RANDOM REGRESSION MODELS IN THE ANALYSIS OF FEED INTAKE AND BODY WEIGHT OF INDIVIDUALLY FED BEEF BULLS IN SOUTH AFRICA

BY

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CHAPTER 1

1. General introduction

The South African National Beef Cattle Improvement Scheme (NBCIS) of the Agricultural Research Council (ARC) records measurements of feed intake, body weight and other traits such as scrotum circumference, body measurements, functional appearance scoring and condition scoring during Phase C of bull performance tests. During these tests, young bulls are fed individually and their post-weaning growth rate and feed conversion ratio are evaluated under standardized conditions. Measurements of feed intake, which is the quantity of feed consumed by the animal, are difficult to take and are the most costly inputs of beef production systems. Feed intake (FI) has been used for assessing feed efficiency in beef cattle (Schenkel *et al*., 2002a).

Traits, such as feed intake and weights of animals, which are recorded repeatedly over a lifetime of an individual, are referred to as longitudinal data where the trait of interest changes gradually but continually, overtime (Meyer, 1999). The South African National Genetic Evaluation Program uses averages (i.e. average daily gain and daily feed intake) and therefore do not take into account the longitudinal nature of the data. In animal breeding, the simple repeatability models have also been applied to analyze longitudinal data, i.e. assuming all records are repeated measurements of the same trait with constant variances.

Random regression models (RRM), a statistically better way of dealing with traits that are measured over time, were introduced by Henderson (1982) and Laird and Ware (1982). RRM provide more accurate estimates of variation in traits and fit a continuous covariance function to an existing covariance matrix or fits a set of random coefficients for each individual to allow for individual variation in the course of the trajectory (Kirkpatrick and Heckman, 1989). Currently, measurements are corrected towards certain landmark ages in the South African beef cattle evaluation, because it is not practical to measure all animals at the same age or time. This study focuses on a method of genetic evaluation (RRM) that does not require measurements to be corrected towards certain landmark ages.

The RRM procedures are already being applied in the National Genetic Evaluation of livestock in many countries. RRM were introduced to the South African beef cattle industry by Nephawe (2004), analyzing mature body weight data of Bonsmara cows. However genetic parameters, which are required inputs for genetic evaluation, are not available for Phase C measured traits in South Africa. The aim of this study was to apply random regression models in analyzing feed intake and body weight of individually fed Bonsmara bulls at central performance testing stations in South Africa. RRM is expected to increase the accuracy of the genetic evaluation of feed intake and body weights. Specific objective was to estimate genetic parameters for weekly cumulative feed intake and body weights for Bonsmara bulls participating in the centralized performance tests of the South African National Beef Cattle Improvement Scheme using random regression models. The Bonsmara is the most numerous beef breed participating in the NBCIS.

2. Literature review

2.1. The South African National Beef Cattle Improvement Scheme

The NBCIS, which is administered by the ARC, is aimed at performance recording of beef testing beef cattle in order to enhance profitability of beef cattle enterprises. The scheme supplies beef cattle farmers with the objective performance information and estimated breeding values (EBVs) for selection of breeding stock.

The scheme comprises five phases namely Phase A, B, C, D and E, to cover the production cycle. Phase A is the reproduction phase where reproduction and ease of calving of cows are evaluated using calving data. Mothering ability and efficiency of cows and the pre-weaning data on growth rate of their calves are also evaluated. During Phase B, post weaning growth rate of young heifers and bulls is evaluated under normal farming conditions by means of their weights at 12 and 18 months of age. Phase C, also called Central Bull Performance Tests, is where young beef bulls are fed individually and their post-weaning growth rate and feed conversion ratio are evaluated under standardized conditions at central bull performance testing centres. During Phase D, the post-weaning growth rate of young beef bulls is evaluated by means of performance tests under controlled farming conditions on the farm of a member. Phase E is the slaughtering phase where meat and carcass quality are evaluated using carcass data from the abattoirs and laboratory analysis of the prime rib cut. Further details of the NBCIS are available in the NBCIS guidelines (NBCIS, 2005).

2.2. The standardized central performance tests of young beef bulls (Phase C)

The Phase C tests are conducted by sending bulls from different herds to central performance testing stations where performance data are collected for a number days on test, following a pre-test adjustment period of 28 days. Before 1990 and between 1991 and 1998, up to 20 and 16 weekly measurements of feed intake and body weights were taken, respectively. As per recommended by Archer and Bergh (2000), from 1999, the test period was shortened to 84 days. During the tests, bulls are placed in pens with electronic gates, which allow individual access to particular feeders. Body weights are recorded every week after a 12-h overnight fast during which animals had no access to food or water. The bulls are fed on a pelleted ration containing 13.0 MJ ME/kg dry matter and 13% protein. The ration was composed of 39% maize, 11.9% wheat pollard, 7.5% cottonseed, 5% lucerne, 20.5% maize straws, 9% molasses, 0.5% urea, 3.4% hominy chop, 0.5% salt, 1.4% limestone ground, 0.35 monocalcium phosphate and 0.2% vitamin-mineral premix which included the rumen modifier rumensin (Archer and Bergh, 2000).

