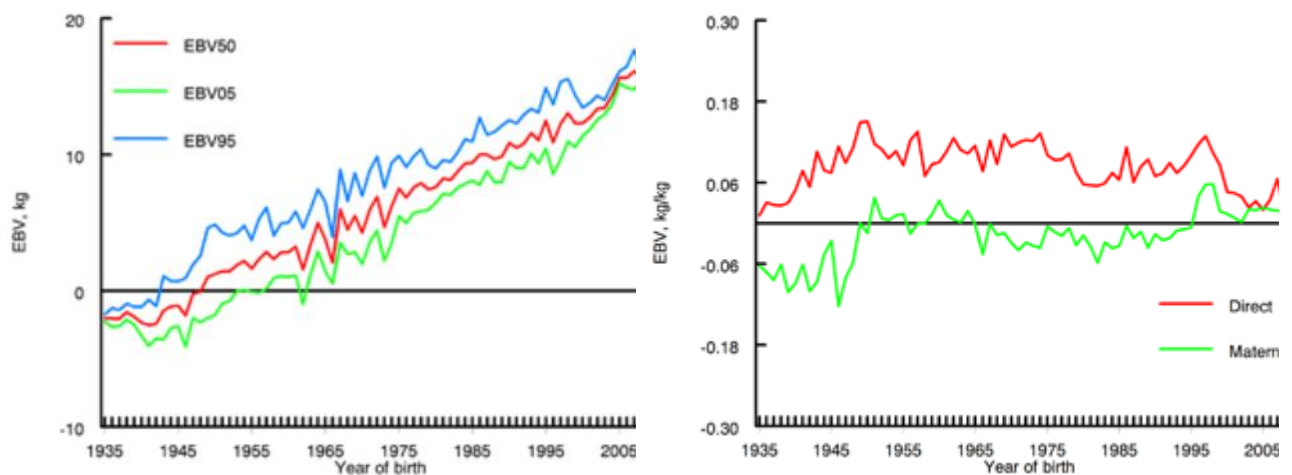
In the latter approach, the genetic effects are modelled as continuous functions of the environmental variable with the slope of the regression indicating the magnitude of the interaction (Cardoso and Tempelman, 2012; Ducrocq et al., 2022).

Numerous studies have undertaken the inspection of possible interactions between genotype and environment by measuring a change in magnitude or a change or rank of genotypes under different environments (Thrift et al., 2000; Montaldo, 2001). For example, a study by Burns et al. (1979) measured line by location interactions in two phases. The first phase used two unrelated lines of Hereford cattle, one of which was established in Montana (MT) and the other in Florida (FL) (M1 and F6, respectively). Birth weights differed significantly between M1 in MT, F6 in MT, M1 in FL, and F6 in FL ( $36.8 \pm 0.17$ ,  $35.0 \pm 0.22$ ,  $29.0 \pm 0.19$ , and  $29.8 \pm 0.27$ , respectively). The second phase included two related lines, M1 and F4, where F4 was established in Florida, however derived from M1 lineage. Lines M1 and F4 varied in performance in a similar manner as was observed in phase one (Burns et al., 1979). Notter et al. (1992) also observed that it might be essential to account for sire  $\times$  herd interaction effects on weaning weight in national cattle evaluations. When the variance due to maternal genetic effects was included in the phenotypic variance, the sire  $\times$  herd interaction component of variance was reduced to 3.3% of phenotypic variance.

MacNeil et al. (2017) examined the relationship of inter-annual environmental variation in effects on gain from birth to weaning on the expression of genetic effects in Line 1 Hereford cattle illustrated in **Figure 2.2**. The environmental variation affected both the direct genetic effects (left panel) and then environmental sensitivity of the direct and maternal genetic effects (right panel) on preweaning gain as illustrated in **Figure 2.3**. These studies provide additional incentive for investigating the potential need for beef production systems to recognize the potential genotype  $\times$  environment interaction. It has been suggested that it is paramount to indicate the best environment for the animals (Santana et al., 2012) and conversely what animal should be selected for in each environment (de Jong and Bijma, 2002).



**Figure 2.2** Inter-annual environmental effects on gain from birth to weaning for Line 1 Hereford calves that were born between 1935 and 2011, taken from MacNeil et al. (2017)



**Figure 2.3** Genetic trends in direct additive effects on preweaning gain as a function of the level of the environmental year effect wherein EBV50 indicates the mean year effect, EBV05 indicates the fifth percentile year effect, and EBV95 indicates the 95th percentile year; and the genetic trends in environmental sensitivity of the direct and maternal genetic effects on preweaning gain, taken from MacNeil et al. (2017)

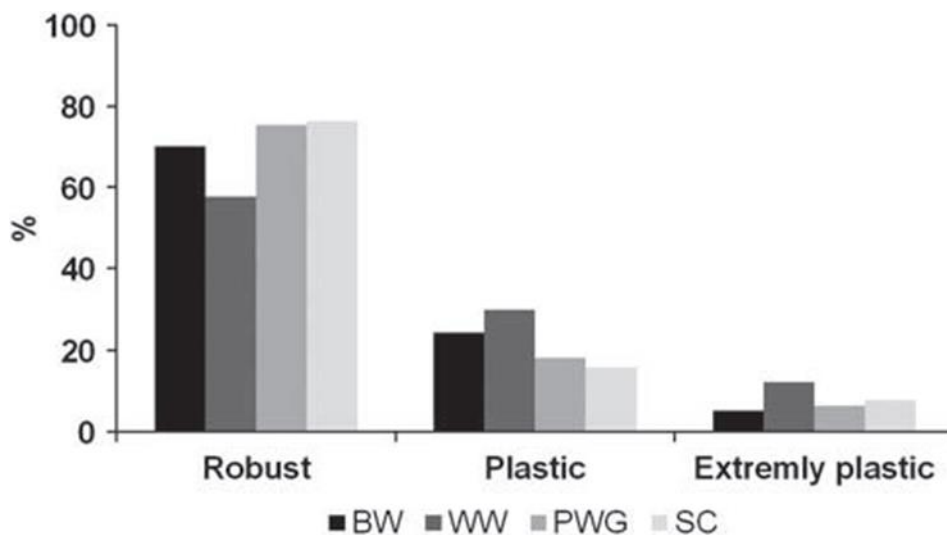
## 2.4 Plasticity

Phenotypic plasticity allows a particular genotype to develop systematically different phenotypes in different environments. Thus, the term plasticity is used to describe all phenotypic responses to environmental change (Kelly et al., 2021). Phenotypic plasticity confers a fitness advantage to an organism by tailoring its phenotype to the environmental circumstances in which it resides (Kingma et al., 2020).

Genotypes that exhibit highly variable phenotypes across environments are 'plastic', whereas genotypes that show little variability across environments are 'robust' (de Jong and Bijma, 2002). Plasticity in beef cattle production is important because it allows producers to raise cattle of a similar genotype in a variety of environments and achieve good productivity. It is also important for the sustainability of beef production, as it also allows cattle to adapt to changing environmental conditions (Santana et al., 2012) including climate change (Rovelli et al., 2020).

Quoting from Bateson and Gluckman (2012) "The size of unborn offspring is influenced by the nutritional and other physiological conditions, such as parity, of the mother. When the fetus responds to an adverse environment by reducing its growth, it makes an adaptive trade-off. It increases the likelihood of immediate survival even though the risk of a shorter life is enhanced by being born small. Nevertheless, the potential exists for the offspring to survive and reproduce as opposed to a greater likelihood of intrauterine death." While Bateson and Gluckman (2012) were addressing human physiology, parallel observations may be made with respect to cattle.

Certainly, parity of the dam affects birth weight of her progeny (Tong, 1983; Rumph and Van Vleck, 2004). In cattle, more emphasis has been put on the consequences of overly large calves experiencing dystocia (Nix et al., 1998). However, calves that are small relative to the size of their dams may be also prone to an increased risk of mortality (Johanson and Berger, 2003). Hay and Roberts (2018) assessed the performance of calves produced by dams that had their energy intake restricted during gestation with those whose dams were managed conventionally. They observed the across environment genetic correlation of ADG indicated a GxE that might have been mediated via fetal programming. The processes of plasticity that are elicited by those conditions normally provide useful adaptations to the environment (Bateson, 2007). For example, calves born to dams in harsher environments may be able to adapt better to a similar environment, rather than to a relatively lush circumstance. Conversely, the genetic variation that exists in the response of animals to the environment could be used to select animals that are robust against environmental changes (Hay and Roberts, 2018). Illustrated in **Figure 2.4** is the distribution of robust and plastic animals for birth weight, weaning weight, postweaning gain and scrotal circumference in a composite population of beef cattle (Santana et al., 2012). It is notable that robust animals were more common than plastic ones. The degree to which beef cattle alter their behavior in response to short-term perturbations in the environment during the postweaning period remains poorly understood.



**Figure 2.4 Percentages of robust, plastic and extremely plastic animals for birth weight (BW), weaning weight (WW), postweaning gain (PWG) and scrotal circumference (SC) in a composite beef cattle population, taken from Santana et al. (2012)**

Several genetic models have been used to explain the genetic basis of plasticity. In a simple case, plasticity might be generated by differential expression of either of two alleles at one locus (Des Marais and Juenger, 2010; Moulherat et al., 2017). Not surprisingly, evolution in a fluctuating environment results in phenotypic plasticity. However, evolution in a constant environment can also lead to phenotypic plasticity due to a pleiotropic coupling of different traits (Moulherat et al., 2017). Plasticity may also be due to epistatic interactions between genes determining the degree of response to environmental influences (Remold and Lenski 2004). It is less likely that environmentally induced mutation leads to plasticity because mutations are infrequent and generally harmful (Krašovec et al., 2014). Phenotypic plasticity designates the alteration within a population of inheritable appearances across generations, thus it is important for its effects on existing geocentric evolutionary theory (Wess, 2003). Thanks to the phenotypic plasticity, the environment appears to play a double role in creating phenotypic variation and enabling selection between the diverse variants within a population (Mohn and Dirk, 2009).

In population genetic studies, phenotypic variance can be used as a measurement of phenotypic plasticity (VandeHaar et al., 2016). Several statistical models for phenotypic plasticity have been considered in animal breeding: 1) the reaction norms or random regression model; 2) the character state or multi-trait model; and 3) the infinite-dimensional or covariance-function model.

These models differ in the way phenotypic plasticity is dissected into quantitative traits, but all of them are based on the general expressions for the change in mean value of a quantitative trait undergoing simultaneous selection (VandeHaar et al., 2016).

The measure of phenotypic plasticity may be used to select animals for robustness or can be used in breeding programmes that produce genetic material for a multiple of production environments (De Jong and Bijma, 2002). Climate change has the potential to affect livestock adversely. Heat stress has been reported to be economically detrimental to the livestock industry (Scholtz et al., 2010a). However, selection and experimental evolution approaches have shown that plasticity can be altered genetically, furthermore various crosses among breeds of beef cattle allow for different genetic reactions to adverse environments (Santana et al. 2013). A few studies document variability in heritability estimates for postweaning performance in beef cattle over an environmental gradient, with the general observation of a greater proportion of phenotypic variation being due to genetic influences occurs in more favourable environments (Cardoso et al., 2011; Mattar et al., 2011; MacNeil et al., 2017).

As stated by de Jong and Bijma (2002), phenotypic plasticity must be highly considered in the selection of livestock because it affords the opportunity to embrace the environment in line with a specific breeding goal. According to Stearns (1989), populations of plastic animals may shift their genetic makeup in accordance with the environment which they inhabit.

Genotypes that are more plastic may thrive under changing environmental conditions, whereas their less plastic counterparts may be unable to endure under adverse conditions (Santana et al., 2013) environment. Charmantier et al. (2008) and Noonan et al. (2018) have shown the ability of animals to adapt rapidly in a changing environment. However, response to environmental changes due to the inherent plasticity of animals is not necessarily favorably adaptive and may have adverse impacts on fitness (Hale et al., 2016; Velotta and Cheviron, 2018). Furthermore, natural selection may not yield change quick enough to mitigate the impacts of adverse climates (Rovelli et al., 2020). Therefore, new breeding objectives and criteria for breed selection should be developed for livestock species in order to use their potential plasticity; especially for ruminant animals with a long generation interval (Rovelli et al., 2020).