Animal feeds and feed measuring techniques are major expenses of the central bull performance testing stations. The duration of the bull performance tests affects the costs of central performance testing station (i.e. the longer the performance tests the higher the feeding costs). The reduction of the duration of the performance tests was of much concern in the late nineties and the early twenties, where several studies (Archer *et al*., 1997; Archer and Bergh, 2000) have been published between 1991 and 2000. In order to minimize the costs of animal feeds and bull performance tests, the test should be optimized in terms of length of test and amount of data without compromising accuracy (Archer *et al*., 1997). Brown *et al*., (1991) assessed the possibility of reducing the duration performance tests from 140 day to 112 or 84 days using data from tests in which a moderate-energy diet, were fed. In their study, bulls representing 13 breeds were evaluated. Models were fitted to average daily gain, daily feed intake and feed conversion for day 1 to 140 and from day 1 to day 112. The regression coefficient indicated that bulls ranked similarly for performance traits at 84, 112, and 140 day. It was concluded that the information upon which selection decision are based is similar, then, there is no advantage of feeding bulls beyond 84 days of age.

Liu and Makarechian (1993) investigated the possibility of increasing the adjustment period using the ten breeds of cattle in Canada. The results indicated that the period between day 28 and day 112 of the standard test was less affected by the herd of origin as compared with the 140-day test period and therefore could be considered as the shortest optimum test period. Average daily gain in this period was least affected by herd of origin and had relatively high heritability estimates which would ensure satisfactory selection response. The study concluded that, in order to properly evaluate growth potential of beef bulls and economically make use of the testing facilities, it would be appropriate to have an adjustment period of 56 days (instead of the original 28 days) followed by a test period of 84 days. The implementation of that kind of performance test was believed that it would result in reduction in management costs while providing a more accurate evaluation of growth potential of young beef bulls.

The optimum duration for bull performance test was suggested to be 70 days by Archer *et al*., (1997). The duration was examined from data on four British breeds (Angus, Hereford, Polled Hereford and Shorthorn). Variance components, heritability estimates, phenotypic and genetic correlations and the efficiency of selection using shortened tests compared with a 119-d test were used as criteria to assess the optimum test length. The results indicated that a 35-day test was sufficient for measurement of feed intake, whereas a 70-day test was sufficient for growth rate, feed conversion and residual feed intake without compromising the accuracy of measurement. The study concluded that a 70-day test with cattle weighed every second week seems to be optimal for measuring these traits in British cattle.

The study of Archer and Bergh (2000) assessed the duration for accurately measuring traits at central performance testing stations in South Africa. Data representing five breeds from the central beef bull performance testing stations were used. The results indicated that a test period of between 42 and 56 days was sufficient for measurement of growth rate when a linear regression equation is used to model weight against time. Feed intake needed 56 to 70 days to be measured accurately. Feed conversion ratio and residual feed intake both required around 70 to 84 days. It was concluded that the duration of performance tests could be shortened from 112 days to 84 days for all breeds with no loss in accuracy.

2.3. Different measures of efficiency and relationship with growth traits

Animal feeds are one of the important costly inputs of animal production. Owing to the difficulty and high cost of feeds and the mechanical systems used to measure feed intake, little attention has been paid to the genetic improvement of the efficiency of feed utilization in beef cattle (Arthur *et al*., 2001). Lately, there have been some advances in electronics and computing techniques that make it relatively easy to measure feed intake in livestock.

In order to increase beef productivity, cattle that are capable of efficiently converting feed to live-weight should be identified. There are a number of factors that influence feed conversion ratio or the efficiency of feed use, such as live-weight, sex, live-weight gain and breed of the animal (Morris, 2003). All of these factors are essential when comparing feed efficiency or feed conversion among groups of cattle from various production systems. Live-weight affects FCR through its effect on maintenance requirements. The heavier the animal, the greater its maintenance requirements to be able to grow at the same rate as lighter animals, which mean that their production requirements are higher. Therefore lighter animals with lower maintenance and production requirements need less feed to grow at the same rate as heavier animals, which means they use feed more efficiently.

The sex of animal can also influence FCR. At maintenance, the requirement of feed by bulls is actually greater than that of steers of the same live-weight. Sex can also affect FCR through the composition of live-weight gain, which contains more protein and less fat in bulls than that of steers (Morris, 2003). The other difference between sexes is their potential for live-weight gain, with entire males having a greater potential than castrates or females, due to the composition of gain effect and mature body weight.