## 2.5 Feed intake

There are numerous research studies currently on-going that are directed towards genetic improvement in overall beef cattle production efficiency in order to decrease production costs and improve profitability of beef production (Burns et al., 2010). Feed intake, a component of efficiency, may be incorporated directly into genetic evaluations as an economically important trait. Genetic parameter estimates for DFI provide the basic information required to develop selection strategies and to predict rates of direct and correlated responses to selection (Nkrumah et al., 2007). Feed efficiency has a significant effect on the unit cost of production, and thus on the affordability of meat products in both domestic and international markets. In beef production, only 5% of the total life cycle dietary energy ingestion is used for protein deposition, whereas pork and poultry are more energetically efficient at 14 and 22%, respectively (Ritchie, 2000).

Major reasons for the inadequacy of beef production systems comprise the relatively low and slow reproductive rates of cattle and the high energetic cost of maintaining them. About 70–75% of the total dietary energy cost in beef production is used for maintenance, including maintenance of the breeding female (Ferrell and Jenkins, 1985). Maintenance requirements of cattle are moderately to highly heritable ( $h^2 = 0.22\text{--}0.71$ ) (Carstens et al., 1989; Bishop, 1992). Thus, there exists a prospect to select for cattle that are more efficient. Selection for lower maintenance requirements is challenging. Measures of feed efficiency, such as feed to gain ratio, are associated to measures of body size, growth rate, and composition of gain as well as appetite (Arthur et al., 2001). An important component of feed efficiency for growing beef cattle is ADG (Nielsen et al., 2013). The mathematical associations among traits causative to efficiency suggest that for a pair of calves with the same initial body weight, the one with a faster ADG will attain a target market weight with less days on feed. Moreover, these animals will be more efficient due to the allocation of less feed to maintenance. Byerly (1941) first found variation in feed intake independent of body weight and level of production.

Today residual feed intake (RFI) is commonly adopted as the appropriate measure of feed efficiency. While also considering RFI, Koch et al. (1963) recommended the use of gain adjusted for feed intake as the preferred measure of biological efficiency because it was considered the most accurate mathematical description of cause and effect. Various measures of feed efficiency, including RFI, appear to be moderately heritable ( $h^2 = 0.29\text{--}0.46$ ), suggesting the potential for its improvement (Archer et al., 1998; Arthur et al., 2001). Few adverse correlated responses to selection for reduced

RFI have been identified, though a single generation of selection for RFI was related with reduced carcass fat content (Richardson et al., 2001).

The time spent eating, and the pattern of meals, is another aspect of beef production systems that may impact total daily intake of dairy cattle (Grant and Albright, 2000). Thus, recent research in dairy nutrition and management has concentrated not only on variations in intake, but also on variations in feeding behaviour. Estimates of genetic correlations between feed behaviour/intake and both performance as well as feed efficiency traits in cattle suffer from a general lack of precision and have large standard errors. Genetic correlations varying from  $0.03 \pm 0.13$  (Robinson and Oddy, 2004) to  $0.56 \pm 0.20$  (Nkrumah et al., 2007) have been reported between DFI and feeding times per day. In a population of 1,394 crossbred replacement beef females fed a roughage-based diet, Olson et al. (2020) determined heritability estimates ( $\pm$  SE) of  $0.25 \pm 0.05$  and  $0.26 \pm 0.06$  for the time spent feeding per day, and the number of feeding events per day, respectively. Estimated genetic correlations between feeding behaviour, performance and feed efficiency metrics also may differ in magnitude and direction among breeds.

Perhaps differences in feeding behaviour are of direct economic value or can be considered as indicator traits in these evaluations. The feeding behaviour of individual animals is generally consistent and repeatable and may be used to predict differences in animal performance and efficiency (Gibb et al., 1998; Oddy and Herd, 2001). Several reports relate animal feeding behaviour to health (Sowell et al., 1998), feed conversion ratio (FCR) and performance (Schwartzkopf-Genswein et al., 2003; Robinson and Oddy, 2004; Cammack et al., 2005).

Variation in the efficiency of growth may be also due to alterations in composition of live weight gain (Ferrell and Jenkins, 1998). For example, differences in rates of water and protein accretion have an influence on rate and efficiency of body weight gain, primarily because of the lower energy content of water and protein relative to fat. Genotype may have a significant influence on rate of growth, feed efficiency, and body composition. Many studies investigating breed differences have been conducted utilizing *Bos taurus* cattle. However, *Bos indicus* and other tropically adapted genotypes of cattle have received less research attention regarding variation in the efficiency of growth. Scholtz and Theunissen (2010) indicated that, on an age or weight-constant basis, cattle with a larger mature size, grow faster, have a decreased FCR, and vary in body composition.

When investigated on a fat constant basis or energetic efficiency basis, those advantages are generally not evident (Ferrell and Jenkins 1998). Thus, variation in feed efficiency may be explained by increased maintenance costs in cattle that have higher growth rates or larger mature size.

Studies in South Africa relating to the variation in feed efficiency, such as MacNeil et al. (2019), indicated that various metrics have been used as measures of efficiency. These include FCR, which Armsby (1880) referred to as the 'nutritive ratio', RFI and residual gain (Koch et al., 1963), as well as residual intake and gain (Berry and Crowley, 2012). Utilization of these metrics as a selection criterion does not result in as much genetic improvement in efficiency as a suitably constructed selection index (MacNeil et al., 2019). MacNeil et al. (2013) reported that estimates of heritability for ADG and DFI for Bonsmara cattle were  $0.25 \pm 0.05$  and  $0.37 \pm 0.05$ , respectively, and their genetic correlation was 0.66. Previous reports of heritability estimates for DFI include: 0.54 for crossbred cattle in Canada (Nkrumah et al., 2007); 0.48 for Charolais cattle in France (Arthur et al., 2001b); 0.48 for Brangus heifers in Texas (Lancaster et al., 2009); 0.45 and 0.39 for Hereford and AN cattle in the Northern Plains of North America (MacNeil et al., 1991), and 0.36 for AN cattle in Australia (Arthur et al., 2001a).

Similarly, prior estimates of the genetic correlation between DFI and ADG were 0.55 in both MacNeil et al. (2011), as well as Berry and Crowley (2012). There is substantial variation in the DFI of beef cattle, independent of size and growth rate (van der Westhuizen et al., 2004) with this recognition motivating interest in using RFI as a measure of feed efficiency. Van der Westhuizen et al. (2004) explored the genetic (co)-variances (and ratios) between weaning weight and other traits, in order to compare relationships of RFI and FCR with growth. The results of this study stated that the estimated genetic correlation of RFI and FCR of 0.75, which was very similar to the estimate of 0.74 in broilers (van Bebber and Mercer, 1994). Ultimately, in South African circumstances, the genetic correlations of weaning weight with other traits that influence feedlot profitability indicates that the correlated responses achieved in these traits through direct selection on weaning weight would be small, if any (van der Westhuizen et al., 2004).

Many central test stations measure body weights and DFI in order to estimate feed efficiency traits including RFI (Manafiazar et al., 2016). It is complex for these traits to be applied by the entire beef industry, and to be inclusive of the national selection indexes due to the great cost involved in individual data collection as well as the limited infrastructure to measure and record DFI (Manafiazar et al., 2016).

By decreasing the test period (from 84 to 42 days) the number of animals to be tested using the same facilities may possibly be doubled, and statistical power-of-the-test (defined as the probability of correctly rejecting the null hypothesis when it is false; a test's power is influenced by the choice of significance level for the test, the size of the effect being measured, and the amount of data available) may be increased. Using the shorter test period Manafiazar et al. (2016) observed that the power-of-the test for the comparison of two treatments was increased to 0.80 from 0.51. Thus, under the circumstances that were evaluated by Manafiazar et al. (2016), there was a 29% higher chance of properly accepting the null hypothesis when it was in fact true by testing a larger number of animals for a shorter length of time despite the reduced accuracy of each of the RFI value for each animal.

Retallick et al. (2017) observed that measuring inter-breed variation in DFI and growth could enable more efficient use of differences among breeds. As in the study of Manafiazar et al. (2016), shorter test periods allowed for more animals to be tested given the limited infrastructure that is available for measuring DFI in the United States (Retallick et al., 2017). In addition to facilitating the better use of breed resources, increasing the number of animals with phenotypes would increase the accuracy of genomic predictions for feed intake.

## **2.6 Partial body weight**

In-pen weighing positions (IPW) can be used in feed and growth efficiency trials to collect daily weights from individual animals in real-time. When an animal stands with its front feet on a scale that has been positioned at the access point to a water fountain, PBW can be recorded in real time. Recorded observations of PBW can be filtered to remove spurious data points and summarized over visits to the waterer to produce a single daily value for each animal. Further, Wells et. al. (2021) indicated that PBW might be transformed to estimate the corresponding entire body weight for the animal.

Accumulating daily weights during a feed efficiency trial, through use of the IPW not only reduces the labour and stress associated with collecting chute weights, but it increases the accuracy of body weight collection and has the potential to reduce the trial lengths. When using chute weights to calculate ADG for RFI determination, trials are traditionally a minimum of 70 days in length in order to calculate ADG accurately (Basarab et al. 2003).

Average daily gain is an important component of production efficiency for growing beef cattle (Nielsen et al., 2013). The mathematical relations among traits that are components of efficiency suggests that for a pair of calves with identical initial body weight, the one with rapid ADG will reach a target market weight with fewer days on feed, and thus would be more efficient due to less feed being used for maintenance (MacNeil, et al., 2021). The most important reason for the length of a postweaning performance evaluation has been shown to be the time necessary to acquire an adequately accurate measurement of ADG rather than feed intake. Archer and Bergh (2000) specified that a period of 42-56 days was acceptable to measure ADG in growing calves. Kearney et al. (2004) also recommended that use of automated live weight evaluation would allow for the period of tests to be reduced to 56 days without decreasing the accuracy of estimates of live weight change.

In a recent study by MacNeil, et al. (2021), an assessment of PBW and predicted body weight as predictors of recorded body weight was carried out. At the beginning of the test period, PBW accounted for between 73.4-99.5% of the variation in recorded body weight ( $P < 0.01$ ), while predicted body weight accounted for between 86.5-99.6 % of the variation in recorded body weight ( $P < 0.01$ ). Moreover, the recorded body weight from predicted body weight had a larger coefficient of determination from 0.91 to 0.95 and decreased the average standard error of the estimate from 0.19 to 0.07 compared to the prediction of recorded body weight from PBW. For the eight contemporary groups, the intercept of the regression of recorded body weight on PBW was positive ( $P < 0.05$ ). Thus, for these contemporary groups utilization of a multiplicative alteration to predict recorded body weight from PBW would result in an under- and over- estimate of the recorded body weight for animals with above or below average PBW, respectively MacNeil et al. (2021).

It was recommended that the suggested length of test should be contingent on the expected use of the resulting data. In the context of genetic assessments and for many experimental trials, power of the test can be increased, and supplementary accuracy may result from testing more animals, even if the individual estimations themselves are less precise (Manafiazar et al., 2017). Thus, a test of 50 days may suffice for many purposes. However, as the postweaning gain test lessens, the impact of any discrepancies in accuracy in the prediction of body weight affecting ADG may be overstated if the body weight records early and late in the test are not similarly affected (MacNeil et al., 2021).

## CHAPTER 3

### Plasticity of breed direct and individual heterosis effects on preweaning traits of beef cattle under extensive conditions<sup>1</sup>

#### 3.1 Introduction

A crossbreeding trial was conducted at the Vaalharts research station near Jan Kempdorp in the Northern Cape Province of South Africa, in which Afrikaner, Bonsmara and Nguni cows (Sanga types) were mated with Afrikaner, Bonsmara, Nguni, Angus and Simmentaler (exotic) bulls in all possible combinations (Pyoos, 2018). This created 15 different genotypes. Large variation was observed in the weaning weights of the different crosses between years. For example, Sanga- and exotic sired calves had the same 205-day corrected weaning weight (171 kg) in the 2015/16 summer, which was very hot (average maximum summer temperature 32.2°C) with well below average season rainfall of only 302mm. In contrast, the summer of 2016/17 was cooler (31.1°C) and wetter (469mm) and the weaning weights of the Angus and Simmentaler sired calves were 27 kg heavier than the Sanga sired calves.

This phenomenon led to the study on plasticity of breed direct and individual heterosis effects in beef cattle under the extensive conditions where the crossbreeding trial is carried out. Plasticity refers to changes in an organism's behaviour or performance in response to a specific, sometimes unique environment (Price et al., 2003). Plasticity is a way for an organism to cope with environmental variation and encompasses all types of environmentally induced changes. These changes may be temporary or permanent (Kelly et al., 2021).

Santana et al. (2013) found superior genotypes in favorable environments may not perform the best in unfavorable environments. This was demonstrated for weaning weight. They concluded that there is genetic variation in the sensitivity of animals to the environment. This will allow the selection of more robust or plastic genotypes for crossbreeding in a specific environment.

The aim of this study was to investigate the plasticity of breed direct and individual heterosis effects on birth weight and 205-day weight of the breeds used in the crossbreeding project.

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<sup>1</sup>Pyoos, G.M., MacNeil, M.D., Scholtz, M.M., Seshoka, M.M., Weepener, H.L. and Naser, F.W.C., 2022. Plasticity of breed direct and individual heterosis effects in beef cattle under extensive conditions. Proceedings 12th World Congress on Genetics Applied to Livestock Production, 3 – 8 July 2022, Rotterdam, the Netherlands.

### 3.2 Materials and methods

The Vaalharts research station is located in the centre of South Africa at 27°57'19" South and 24°50'41" East at an altitude of 1175 meters and is in an area with sandy red soil with lime rock underneath (Laker, 2003). The veld type is mixed *Tarchonanthus* veld, Veld type No 16b, 4 (Acocks, 1988). The research station has a recommended carrying capacity of 10 ha/Large Stock Unit. The climate at the Vaalharts research station is characterized by hot summers and cold winters with frost being a common occurrence. The highest monthly average temperature is around  $\pm 32^{\circ}\text{C}$  and is experienced during December and January. The average precipitation is 440 millimetres per annum of which 88% is from thunderstorms during the summer months from October to April. Cattle would typically graze native vegetation throughout the year. However, cattle from the Free State may have grazed maize stowage over the winter before their arrival at Vaalharts.

A crossbreeding trial was conducted at Vaalharts over a period of eight years. It included calves that were weaned from 2015 until 2022. Afrikaner, Bonsmara and Nguni dams were mated with Afrikaner, Bonsmara, Nguni, Angus, and Simmentaler sires. The Afrikaner and Nguni breeds are indigenous to Southern Africa and classified as *Bos taurus africanus* (Meyer, 1984), and are referred to as Sanga breeds. The Bonsmara is a composite breed developed from the Afrikaner, Hereford, and Shorthorn breeds in a combination of 5/8 Afrikaner and 3/8 British (Scholtz, 2010a). The Angus is a British breed and the Simmentaler a European breed. This resulted in producing 12 crossbred- and 3 purebred genotypes. Cows that were used in this study either were from the Vaalharts Research Station or were purchased from farms in the Free State, Northern Cape, North West, Eastern Cape, Limpopo, and Mpumalanga provinces, as well as from Namibia.

The data was collected according to the approved standard operating procedures the National Beef Recording and Improvement Scheme in South Africa, which is accredited with the International Committee for Animal Recording (ICAR). In the first of the three years of data collection (2014 to 2017) the cows of each breed were stratified by age, weight, and estimated breeding values. They were then assigned to mating groups within strata to avoid the possibility of uneven genetic merit of cows mated to any breed of bull. With the exception that some of the Afrikaner cows that were pregnant when they were purchased, each bull was used across the three breeds of dam and there was connectedness of sires across years. At least two bulls of each breed were assigned to a specific mating group.

In year 1, single sire mating was used, whereas in years, 2 and 3 multiple sire mating was used, and paternal parentage is therefore unknown. The data resulted from mating Afrikaner, Bonsmara, Nguni, Angus and Simmentaler bulls to Afrikaner, Bonsmara, and Nguni cows over a six-year period. In total 212, 324, 303, 179 and 234 calves were sired by Afrikaner, Nguni, Bonsmara, Angus and Simmentaler sires, respectively. There were 182, 633 and 437 calves produced by Afrikaner, Nguni and Bonsmara cows, respectively. The breeding season, which ran over December to February, occurred on natural veld and all calves were raised by their dams from birth through weaning at approximately 205 days of age. Birth dates were recorded, and calves were weighed within 48 hours of birth. Each year, all calves were weaned and weighed on the same day. It should be noted that calves are born in spring and weaned in the autumn of the next year.

The climate information from the Vaalharts location is unfortunately not complete, with some missing data. The climate information from the nearby town Hartswater, which is 25 km from Vaalharts, was thus used. The Temperature-Humidity Index (THI) was calculated as follows (National Research Council, 1971):

$$\text{THI} = 0.81 \times T (\text{dry bulb}) + 0.143 \times \text{RH} + 0.0099 \times \text{RH} \times T (\text{dry bulb}) + 46.3$$

Where: T (dry bulb) = ambient dry-bulb temperature (°C) and RH = relative humidity (%).

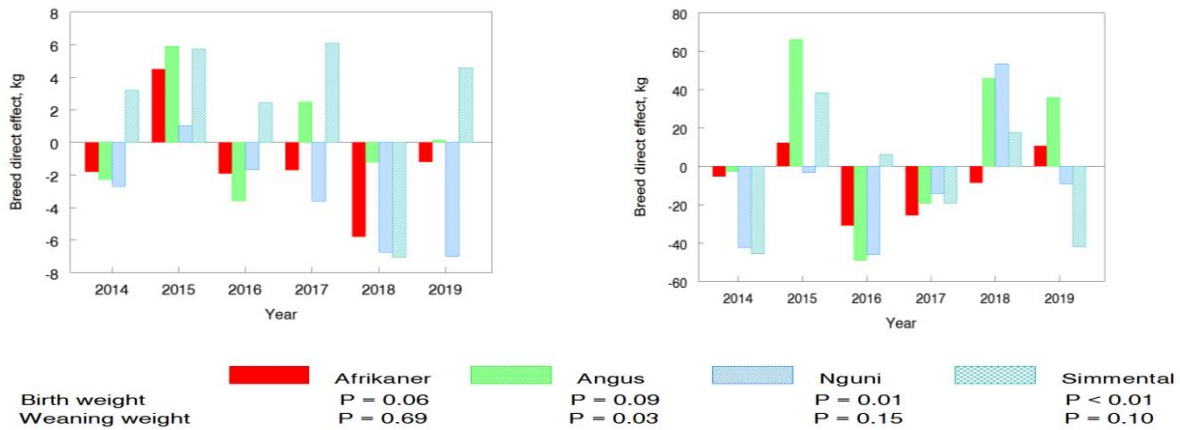
Daily THI values were calculated for the summer months from September to April. The length of the rainfall season was calculated from the first rains (at least 5 mm) to the last rains of the spring to autumn season. The number of heat wave days was calculated as the number of days within the rainfall season with THI values  $\geq 72$ .

The data were analysed using PROC Mixed of SAS. The linear models for birth weight and 205-day weight included effects of year, sex, age of dam, the genetic expectation for breed group as proposed by Dickerson (1969), and the interactions of year with the breed direct and maternal effects and individual heterosis. The direct effects of the Bonsmara in each year were set to zero to make the other effects estimable.

### **3.3 Results and discussion**

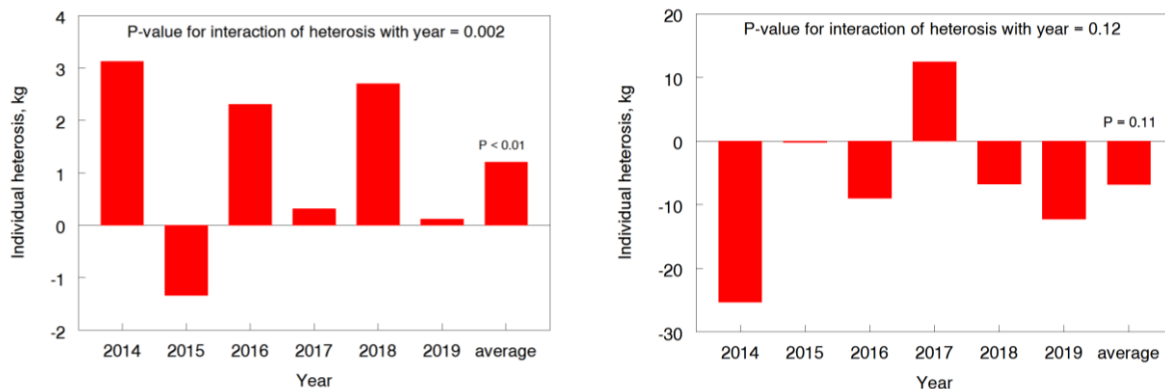
The degree of plasticity is depicted by the *P*-values for the interaction terms, where a numerically larger *P*-value indicates less plasticity. Overall, birth weight, a manifestation of growth *in utero*, appeared more plastic, i.e., more sensitive to the variation among years, than 205-day weight.

The *P*-values for the interaction effects of breed direct effects and year on birth weight indicate considerable plasticity with respect to the inter-year environment presented in **Figure 3.1**. The *P*-values for the interaction effects of breed direct effects and year on 205-day weaning weight indicate the direct effects of Afrikaner and Nguni being less plastic with respect to the variation among years than were the direct effects of Angus and Simmentaler.



**Figure 3.1 Interactions of the breed direct effects with year for birth (left) and 205-day (right) weights expressed as a deviation from the Bonsmara**

Individual heterosis effects on birth weight varied considerably among years with the effects being large in 2014, 2016 and 2018, and essentially nil in the other years presented in **Figure 3.2**. However, the inter-year variation in heterosis effects on 205-day weight was smaller and overall, not different from zero.



**Figure 3.2 Interactions of the heterosis effect with year for birth (left) and 205-day (right) weights expressed as a deviation from the Bonsmara**

The rainy season THI during the study period varied between 78.5 and 81.6, whereas Bohmanova et al. (2005) indicated that heat stress is induced if  $\text{THI} \geq 72$  in semi-arid regions. This indicates that the environment is very harsh. The rainfall varied between 240mm and 788mm per season, the length of the rainfall season varied from 156 days to 228 days and the number of heat wave days within the rainfall season between 171 and 232 days.

It is clear that the breed direct effects for birth weight varied from year to year, and it may be influenced by climate. There also appears to be large interactions between breed direct effects and year for 205-day weaning weight. The Afrikaner shows the least interaction, followed by the Nguni. This demonstrates low plasticity in the indigenous breeds, indicating more tolerance to variation in climate. The exotic breeds demonstrated more plasticity. Future studies will use weather data such as maximum temperature, seasonal rainfall, and length of the growing season, THI, and number of heat waves per season, to see whether it can be linked to the plasticity expressed between different genotypes.

Producing beef cattle can simultaneously optimize the use of additive (breed differences) and non-additive (heterosis) effects (Akanno et al., 2018). However, it is impossible to change the breeding scheme on an annual basis to best account for inter-year environmental variation.