Feed conversion ratio can also be affected by breed type. Faster growing breeds have leaner gain and therefore a higher FCR. On the other hand, faster growing breeds also become heavier and this counts against FCR. Lighter cattle of the same breed and sex, growing at the same rate, as heavier ones will require less feed per unit of gain (Morris, 2003).

Although FCR is an important component of intensive beef production, the seasonal pattern of the feed demand is also of significance. The lower the winter demands and the higher the spring demands, the lower the need for expensive pasture conservation. When selecting animals that are more efficient in their feed utilisation, the major disadvantage of selecting for FCR is that it increases mature weight and there is a highly undesirable correlated response in the breeding cowherd (Morris, 2003).Feed intake and measures of feed efficiency are known to be heritable in beef cattle. It has also been known that most of the measures of feed efficiency are related to each other and to measures of growth (Arthur *et al*., 2001). It is therefore of importance to know to which extent these traits are related.

Arthur *et al*., (2001) computed the genetic and phenotypic relationships among different measures of growth and feed efficiency in young Charolais bulls. The genetic and phenotypic variation and correlation among post weaning growth and feed efficiency traits were estimated using performance and progeny test data on young Charolais bulls in France. Nine growth and efficiency traits were studied and (co) variances were estimated by multivariate analysis using an animal model. Heritability estimates were high; 0.34 for ADG and 0.48 for FI, 0.46 for FCR. FCR showed a negative genetic correlation (-0.46) with ADG and a positive genetic correlation with FI (0.64). FCR was highly correlated with relative growth rate (r_g = 0.90) and Kleiber ratio, defined as weight gain per unit of metabolic body weight, (r_g = -0.81), two traits which do not require measurement of feed intake. The measure of residual feed intake (RFI) where the expected feed intake (EFI) was calculated from the data set was highly correlated genetically (r_g = 0.89) with RFI where EFI was calculated from feeding standards formulae. Both RFI measures had a high genetic correlation ($r_g \geq 0.85$) with FCR.

Van der Westhuizen *et al*. (2004) analyzed the genetic relationship between feed efficiency and profitability traits in Bonsmara cattle. The heritability estimates for the three traits, ADG, RFI and FCR, were also found to be moderate (0.37, 0.31 and 0.34 respectively). The study revealed a negative genetic correlation between FCR and ADG (-0.69) and a positive one between FCR and RFI (0.75). The genetic correlation between ADG and RFI was negative (-0.09).

2.4. The effect of the herd of origin on individual bull performance in central performance testing stations

The central performance testing stations are essential to sire selection and breed utilization. However individual bull performance in central test stations depends upon several pre-weaning and post-weaning genetic and environmental factors (Cain and Wilson, 1983). Therefore, in order to select superior sires from within and among central testing stations, it is necessary to determine the influence of genetic and environmental factors contributing to test performance and to have an understanding of the variability of test traits (Cain and

Wilson, 1983). The effects that contribute to the variation in phenotypic observations during performance tests start as far as the bull's herd of origin. There have been several studies analyzing the effect of the herd of origin on performance of bulls at central performance testing stations. Tong *et al*., (1986) examined the effect of herd of origin and the relationship between pretest and station test environments from pre-weaning and post-weaning performance records of Hereford, Angus and Shorthorn calves. The herd of origin by year effects was significant for all performance traits studied. The herd of origin by year mean squares accounted for 26% of the total variation in the pretest period to a maximum of 54% in the adjustment period and decreased to 7% in the 140 day period. The low environmental correlations suggested that the performance of calves at Brandon and Lacombe central performance testing station were not affected by variation in pretest herd environment.

The effect of herd of origin on genetic evaluation of weight gain of beef bulls in central performance testing stations was examined by Schenkel *et al*., (2004) using a univariate and bivariate analyses. The model included bull's estimated weight gain on test and pre-weaning gain of bulls and their contemporaries in the herd of origin. Estimated weight gain on test was estimated fitting fixed linear regressions to the weights on test of each bull. The bivariate model included random direct additive genetic and dam effects and fixed breed effects for both traits, fixed management group and sex of calf by age of cow effects for pre-weaning gain and fixed test group and random herd of origin by year effects for estimated weight gain on test. Variance components and breeding value estimates were obtained with or without herd of origin effect, which were compared using likelihood ratio test statistic and two information criteria. The effect of herd of origin was significant on estimated weight gain on test, contributing 8% to total phenotypic variation. The interaction between the sire and the herd of origin was found not to be of concern.