### **3.4 Conclusion**

Adequately resourced commercial producers may choose to provide exogenous inputs to offset environmental variation, for example through the purchase of feedstuffs in drought years. They may therefore choose to use breed resources with high average genetic potential for production without regard to their plasticity. However, some commercial producers and probably all subsistence producers might choose a less plastic and more robust set of breed resources that can be depended upon to produce even under less favorable environmental circumstances.

## CHAPTER 4

### **Breed direct and heterosis effects on feed intake and partial body weight and their interactions with temperature humidity index during the postweaning period**

#### **4.1 Introduction**

Breed differences in feed intake and body weight have been observed in young growing beef cattle and these differences have been attributed to genetic effects (Retallick et al., 2017; Freetly et al., 2020). There are 34 recognized beef breeds in South Africa as recorded by the Animal Improvement Act (Act No 62 of 1998). The Afrikaner, Drakensberger, Nguni, Bonsmara and Hugenoot have been declared as Landrace breeds (indigenous or locally developed). The first three are regarded as indigenous to South Africa and referred to as Sanga breeds, whereas the latter two were locally developed from the indigenous Afrikaner breed and other *Bos taurus* breeds. Makina et al. (2017) recently confirmed the lack of *B. indicus* influence in the modern-day Afrikaner and Nguni. Thus, these breeds can be described as taurine tropical adapted breeds, which make them unique.

The past decade saw the warmest years on record, with the 2015/16 season the warmest and driest recorded in South Africa (Scholtz et al., 2013). The absence of information about the tolerance to heat in different breeds is already observed as a major restraint to production in sub-Saharan Africa. The indigenous breeds of South Africa may be better adapted to high heat temperature and humidity than European *Bos taurus* breeds (Scholtz et al., 2010a). However, these effects lack substantial documentation. Thus, it is important to understand the effects of temperature and humidity on the DFI and PBW during the post-weaning period of different crosses among breeds of beef cattle under feedlot conditions. Measurement of adaptation is complex and difficult, and an improved understanding thereof is important and relevant to South Africa. Some authors speculate that there will be a need to replace breeds or genotypes in production systems over the next 25 - 30 years due to changes in the environment (Wolfe et al., 2008; Yahdjian and Sala, 2008). Adapted or heat-tolerant breeds have a genetic advantage that is more distinct under heat stress circumstances. This suggests that use of heat-tolerant breeds will be an important strategy for successful beef cattle production.

The first objective of this investigation was to assess breed additive and heterosis effects on DFI and PBW of Afrikaner, Bonsmara and Nguni in comparison with European Angus and Simmentaler. The

second objective was to determine the effects of THI greater than 72 on DFI and PBW, since a THI of greater than 72 is indicative of heat stress (Du Preez, et al., 1990; Armstrong, 1994).

However, there are no unified critical thresholds of THI for delineating different degrees of heat stress in different breeds.

#### 4.2 Materials and methods

The crossbreeding experiment was conducted on at the Vaalharts Research Station, situated near Jan Kempdorp. Briefly, calves were produced in a three-breed diallel cross of Afrikaner, Bonsmara and Nguni augmented with topcrosses to Angus and Simmentaler sires. For the complete description of the experimental terrain, animals, the environmental conditions, and management practices see Chapter 3. After weaning, the bull calves were transported from Vaalharts to Irene at weekly intervals in groups of 25-28 according to their weight. Upon arrival in Irene the animals were given a period of 2 weeks to adapt to the facilities and diet and were then allocated to pens in the GrowSafe system according to body weight in accordance with the animal ethics committee and given 2 weeks to adapt to the facilities and diet. This system of allocation of animals to experimental units resulted in the partial confounding of breed groups and the contemporary groups in which the animals were fed. Raw data was summarized from the GrowSafe system in order to standardize the time period in which the trial occurred each year for all of the breed groups. Outliers were identified as having residuals more than 3 standard deviations from zero after preliminary analysis of the data and the data from these animals was discarded.

The **Afrikaner** is among the oldest indigenous breed in South Africa. It was created from cattle originating from the tribes of Koi (Hottentot/San) people that owned them during the 17th and 18th centuries (Epstein, 1956). By the end of the 18th century settlers around the Southern Cape had developed the Afrikaner into a well-defined breed that was principally adapted to extensive production systems and esteemed for its exceptional draught tenacities, meat, and milk production (Scholtz, 2010a). The Afrikaner Cattle Breeders' Society, founded in 1912, was one of the first breed societies to be instituted in South Africa. In South Africa, the Afrikaner was also successively used in the development of six composite breeds: Bonsmara, Afrigus, Afrisim, Hugenoet, Sanganer and S.A. Braford (Scholtz, et al., 2016). While the Afrikaner was the dominant breed in the 1960's, its numbers have promptly weakened in years that are more current. Results of a study by Collins-Lusweti (2000) specify that under extreme conditions the Afrikaner may outperform the Bonsmara breed.

The **Bonsmara** is a breed of cattle notorious for its high-quality beef. It originated in South Africa as a scientific experiment of Professor Jan Bonsma conducted at the Mara and Messina Research stations from 1937 to 1963. The Bonsmara was created after many cross matings and backcrosses and had an estimated breed composition of five-eighths Afrikaner (Sanga-type), three-sixteenths Hereford, and three-sixteenths Shorthorn (both taurine types) (Maule, 1990). The Bonsmara is functionally economical, well adapted to extensive production in Southern Africa, as well as the adverse climatic conditions. They are very fertile with small to medium size calves for easy calving, while producing a calf that is sought after by the feedlot industry (Scholtz, 2010). The Bonsmara became world-renowned as the first breed of beef cattle established through a crossbreeding program with the assistance of objectively recorded performance data. The Bonsmara SA Society was founded in 1964 (Scholtz, 2010).

The Sanga cattle that were originally found along the East coast of Southern Africa are known as the **Nguni**. They were found in Swaziland, Zululand, Mozambique, Zimbabwe where the original African Nguni tribes settled during their migration to Southern Africa between 600 and 1400 AD (Scholtz, 2010a). Since then, these animals have played a vital social and economic role in the advancement of these people. Nguni cattle are known for their fertility, resistance to diseases, and adaptability to penalising climates (Scholtz, 2010a). It should be noted that less than 20% of registered Nguni cattle are subjected to performance recording.

**Angus** or Aberdeen Angus is a breed that is commonly used in beef production, particularly in North America. They were developed from cattle native to the counties of Aberdeenshire and Angus in Scotland (Encyclopædia Britannica 15th Ed. Vol.10 p.1280). Contemplating cow weight and efficiency (weaning weight as a percentage of cow weight) Angus cows have increased in weight and have become more efficient (Pyoos, 2018). They are also known for maintaining birth weight below the South African national average (34.1kgs). The Angus is the most abundant beef breed in the world and the most abundant British breeds in South Africa (Scholtz, 2010a).

**Simmentaler** cattle had their origin near the Simmerom river of Switzerland. The first bulls and heifers were imported to Namibia in 1895 and then to South Africa in 1905 as dual-purpose milk/beef cattle as termed by Theunissen (2011). The Simmentaler Cattle Breeders' Society was formed in 1964, and since then the breed has seen endless popularity for crossbreeding (Scholtz, 2010a). Simmentaler cattle have substantial frames, high milk production and the calves grow swiftly after weaning when provided sufficient feed.

In total 307, 406, 431, 269 and 347 calves were sired by Afrikaner, Bonsmara, Nguni, Angus and Simmentaler sires, respectively as presented in **Table 4.1**. There were 300, 656 and 804 calves produced by Afrikaner, Bonsmara and Nguni cows, respectively. Breeding occurred on natural veld and all calves were raised by their dams from birth through weaning at approximately 205 days of age. Birth dates were recorded, and calves were weighed within 48 hours of birth. Each year, all calves were weaned and weighed on the same day. It should be noted that calves born in spring were weaned in the autumn of the next calendar year.

**Table 4.1 Numbers of calves produced by Afrikaner, Bonsmara, Nguni, Angus and Simmentaler bulls when crossed on Afrikaner, Bonsmara and Nguni cows**

Dam breed	Sire breed				
	Afrikaner	Bonsmara	Nguni	Angus	Simmentaler
Afrikaner	100	55	56	43	46
Bonsmara	62	200	167	114	113
Nguni	145	151	208	112	188

Previous research in South Africa has shown large differences in average daily gain (ADG) and feed conversion ratio (FCR) in standardized growth tests between diverse beef cattle breeds (**Table 4.2**). It should be noted that these results are based on centralized testing of weaner beef bulls in confinement and are not the result of contemporaneous evaluation of the indicated breeds.

**Table 4.2 Growth rate and feed conversion ratio in diverse beef cattle breeds in South Africa taken from Scholtz (2010)**

Breed	Final weight (Kg)	ADG (g/day)	FCR	n
Nguni	338	1 284	5.88	30
Afrikaner	361	1 350	6.31	360
Bonsmara	438	1 743	5.97	7 650
Angus	469	1 885	6.09	470
Simmentaler	485	1 954	6.02	310

The objective of practicing an effective crossbreeding system would be to optimize performance (Kinghorn, 1980, 1982; MacNeil et al., 1988). The quantification of breed additive direct ( $g^I$ ) and maternal ( $g^M$ ) effects provide a suitable basis for evaluating crossbreeding systems; since according to additive genetic theory, the predicted performance of such crossbreds will be proportional to breed contributions. Heterosis and breed complementarity also provide opportunities for additional “gains” in crossbreeding and that may in part offset deficiencies in the additive genetic effects.

Dickerson (1969, 1973) presented general models for breed-specific genetic effects that can be used to predict differences in performance of a wide variety of breed crosses. Robison et al. (1981) and MacNeil et al. (1982), respectively first used multiple regression to quantify the effects in these models in analysing crossbreeding experiments and field data.

When partitioning the performance of crossbred animals into genetic effects, assuming that there are no epistatic effects (between-locus interactions) and no interactions among the effects (parameters), the model for a F1 cross of breeds A (sire) and B (dam) can be written as follows:

$$P_{X(AB)} = \frac{1}{2}g_A^I + \frac{1}{2}g_B^I + g_B^M + h_{AB}^I + e$$

Where:

$P_{X(AB)}$  = the phenotypic value of individual X, that is sired by breed A and out of a breed B dam;

$g_A^I$  and  $g_B^I$  = the direct (additive genetic) effects of breeds A and B, respectively;

$g_B^M$  = maternal additive effect of the breed B dam, which provides an environment for her offspring;

$h_{AB}^I$  = the individual heterosis effect which is expressed in AB crossbred progenies; and

$e$  = the temporal environmental effect to which the calf is subjected.

In the case of a three-breed cross (e.g. sire breed C mated to an AB crossbred dam) the above-mentioned model can be extended to include an additional parameter, namely the maternal heterosis effect ( $h_{AB}^M$ ), due to the dam being a F<sub>1</sub> cross. The model then becomes:

$$P_{X(C.AB)} = \underbrace{\frac{1}{4}g_A^I + \frac{1}{4}g_B^I + \frac{1}{2}g_C^I}_{\text{direct effects}} + \underbrace{\frac{1}{2}g_A^M + \frac{1}{2}g_B^M}_{\text{maternal effects}} + \underbrace{\frac{1}{2}h_{AC}^I + \frac{1}{2}h_{BC}^I + h_{AB}^M}_{\text{individual and maternal heterosis effects}} + e$$

Here, the breed additive effects were modeled with fixed continuous linear variates for the direct and maternal effects and were expressed as deviations from the Bonsmara as presented in Table 4.3. Breed specific heterosis effects were modeled as being proportional to expected heterozygosity with additional fixed linear continuous effects. Heterosis in crosses with Simmentaler and Angus was assumed equal to the average of the estimable heterosis effects.

**Table 4.3 Genetic expectations for Afrikaner (AF), Angus (AN), Bonsmara (BN), Nguni (NG), and Simmentaler (SM) sired calves from AF, BN and NG dams (breed of sire x breed of dam). Breed direct and maternal additive effects of BN were assumed to be 0.0.**

Breed group	Genetic effects <sup>1</sup>								
	$g_{AF}^i$	$g_{NG}^i$	$g_{AN}^i$	$g_{SM}^i$	$h_{AF \times BN}^i$	$h_{AF \times NG}^i$	$h_{BN \times NG}^i$	$g_{AF}^m$	$g_{NG}^m$
AF	1.0							1.0	
NG		1.0							1.0
BN x AF	0.5				1.0			1.0	
AF x BN	0.5				1.0				
BN x NG		0.5					1.0		1.0
NG x BN		0.5					1.0		
AF x NG	0.5	0.5				1.0			1.0
NG x AF	0.5	0.5				1.0		1.0	
AN x AF	0.5		0.5		0.333...	0.333...	0.333...	1.0	
AN x BN			0.5		0.333...	0.333...	0.333...		
AN x NG		0.5	0.5		0.333...	0.333...	0.333...		1.0
SM x AF	0.5			0.5	0.333...	0.333...	0.333...	1.0	
SM x BN				0.5	0.333...	0.333...	0.333...		
SM x NG		0.5		0.5	0.333...	0.333...	0.333...		1.0

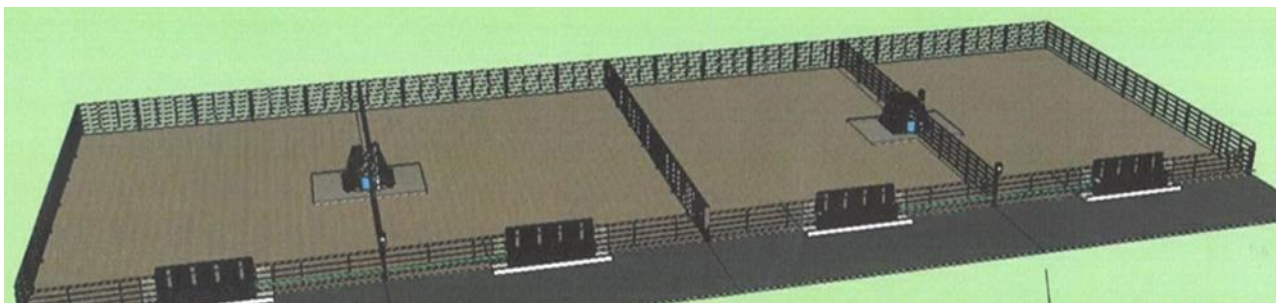
<sup>1</sup>  $g^i$  designate the direct additive effect of the breed indicated by the subscript,  $h^i$  designates the individual heterosis effect attributable to the combination of breeds indicated by the subscript, and  $g^m$  designate the maternal additive effect of the breed indicated by the subscript.

All the data was collected in terms of the guidelines of the National Beef Cattle Recording and Improvement Scheme as mandated by government under the Animal Improvement Act 83 of 1989. Ethical clearance was granted by the ARC-AP, number: APIEC18/16. The ARC - Irene campus is located at 25055' south latitude and 28012' east longitudes in Pretoria, South Africa and is situated

on the highveld with altitude of 1525m above sea level. A radio frequency identification ear tag uniquely identified each animal.

The feeding facility consisted of two double pens measuring 29 m × 51 m as illustrated in **Figure 4.1**. Each pen was deemed to have a capacity of between 35 and 40 weaned bull calves aged between 8 and 10 months. The calves were allotted to the pens according to their size and weight in accordance with the rules of the local animal ethics committee. In this regard, the structure of the experiment was confounded due to the allocation of breeds in the pens, which may ultimately affect some results. In an attempt to ensure a constant environment within a year, only data that was collected contemporaneously from all pens was used in this study.

For a period of two weeks after being transported from Vaalharts to Irene, the animals were adapted to the facility and fed a standard diet for the duration of the test. The diet was presented as a meal that contained a minimum of 11.0 MJ/kg DM of metabolizable energy, between 135 and 150 g/kg DM of crude protein, 125 g/kg DM of crude fibre, and 30 g/kg fat. Vitamins and minerals were added to the ration to meet the requirements of the animals. In addition, monensin-sodium and zinc-bacitracin were fed at 29 g/ton and 25 g/ton, respectively. Each pen of animals was fed for 80 days with 15 different tests occurring during the study. The pens were equipped with four feed intake nodes and an IPW to collect DFI and PBW (Vytelle Inc., Lenexa, Kansas, USA).



**Figure 4.1 Feeding facility used for the collection of daily feed intake and partial body weight**

Partial body weight and feed intake were recorded in real-time. To access the feed bunk, an animal must pass its head through a gate that limits access to one animal at a time and an antenna in the inner rim of the bunk recognizes a radio frequency identification tag in the animal's ear. Every 10 seconds the tag is scanned to confirm the animal has continued presence at the feed trough and the trough is weighed with a resolution of 10 grams as shown in **Figure 4.2**. Feed intake is measured by feed disappearance from the trough. Partial body weight is measured as the animal places itself on

the weigh scale whilst drinking water at the trough, only the front quarter is on the scale (Benfield et al., 2017). Briefly, a platform scale was positioned such that an animal must place its front feet on the scale in order to drink from a water trough as shown in **Figure 4.3**. The feed intake and PBW data are summarized to a daily basis with methods that are the intellectual property of Vytelle, Inc.



**Figure 4.2** An animal feeding from trough suspended on two load cells at a feed intake node (photo taken by Pyoos)



**Figure 4.3** An animal on an in-pen-weigh-point at a water trough to measure partial body weight (photo taken by Pyoos)

Weather data were obtained from the South African Weather Services (SAWS) REF - WCS-CLS-FRM-004.1. The THI proposed by Thom (1959) was calculated and used to summarize the thermal environment of each day. The THI was calculated as:

$THI = 0.81 \times Tdb + 0.143 \times RH + 0.0099 \times RH \times Tdb + 46.3$  (National Research Council, 1971); wherein, Tdb = dry bulb temperature ( $^{\circ}C$ ) and RH = relative humidity (%).

Results reported here were generated using PROC MIXED of the SAS™ System for Windows (Version 8.2, ©1999-2001 by SAS Institute Inc., Cary, NC, USA). The linear models that were initially used to analyze DFI and PBW included the fixed effect of test group comprised of pen and date at the beginning of the test, and a fixed breed group effect. Due to the study being run over a set period of days, this served as a fixed linear effect of days on test to account for the general growth of the animals over time while contained in the GrowSafe system.

In addition, a random effect for animals within breed and test group was included to account for the repeated measures of each animal. This effect was used as error to test the breed group effect. An additional analysis of the DFI measures also included PBW as a covariate. A set of analyses were conducted that were similar to those described above except that a binary fixed effect of stress coded as 1 when the THI was greater than 72 and 0 otherwise was also included. The breed group effect was subsequently partitioned using the genetic expectations proposed by Dickerson (1969) (see **Table 4.3**).

In doing so, the direct and maternal additive effects of the Bonsmara were set to zero to make the corresponding effects of the other breeds estimable. In the analyses that included the stress effect, including its interaction of breed, made the stress effect non-estimable due to the way in which animals had been allotted to test groups.

### **4.3 Results and discussion**

Before any discussion of the genetic effects on DFI and PBW, some comments regarding the effect of the experimental design on the results are warranted. The partial confounding of breed group with test group results in not being able to derive estimable effects from the linear models that might be deemed most appropriate. In addition, the sample sizes for the individual breed groups are small enough that the power of the test for differences among them is somewhat compromised.

Shown in **Table 4.4** are analysis of variance results from the linear models that included the categorical effects of test group and breed group and the continuous effect of days on test. In this analysis, breed group effects on DFI and PBW were not detected ( $P > 0.05$ ). As expected, the animals ate more and became heavier as the test progressed ( $P < 0.05$ ). The breed groups differed in their growth rate as evidenced by the significant interaction between the breed group effect and the linear effect of days on test for PBW. However, the rate at which animals increased their DFI was invariant to their genotype. These findings are interpreted to suggest further analyses of the data

regarding the level of postweaning performance can disregard the effect of the breed groups. In partitioning the interaction of breed group with days on test into single degree of freedom effects, only the individual heterosis on PBW ( $0.99 \pm 0.35$  kg/day) was significant ( $P < 0.01$ ).

**Table 4.4 Analyses of variance for feed intake and partial body weight of cattle representing 15 breed groups that could be used for beef production in South Africa**

Source	Numerator degrees of freedom	Denominator degrees of freedom	Feed intake		Partial body weight	
			F-value	Probability	F-value	Probability
Test group	14	337	2.26	<0.01	144.62	<0.01
Breed group (B)	14	337	0.64	0.83	1.56	0.09
Days on test (D)	1	16 897	5.68	0.02	8922.36	<0.01
B x D	14	16 897	1.01	0.44	2.01	0.01

Adding the binary indicator of heat stress to the linear model shown above indicated highly significant ( $P < 0.01$ ) effects on both DFI ( $-9.69 \pm 1.31$  g/day) and PBW ( $48.2 \pm 2.1$  g/day). Significance levels for the other effects in the model were similar to those that had been observed previously. Thus, on days when the THI was greater than 72, the animals consumed slightly less feed, but probably drank more water than on the days when they were not stressed, and that is why they tend to be heavier. With increased thermal discomfort, animals pursue ways to lose heat using a series of adaptations of their respiratory, circulatory, excretory, endocrine, and nervous systems (McManus et al., 2009). These adaptive mechanisms can regulate the tolerance of each breed to its environment (McManus et al., 2009).

Lucas et al. (2021) characterized the effect of grazing toxic fescue across Hereford- and Charolais-sired cows for known and new stress-associated phenotypes. In general, cows on toxic fescue practiced a decrease in hair shedding efficacy ( $P < 0.001$ ), higher vaginal temperatures ( $P < 0.001$ ), and a decrease in average daily gain ( $P < 0.001$ ). Hereford cows had a weaker ability to shed their winter coat and standardize body temperature together with lower serum mineral concentrations compared to Charolais cows. These differences between sire breeds provide further evidence of genetic variation in response to stress.

The general guideline is that the water intake of ruminant livestock is four litres of water per kg dry matter consumed, but that it can increase by 50% during hot weather periods (Scholtz et al., 2013). Unpublished results also indicated that the Nguni doubles its water intake during periods of heat stress. The observed increase in PBW during periods of heat stress can thus be explained by an increase in water intake.

Efficiency was assessed by incorporating 1) a linear effect of PBW into the model for DFI that also included the stress effect, and 2) by incorporating a linear effect of DFI into the similar model for PBW. Breed group effects on either measure of efficiency were not detected.

Animals that were heavier consumed more feed ( $37.7 \pm 4.8$  g/day;  $P < 0.01$ ) and animals that consumed more feed were heavier ( $57.1 \pm 9.3$  g/kg;  $P < 0.01$ ), as expected. In a population of 1,394 crossbred replacement beef females fed a roughage-based diet, Olson et al. (2020) determined heritability estimates ( $\pm$  SE) of  $0.25 \pm 0.05$  and  $0.26 \pm 0.06$  for specific times of feeding per day, and the number of feeding events per day, respectively. Estimated genetic correlations between feeding behaviours, performance and feed efficiency metrics have also varied in scale and direction among dissimilar cattle breeds. Genetic correlations fluctuating from  $0.03 \pm 0.13$  (Robinson and Oddy, 2004) to  $0.56 \pm 0.20$  (Nkrumah et al., 2007) have been reported between DFI and feeding time per day. Conceivably, differences in feeding behaviour are of direct economic value or can be considered as indicator traits in these evaluations.

In another recent study by MacNeil, et al. (2021), an assessment of PBW and predicted body weight as predictors of recorded body weight was conducted. At the beginning of the test period, PBW accounted for between 73.4–99.5% of the dissimilarity in documented body weight ( $P < 0.01$ ), while predicted body weight accounted for between 86.5–99.6 % of the deviation in documented body weight ( $P < 0.01$ ). Moreover, the prediction of recorded body weight from predicted body weight had a larger coefficient of determination, from 0.91 to 0.95, and reduced the average standard error of the estimate from 0.19 to 0.07, compared to the prediction of recorded body weight from PBW. For the eight contemporary groups in the study, the intercept of the regression of recorded body weight on PBW was positive ( $P < 0.05$ ). Thus, for these contemporary groups, application of a multiplicative modification to predict recorded body weight from PBW may yield in an under- or over- estimation of the recorded body weight for animals with above or below average PBW, respectively MacNeil et al. (2021).

#### **4.4 Conclusion**

First, and perhaps obviously, proper experimental design matters. Given the allocation of animals to pens, the opportunity to estimate some effects of interest was compromised in these data. Breed additive effects on postweaning DFI and PBW were similar. Direct heterosis effects increased PBW but altered neither DFI nor efficiency. One potential reason for animals being heavier on days when the THI was greater than 72 could be that they may have consumed higher amounts of water under heat stress. However, no water consumption data was captured in this study. Thus, future research could consider water consumption. The Nguni bull calves ate more feed, which may be due to the smaller animals being transported and fed together separately from the larger animals. Concurrent measurements of feeding behavior and growth will significantly enrich the amount of data for understanding breed differences and genetic effects amongst crossbred cattle. Future studies should also record feeding behavior traits to better understand the variation in feed efficiency in stressful and stress-free environments.

## CHAPTER 5

### Serial correlations of partial body weight and feed intake in crossbred cattle

#### 5.1 Introduction

Feed consumption is essential for survival because it replenishes an animal's energy and nutrient stores (Petrovich, 2018). Feeding behavior in cattle affects feed efficiency, which is important for increasing the profitability of production while simultaneously reducing the environmental impact (Llonch et al., 2018). In beef production, understanding and managing feed is essential for optimal production (Nielsen et al., 2013). Cattle that are able to eat comfortably and without stress are more likely to consume the amount of feed they need to attain their genetic potential for growth (Archer and Bergh, 2000). Recent automated advances can be used to measure individual DFI efficiently. These include the upgraded Calan® Gate System (American Calan, Northwood, New Hampshire), the newer GrowSafe® Systems, Ltd. (Airdrie, Alberta, Canada) and the Insentec® Systems (Marknesse, Netherlands). All these systems use electronic scales and radio frequency identification ear tags to record individual feed intake records in real time (Retallick et al., 2017).

Serial correlation occurs in a time series when a variable and a lagged version of itself (for instance data values recorded at times  $t$  and  $t-1$ ) are observed to be correlated with one another. A positive value of the serial correlation indicates an animal that consumes an above average amount of feed on one day will again do so on the next. Conversely, a negative value of the serial correlation indicates a cyclical feeding behavior. In the context of beef cattle breeding, the concept of most probable producing ability is a well-known tool for the evaluation of individual cows. The accuracy of the most probable producing ability for a cow depends on the correlation among the performance records of her calves (i.e. the correlation of the weaning weight of her first and second calves, etc.). In a similar manner, a potential use of the serial correlation of feed intake is to estimate the number of days feed intake must be recorded to achieve a specific accuracy for the average DFI of animals being evaluated.

Therefore, the objective of this study was to estimate the serial correlation (lagged 1 day) for DFI and PBW records of individually fed beef bulls. Further analysis will attempt to partition the estimates obtained for the individual animals to breed-specific genetic effects.

## 5.2 Materials and methods

Crossbreeding experiments conducted at the Vaalharts Research Station, and described in the previous chapters provided the data that was used herein. Estimates of the serial correlations of DFI and PBW were calculated for each animal. In general, correlations are not normally distributed. Thus, the serial correlations were transformed to z-statistics (Fisher, 1915).

Fisher's z-transformation is as follows:

$$z = \ln\left(\frac{1+r}{1-r}\right)/2$$

and conversely,

$$r = \frac{e^{(2z)} - 1}{e^{(2z)} + 1}.$$

Wherein:  $r$  designates the estimated product-moment correlation, and  $\ln$  indicates a natural logarithm. For example, if the Pearson correlation coefficient between two variables was found to be  $r = 0.55$ , then  $z_r$  would be:  $z_r = \ln((1+0.55) / (1-0.55)) / 2 = 0.618$ . Because these z-statistics are normally distributed (Gayen, 1951), inferences with regard to the correlations can be made using analysis of variance procedures. The z-transformed values of the serial correlations were analysed using PROC MIXED of the SAS™ System for Windows (Version 8.2, ©1999-2001 by SAS Institute Inc., Cary, NC, USA). The lower bound (lb) of a 95% confidence interval for  $z$  is:  $z_{lb} = z - \sqrt{\frac{1.96}{N-3}}$  and the upper bound (ub) of the 95% confidence interval is:  $z_{ub} = z + \sqrt{\frac{1.96}{N-3}}$ ; wherein  $N$  = the number of observations. The linear model included the fixed effect of test group comprised of pen and date at the beginning of the test and a fixed breed group effect. Estimates of the genetic effects were obtained as linear functions of the breed group effects following Dickerson (1969) presented in **Table 5.1**. The accuracy of an n-day long test for feed intake was calculated from back-transformed values of  $z$ :

$$r = \frac{e^{(2z)} - 1}{e^{(2z)} + 1}$$

as:

$$Accuracy = \frac{nr}{(1+(n-1)r)}.$$

**Table 5.1 Coefficients for linear functions of the breed group means to estimate breed direct and maternal effects and individual heterosis**

Breed group	Genetic effects						
	$g_{AF-BN}^i$	$g_{NG-BN}^i$	$g_{AN-BN}^i$	$g_{SM-BN}^i$	$h^i$	$g_{AF-BN}^m$	$g_{NG-BN}^m$
AF	1.0	0.0	0.0	0.0	-0.333	1.0	0.0
AFxBN	0.0	-0.5	-0.25	-0.25	0.167	-1.0	-1.0
AFxNG	0.5	0.5	0.0	0.0	0.167	0.0	1.0
ANxAF	0.5	0.0	0.5	0.0	0.0	1.0	0.0
ANxBN	-0.5	-0.5	0.0	0.0	0.0	-1.0	-1.0
ANxNG	0.0	0.5	0.5	0.0	0.0	0.0	1.0
BNxAF	0.0	-0.5	-0.25	-0.25	0.167	1.0	0.0
BN	-1.0	-1.0	0.0	0.0	-0.333	-1.0	-1.0
BNxNG	-0.5	0.0	-0.25	-0.25	0.167	0.0	1.0
NGxAF	0.5	0.5	0.0	0.0	0.167	1.0	0.0
NGxBN	-0.5	0.0	-0.25	-0.25	0.167	-1.0	-1.0
NG	0.0	1.0	0.0	0.0	-0.333	0.0	1.0
SMxAF	0.5	0.0	0.0	0.5	0.0	1.0	0.0
SMxBN	-0.5	-0.5	0.0	0.0	0.0	-1.0	-1.0
SMxNG	0.0	0.5	0.0	0.5	0.0	0.0	1.0

$g_{A-B}^i$  = direct genetic effect for breed A expressed as a deviation from breed B;  $g_{A-B}^m$  = maternal genetic effect for breed A expressed as a deviation from breed B;  $h^i$  = individual heterosis effect; AF = Afrikaner, AN = Angus, BN = Bonsmara, NG = Nguni, SM = Simmentaler; crosses are designated as breed of sire x breed of dam

### 5.3 Results and discussion

Analyses of variance for the z-transformed serial correlations of DFI and PBW are presented in **Table 5.2**. Denominator degrees of freedom were 332 and 198, respectively. This difference in degrees of freedom from the previous analyses and between traits here was due to missing data.

**Table 5.2 Analyses of variance for z-transformed serial correlations of feed intake and partial body weight of cattle representing 15 breed groups that could be used for beef production in South Africa.**

Source	Numerator degrees of freedom	Feed intake		Partial body weight	
		F-value	Probability	F-value	Probability
Test group	14	2.37	<0.01	3.53	<0.01
Breed group (B)	14	1.08	0.37	0.98	0.47

The test groups differed significantly ( $P < 0.01$ ) in the patterns of feeding behaviour and growth as documented by their effects on the serial correlation estimates. Despite the general lack of statistical significance, the genetic effects on the z-transformed serial correlations are presented in **Table 5.3**. However, the results might indicate some difference in the serial correlation of PBW between Afrikaner and Bonsmara.

**Table 5.3 Estimates of genetic effects on z-transformed values of the serial correlations of feed intake and partial body weight of beef bulls**

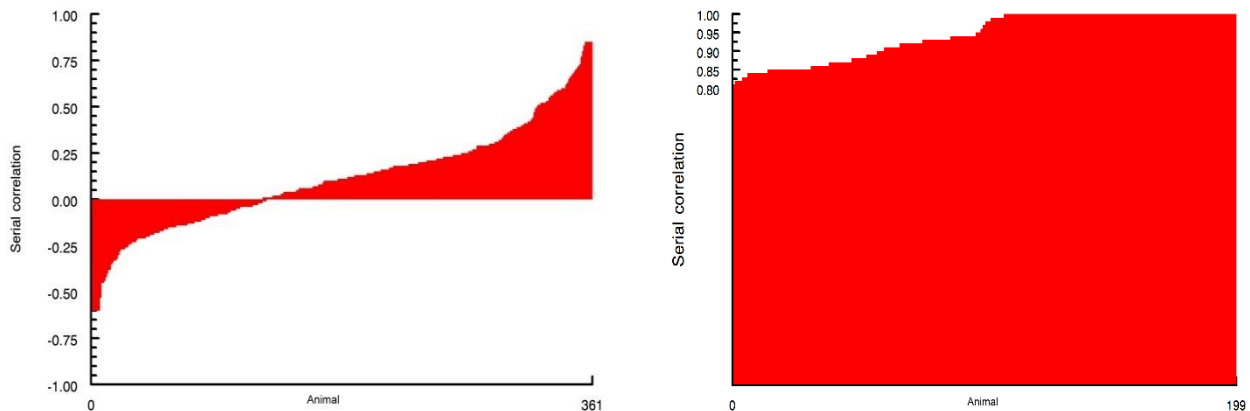
Genetic effect	Partial body weight		Feed intake	
	Estimate	Probability	Estimate	Probability
$g_{AF-BN}^I$	$1.41 \pm 0.71$	0.05	$-0.13 \pm 0.12$	0.29
$g_{NG-BN}^I$	$0.98 \pm 0.57$	0.09	$0.05 \pm 0.12$	0.66
$g_{AN-BN}^I$	$0.53 \pm 0.56$	0.34	$0.03 \pm 0.07$	0.67
$g_{SM-BN}^I$	$0.16 \pm 0.26$	0.55	$0.03 \pm 0.06$	0.59
$h^I$	$0.64 \pm 0.51$	0.21	$-0.07 \pm 0.12$	0.56
$g_{AF-BN}^M$	$2.55 \pm 1.38$	0.07	$-0.25 \pm 0.23$	0.27
$g_{NG-BN}^M$	$0.52 \pm 0.81$	0.52	$0.13 \pm 0.18$	0.50

$g^I$  = breed direct effect contrast for the breeds indicated in the subscript;  $g^M$  = breed maternal effect contrast for the breeds indicated in the subscript;  $h^I$  = individual heterosis effect. AF = Afrikaner, BN = Bonsmara, NG = Nguni, AN = Angus, SM = Simmentaler

Average estimates for the z-transformed serial correlation of DFI and PBW for each animal were 0.1003 and 3.0506, respectively. Using the formula below, these estimates transformed to correlation coefficients were 0.100 and 0.941, respectively. For comparison to other studies

repeatability of DFI was also calculated from the ratio of animal variance to phenotypic variance from the analysis reported in Chapter 4. The measure of the correlation among the repeated records was 0.43.

Thus, the 95% confidence interval for DFI was  $0.095 < z < 0.106$ ; and for PBW it was  $3.041 < z < 3.061$ . **Figure 5.1** shows the distributions of the correlation coefficients back-transformed from the z-statistics for feed intake and PBW, respectively.

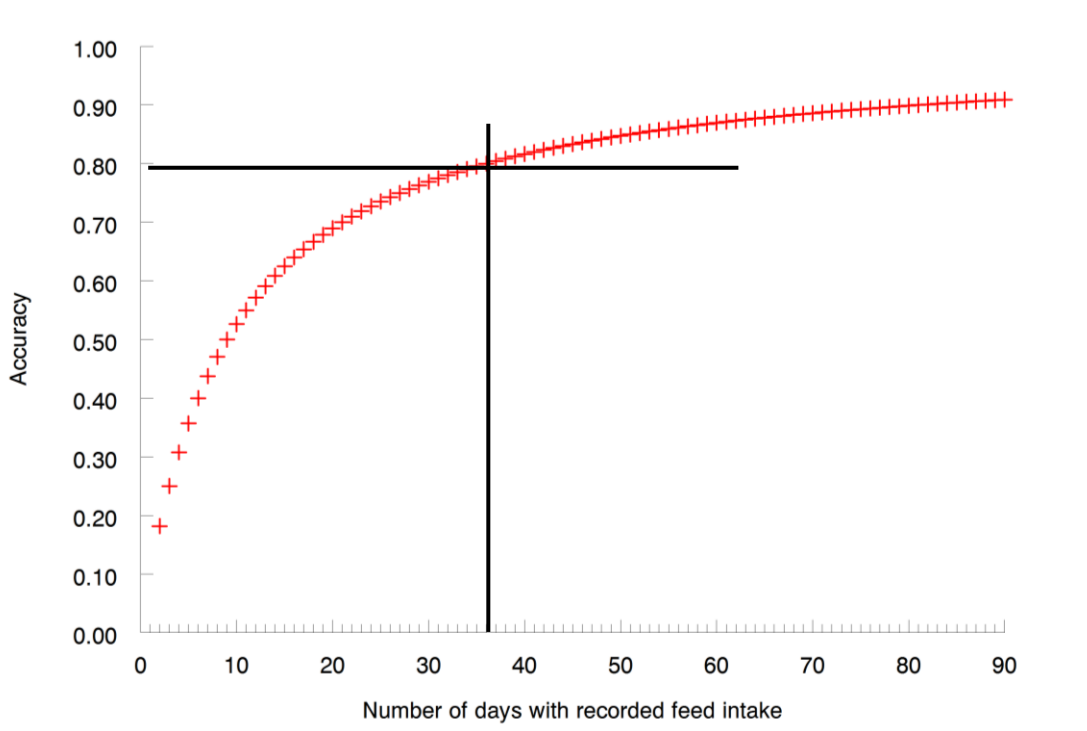


**Figure 5.1** Distribution of serial correlation coefficients for feed intake (left panel) and partial body weight (right panel) recorded daily

An applied question of some importance is the number of days for which data needs to be recorded in order to achieve a pre-specified accuracy of the mean. Accurately calculating and predicting phenotypes in growing animals is, in part, informed by the number of days over which the trait is measured (Swiger et al., 1961; Koch et al., 1982). Feed intake is a crucial data point required to capture as much of the variability as possible with feed efficiency models. It is vital that intake records are collected with high degrees of accuracy. For example, a 10% increase in feed intake may potentially enhance profits by 43% (Fox et al., 2001). Illustrated in **Figure 5.2** is the accuracy of the average of  $m$  repeated daily records for DFI based on an estimated serial correlation of 0.10 (i.e., the value from these data).

Highlighted in **Figure 5.2** is the number of days (36) over which feed intake records need to be accumulated in order to achieve an accuracy of 0.8 for an average animal based on the estimated serial correlation. If the estimate of repeatability (0.43) from the variance components were used in this calculation, then six days of feed intake records would be sufficient to achieve an accuracy of approximately 0.8. Using repeatability estimated from the variance components also produced a

much smaller required number of days of data collection to estimate nutrient intakes in human beings with good accuracy ( $r = 0.8$ ) than relying on within-subject variability (Palaniappan et al., 2003).



**Figure 5.2 Accuracy (+) of the mean of daily feed intake records as a function of the number of days on which feed intake was recorded**

According to Hill (2012), in order to have an accurate value for feed intake, either as total feed intake or average DFI, feed intake should be collected on a continuous basis during the testing or evaluation period. The current Beef Improvement Federation recommendation is that a 42-day test length is sufficient to collect accurate feed intake data. Other research supports test periods that are 35 to 56 days long (Archer et al., 1997; Archer and Bergh, 2000; Wang et al., 2006; Manafiazar et al., 2017). These earlier recommendations were based on the relationship of the proportion of variation in average DFI over a longer test interval that was explained by the feed intake records that were recorded over a shorter period of time. The methodology used in the present study is different in that it does not rely on a part-whole relationship.

The amount a specific character fluctuates from day-to-day varies with the trait that is being measured (Horgan et al., 2021). It is evident in this study, that PBW was much more consistent from one day to the next than was feed intake. The remarkably high serial correlation implies that there is little need to average measurements of PBW from successive days of recording to obtain a point estimate of it as, for example, may be desired to obtain a mid-test weight for the calculation of RFI.

This result does not inform the decision as to the length of an evaluation period that is required to measure any particular trait that is derived from body weight records such as ADG.

Oloo et al., (2023) made use of autocorrelation (equivalent to what is called serial correlation herein) as an indicator of resilience or equivalently robustness and the opposite of plasticity. The serial correlation of milk yield deviations was lowly heritable and insignificant genetic correlations with both longevity and average test-day milk yield. Further, at least for milk production, this measure of plasticity appears to be independent of phenotypic performance.

#### **5.4 Conclusion**

The highly variable serial correlation of DFI indicates marked differences among animals in their feeding behaviour over time. However, it does not appear these differences are related to the breed composition of the animals. The average serial correlation of DFI was interpreted to suggest a test period of 36 days was needed to achieve 80% average accuracy of the mean value for the animals being tested. The similarity and very large estimate of the serial correlation of PBW indicates the values from individual days are quite useful. Thus, there is little need to average values over days to achieve an accurate estimate of PBW at any specific point in time.

## CHAPTER 6

### Plasticity of feed intake of crossbred cattle during the postweaning period

#### 6.1 Introduction

A crossbreeding trial was conducted at the Vaalharts research station near Jan Kempdorp in the Northern Cape Province of South Africa, in which Afrikaner, Bonsmara and Nguni cows (Sanga types) were mated with Afrikaner, Bonsmara, Nguni, Angus and Simmentaler (exotic) bulls in all possible combinations. This created 15 different genotypes. Birth and 205-day weight exhibited large variation between years (**Chapter 3**).

These results stimulated the study of plasticity of breed direct and individual heterosis effects on DFI when the bull calves were transferred from Vaalharts to the bull-testing center at Irene. Palaniappan et al. (2003) observed that even for human beings, day-to-day variability in food consumption makes accurate measurement of the "usual" intake of foods and nutrients difficult. Herein plasticity refers to changes in an organism's behavior or performance in response to a specific, sometimes unique environment (Price et al., 2003).

Plasticity is a way for an organism to cope with environmental variation and encompasses all types of environmentally induced changes. These changes may be temporary or permanent (Kelly et al., 2021). Santana et al., (2013) found that superior genotypes in favorable environments might not necessarily perform the best in unfavorable environments. They concluded that there is genetic variation in the sensitivity of animals to a specific environment. This will allow the selection of more robust or plastic genotypes, or specific crosses that will perform well in a changing environment.

The aim of this study was to investigate the plasticity of breed direct and individual heterosis effects for DFI of the breeds used in the crossbreeding project.

## 6.2 Materials and methods

The crossbreeding experiment that generated the bull calves used in this study was conducted on at the Vaalharts Research Station, situated near Jan Kempdorp. Briefly, calves were produced in a three-breed diallel cross of Afrikaner, Bonsmara and Nguni augmented with top crosses to Angus and Simmentaler sires. After weaning, the bull calves were transported from Vaalharts to Irene at weekly intervals in groups of 25-28 according to their weight. Upon arrival in Irene the animals were allocated to pens in the GrowSafe system according to body weight in accordance with the animal ethics committee and given a period of 2 weeks to adapt to the facilities and diet. This system of allocation of animals to experimental units resulted in the partial confounding of breed groups and the pens in which the animals were fed.

In order to examine the inter-day plasticity of feed intake, the within-animal variance was estimated for each animal. This variance served as the dependent variable for a non-parametric two-way analysis of variance (Friedman, 1940). Within each test group, the inter-day variance of DFI for each animal was ranked. Then the ranks were subjected to two-way analysis of variance (without interaction) and the significance of the breed group effect was tested using a chi-square statistic that was calculated by multiplying the sum-of-squares for treatment by  $12/((t*(t+1)))$  where  $t$  is the number of breed groups. The genetic effects were calculated as linear functions of the breed group means presented in **Table 6.1**. The sums of squares for the single degree of freedom estimates of genetic effects, as described above, were used to test their significance.

**Table 6.1 Coefficients for linear functions of the breed group means to estimate breed direct and maternal effects and individual heterosis**

Breed group	Genetic effects						
	$g_{AF-BN}^i$	$g_{NG-BN}^i$	$g_{AN-BN}^i$	$g_{SM-BN}^i$	$h^i$	$g_{AF-BN}^m$	$g_{NG-BN}^m$
AF	1.0	0.0	0.0	0.0	-0.333	1.0	0.0
AFxBN	0.0	-0.5	-0.25	-0.25	0.167	-1.0	-1.0
AFxNG	0.5	0.5	0.0	0.0	0.167	0.0	1.0
ANxAF	0.5	0.0	0.5	0.0	0.0	1.0	0.0
ANxBN	-0.5	-0.5	0.0	0.0	0.0	-1.0	-1.0
ANxNG	0.0	0.5	0.5	0.0	0.0	0.0	1.0
BNxAF	0.0	-0.5	-0.25	-0.25	0.167	1.0	0.0
BN	-1.0	-1.0	0.0	0.0	-0.333	-1.0	-1.0
BNxNG	-0.5	0.0	-0.25	-0.25	0.167	0.0	1.0
NGxAF	0.5	0.5	0.0	0.0	0.167	1.0	0.0
NGxBN	-0.5	0.0	-0.25	-0.25	0.167	-1.0	-1.0
NG	0.0	1.0	0.0	0.0	-0.333	0.0	1.0
SMxAF	0.5	0.0	0.0	0.5	0.0	1.0	0.0
SMxBN	-0.5	-0.5	0.0	0.0	0.0	-1.0	-1.0
SMxNG	0.0	0.5	0.0	0.5	0.0	0.0	1.0

$g_{A-B}^i$  = direct genetic effect for breed A expressed as a deviation from breed B;  $g_{A-B}^m$  = maternal genetic effect for breed A expressed as a deviation from breed B;  $h^i$  = individual heterosis effect; AF = Afrikaner, AN = Angus, BN = Bonsmara, NG = Nguni, SM = Simmentaler; crosses are designated as breed of sire x breed of dam

### 6.3 Results and discussion

Shown in **Table 6.2** are results for the Friedman's test for differences between breed groups in their plasticity of feed intake. The results indicate that the breed groups differ significantly in their plasticity of feed intake. The breed group effect was partitioned into single degree of freedom genetic effects that are presented in **Table 6.3**. The Nguni, Simmentaler, Afrikaner, and Angus breed direct effects indicated more inter-day variability in daily feed intake than the Bonsmara direct effect. Likewise, the Nguni maternal genetic effect was greater than that of the Bonsmara. The estimated heterosis effect was small and not significant indicating that crossbred cattle would be no more variable over time in feed intake than were their straightbred counterparts. Taken

together, these results indicate that Bonsmara cattle would not be as sensitive to changes in the temporal environment in the feedlot as the other breeds and crosses. Therefore, the daily feed intake of Bonsmara cattle would be more predictable. The fact that the Bonsmara was the most robust (less plastic) in the feedlot may be a result of the breeding policy followed by the breed and its being a locally adapted composite. Performance recording is compulsory in Bonsmara, and a large proportion of young bulls are tested under intensive feedlot conditions. This may have resulted in a breed that is more tolerant (robust) to changes in conditions during the postweaning period.

**Table 6.2** Friedman’s analyses for plasticity of feed intake in cattle representing 15 breed groups that could be used for beef production in South Africa.

Source	Degrees of freedom	Sum of squares	Chi-square statistic	Probability of chi-square
Test group	14	9020.9	451.0	< 0.01
Breed group (B)	14	1327.1	66.4	< 0.01

**Table 6.3** Partitioning the breed group effect on plasticity of postweaning feed intake into single degree of freedom contrast corresponding to explanatory genetic effects

Genetic effect	Sum of squares	Chi-square statistic	Estimate	Probability of chi-square
$g^i$ AF – BN	9.22	55.32	1.35	< 0.01
$g^i$ NG – BN	30.11	180.66	2.39	< 0.01
$g^i$ AN – BN	4.11	24.66	0.54	< 0.01
$g^i$ SM – BN	45.61	273.66	1.45	< 0.01
Heterosis	0.15	0.90	-0.17	0.34
$g^m$ AF - BN	0.01	0.06	-0.06	0.81
$g^m$ NG - BN	142.06	852.36	7.88	< 0.01

$g^i_{A-B}$  = direct genetic effect for breed A expressed as a deviation from breed B;  $g^m_{A-B}$  = maternal genetic effect for breed A expressed as a deviation from breed B;  $h^i$  = individual heterosis effect; AF = Afrikaner, AN = Angus, BN = Bonsmara, NG = Nguni, SM = Simmentaler

In the tropical environment of Kenya, a study by (Oloo et al., 2023) indicated the viability of utilizing log-transformed variance of deviations in milk yield as an indicator of general resilience of dairy cows. In this chapter, rather than using a transformation of the variance, Friedman's test was used to analyse the magnitude of the variance in DMI across the days on test. Oloo et al. (2023) found the log-transformed variance of deviations in milk yield to be heritable. Conclusively, log transformed variance of deviations in milk yield grasps a substantial prospective as an indicator of robustness and plasticity to environmental stressors for dairy animals performing in Sub-Saharan Africa (Habimana, et al., 2023), and might be improved through selective breeding (Oloo et al., 2023).

As the environments in which livestock are reared become more variable, animal robustness becomes an increasingly valuable attribute. The challenge of food security for the increasing human population will unavoidably decrease the use of human-edible foodstuffs for feeding livestock (Schader et al., 2015). Including robustness in future breeding and management plans suggests being able to measure and quantify it, but no single, simple, useful measure of robustness currently exists. This is largely because robustness is a complex trait, which relates to a whole biological system (Friggens et al., 2017). Characteristically, measures of animal performance are only one part of a biological system. For example, there are numerous studies that have examined the aptitude of cows to maintain milk production when feed quality is decreased (e.g. Horan et al., 2006; Beerda et al., 2007).

These can be used to assess the environmental sensitivity of milk production via the slope of the relationship between milk production and environment quality (usually referred to as a reaction norm (Lewontin, 1974)). If the resolution is to identify biomarkers that may be useful for molecular phenotyping or genotyping, the quantities should focus on the physiological mechanisms fundamental to robustness. However, if the determination of measuring robustness is to enumerate the degree to which animals can adapt to restrictive circumstances, then the measurements should focus on the life functions, the trade-offs between them and the animal's capability to increase resource attainment. The time-related aspect of robustness also has important consequences (Friggens et al., 2017).

## **6.4 Conclusion**

The different breed groups differed significantly in their plasticity of feed intake. This resulted in the direct effect of Bonsmara on the plasticity of postweaning DFI being less than the direct effects of the other breeds. It is a given that the environment changed from day to day as each of the test periods progressed. Bonsmara cattle performed more consistently in this changing environment as compared to other breed types. It is important to note that adequately resourced producers may provide exogenous inputs to offset environmental variation and therefore use genotypes with high plasticity. However, subsistence farmers in many parts of sub-Saharan Africa might choose to use more robust genotypes that can produce at a certain level irrespective of the environment.

## CHAPTER 7

### General discussion, recommendations, and conclusion

An evaluation of breed genetic and heterosis effects on variability of growth and efficiency traits in different crossbred beef cattle genotypes whilst measuring the phenotypic plasticity was conducted. Plasticity indicates the degree to which a genetic group alters its phenotype as the environment changes. These alterations can be either permanent or temporary. A low level of plasticity is occasionally, referred to as robustness indicating a genetic group that is not particularly responsive to the environment. A highly plastic genetic group alters its phenotype in response to changes in the environment.

Plasticity permits individuals to 'match' their phenotype to varying environments and may be manifested at various times within the lifespan. It is important to note that there are a few limits to the benefit of phenotypic plasticity. Unreliable information may limit consequence of the production of phenotypes that are not adapted if the environmental triggers are not processed correctly.

The expression of plasticity may exhibit a lag-time limit that arises from the inevitable interruption amid sensing the environmental stressors and producing the corresponding new phenotype. Advancing from a preliminary phenotype to the final one may include transitional phases with poor fitness. This could limit the degree to which the underlying physiology would impinge on phenotypic expression. Finally, it may be that epigenetically influenced traits are affected differently than if the same trait is not subject to epigenetic effects.

Plasticity is an important tool by which organisms can manage a varying environment, including climatic conditions, within their lifetime. Therefore, plasticity is of paramount importance for livestock with long generation intervals as evolutionary changes through natural selection may not produce new variation fast enough to mitigate the effects of a changing environment. Genotypes that are better adapted to a warmer and more consistent climate as is typical of the tropics appear to be less plastic compared to genotypes in more variable temperate habitats. Animals that evolved in areas with variable temperatures may provide a terrific opportunity to identify valuable resources for offsetting the effects of climatic changes due to their apparently greater plasticity.

This investigation examined relatively few phenotypes and evaluating a more comprehensive set of phenotypes including reproduction and body composition is seen as necessary for incorporating plasticity into the decision-making process of animal breeders.

Below are the primary observations resulting from the components of this investigation.

- Overall, birth weight, a manifestation of growth *in utero*, appeared more plastic, i.e., more sensitive to the variation among years, than was 205-day weight. The *P*-values for the interaction effects of breed direct effects and year on birth weight indicate considerable plasticity with respect to the inter-year environment. The interaction of breed direct effects on 205-day weaning weight indicated less plasticity of Afrikaner and Nguni than Agnus and Simmentaler. The individual heterosis effects on 205-day weight did not interact with the year effects. This demonstrates low plasticity in the indigenous breeds, indicating more tolerance to variation in the environment. During the years in which the data for this study were collected, breed additive effects and heterosis were smaller than anticipated.
- During the postweaning period, breed group effects on daily feed intake and partial body weight were not detected ( $P > 0.05$ ). As expected, the animals ate more and became heavier as the test progressed ( $P < 0.05$ ). In partitioning the interaction of breed group with days on test into single degree of freedom effects, only the effect of individual heterosis on partial body weight ( $0.99 \pm 0.35$  kg/day) was significant ( $P < 0.01$ ). Breed group effects were not detected for either the partial regression of daily feed intake on partial body weight or the partial regression of partial body weight on daily feed intake. Thus, the breed-specific genetic effects were deemed unimportant.
- The binary indicator of heat stress was found to be highly significant for both daily feed intake ( $-9.69 \pm 1.31$  g/day) and partial body weight ( $48.2 \pm 2.1$  g/day). Animals that were heavier consumed more feed ( $37.7 \pm 4.8$  g/day;  $P < 0.01$ ) and animals that consumed more feed were also heavier ( $57.1 \pm 9.3$  g/kg;  $P < 0.01$ ), as expected.
- The serial correlation daily feed intake indicates marked differences among animals in their feeding behaviour. However, it does not appear these differences are related to the breed composition of the animals. The average serial correlation in daily feed intake was interpreted to suggest a test period of 36 days was needed to achieve 80% accuracy for the mean feed

intake. The very large estimate of the serial correlation of partial body weight indicates that values from individual days are quite useful. Thus, there is little need to average values over days to achieve an accurate estimate of partial body weight at any specific point in time.

- Plasticity was indicated by interactions of genetic effects with time; year in the preweaning phase and day on test in the postweaning phase. The breed groups differed significantly in their plasticity of feed intake during the postweaning phase. The Nguni, Simmentaler, Afrikaner, and Angus breed direct effects indicated more inter-day variability in daily feed intake than the Bonsmara direct effect. Likewise, the Nguni maternal genetic effect was greater than that of the Bonsmara.
- The estimated heterosis effect was small and not significant indicating that crossbred cattle would be no more variable over time in feed intake than were their straightbred counterparts. Taken together, these results indicate that Bonsmara cattle would not be as sensitive to changes in the temporal environment in the feedlot as the other breeds and crosses would be.

Breeds interact differently with the environment in which they are raised, and this interaction (effects) is more complex than simple differences in average performance. There is currently a follow up project which will investigate more in-depth the use of less plastic genotypes in a structured crossbreeding programme to the benefit of emerging and subsistence farmers, as they do not have sufficient resources to offset temporal environmental effects.

Crossbreeding is a technology that can potentially; 1) aid in alleviating poverty by improving production efficiency; 2) improve food security by increasing the supply of beef; and 3) improve sustainability by achieving a more appropriate balance of meat production relative to its carbon footprint. However, this technology remains underutilized in South Africa. The lack of objective information from local research may be one reason why farmers do not make proper use of crossbreeding. Failure of the research community to formulate experimental results in the context of production systems that benefits farmers is also evident.

Relative few experiments have been conducted to evaluate the crossbreeding technology in South Africa. Internationally, such experiments have not made use of breed resources that are indigenous to South Africa. The experiments that have been conducted in South Africa have not consistently summarized the results at a production system level as opposed to having done so on a trait-by-

trait basis. It is proposed that the available information from locally conducted experiments be collated in a standardized format and summarized at a production systems level. The generated information should be transferred via extension officers to emerging and subsistence farmers that can assist them in choosing bulls that will produce beef more efficiently and facilitate their entry into commercial market channels.

The adoption of the correct crossbreeding technology is anticipated to improve the wellbeing of economically disadvantaged farmers. Particular emphasis should be given to crossbreeding systems that can be implemented with a small number of cows, as opposed to those that require several camps for breeding management.

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## Ethical Approval



Date: 25 January 2021

Dear Prof. M M Scholtz,

Re: Renewal of "Climate-smart beef production systems to mitigate global warming "

Your application for the renewal of ethical evaluation of the project entitled "Climate-smart beef production systems to mitigate global warming" has been finalised and approved. Its Ref no is APIEC 21/06 (old 18/16).

I would like to inform you that the project was evaluated and found to be ethically acceptable.

Please note that should any more amendments or changes be made to the protocol, you are obliged to submit an amended application to the Animal Ethics Committee. A hard-copy of this application letter of approval must be available at the site office where animals are kept, including a copy of the protocol, a copy of the signed ethical application, all related SOP's and data monitoring sheets. Further, you will need to inform the committee when the animals will enter the facility, the starting date of the trial and end date of the trial. This approval is valid for two (2) years, projects that are continuing after this will need to re-apply. Failure to comply may lead to withdrawal of the ethical approval. Any neglect finding against this project may result in the applicant being held personally responsible and subjected to the Animal Protection act (Act 71 of 1962).

Regards,

A handwritten signature in blue ink, appearing to read "Klaas-Jan Leeuw".

Dr. Klaas-Jan Leeuw (D-Tech Agric.)

Chairperson: ARC-API Ethics Committee

Tel. No. 012 672 9320

E-mail / E pos: [kleeuw@arc.agric.za](mailto:kleeuw@arc.agric.za)