Nephawe *et al*., (2006) investigated the effect of herd of origin by year on the post-weaning traits for Bonsmara bulls at central-performance testing station in South Africa. The traits of interest were average daily gain (ADG), daily feed intake (DFI), shoulder height (SH) and scrotal circumference (SCR). A multiple-trait animal model was used to estimate (co)variance components using REML procedures. The contribution of the herd of origin by year to the phenotypic variance were 9%, 10%, 6%, and 5% for ADG, DFI, SDH and SCR, respectively. They concluded that the effect of the herd of origin by year should be included in the model for the national genetic evaluation of post-weaning traits of beef bulls measured at central performance testing stations in South Africa.

2.5. Random regression models

Traits such as feed intake and body weight, which are measured repeatedly were a lifetime of an individual, are termed longitudinal data. In animal breeding, RRM have been used in analyzing data of feed intake (Schenkel *et al*., 2002a; Huisman *et al*., 2002a), intramuscular fat (Hassen, *et al*., 2003), weight gain or growth (Meyer, 1999 and 2004; Huisman *et al*., 2002b, Arango *et al*., 2004) and test-day production in dairy (Swalve, 2000). Traits, such as feed intake and body weight, which are measured repeatedly over a lifetime of an individual, are termed longitudinal data. The RRM have many advantages: (1) they are able to predict covariance structures at any point along a continuous scale, (2) they require fewer parameters to describe longitudinal data and estimate (co)variances smoother and with less bias as compared to multivariate model, (3) they allow for a theoretically more complete model, (4) have better properties for genetic evaluation and, (5) they offer more powerful approach to evaluate repeated measurements to determine genetic merit (Kirkpatrick and Heckman, 1989). RRM allow the researcher to study changes in genetic variability with time and allow selection of individuals to alter the general patterns of response over time; however, more research in this area is still needed (Schaeffer, 2004).

Schenkel *et al*., (2002a) used random regression models in the analyses of feed intake of bulls at central performance testing stations. The objective was to assess the optimum length of test and to estimate genetic and environmental parameters of feed intake using random regression models. The data used in the study was from daily dry matter intakes of crossbred steer calves in Canada. The RRM included fixed linear regression effect on breed composition and fixed regressions on third order orthogonal Legendre polynomials of the actual days on test for starting age and herd of origin effects and third or fifth order Legendre polynomials for test group effect. Random regressions on third order polynomials were included for permanent environment (PE) and additive genetic animal effects. Residuals were assumed independently distributed with heterogeneous variance for each week on test. The results from the genetic and environmental parameters and genetic eigenfunctions indicated that a short period of 28 days, starting between 57 and 85 days on feed, would be sufficient for evaluating feed intake. It was reported that random regression analysis of daily feed intake of beef cattle provided genetic and environmental parameters useful for examining the optimum duration of test.

There have been several applications of random regression models to feed intake in pig production systems. Schnyder *et al*., (2001a) estimated genetic parameters for daily feed intake of performance tested French Landrace and Large White growing pigs using random regression models. A quadratic polynomial in days on test with fixed regressions for sex and batch, random regressions for additive genetic, pen, litter and individual permanent environmental effects was used. Variance components were estimated from weekly means of daily feed intake by means of Bayesian analysis using Gibbs sampling. Genetic eigenfunctions revealed that altering the shape of the feed intake curve for pig breeds in the analysis is difficult.

Schnyder *et al*., (2001b) used random regression models in assessing the impact of variation in length of individual testing periods on estimation of (co) variance components for feed intake of growing pigs. A quadratic polynomial in days on test with fixed regression for sex, random regressions for additive genetic and permanent environmental effects and a constant residual variance was used for a bivariate simulation of feed intake and daily gain. (Co)variance components were estimated for feed intake by means of Bayesian analysis using Gibbs sampling and Restricted Maximum Likelihood (REML). The test day variances calculated from estimates of additive genetic and permanent environmental covariance matrices revealed that no bias in estimates of (co)variance components occurs due to the individual length of testing periods of performance-tested growing pigs.

Schenkel *et al*., (2000b) applied random regression models to analyze weight gain of station tested beef bulls. Two sets of analyses were conducted in this study. Firstly, the two-step model was applied where a linear regression of the weights on the actual days on test for each bull was calculated. Secondly, the bull's calculated gain on test as obtained was used as an "observation" in the genetic evaluation model. The model included fixed effects of the breed, starting age and test group, cubic random regression of the weights on days on test for weaning-herd-year group effect and for permanent environmental and additive genetic effects of the bull. It was concluded that the use of a joint procedure, via random regression model, for analysis of bull's performance records allows the use of more complete than the usual two-step procedure and random regression model could accommodate deviations from linearity and would be a step forward to a more accurate model.

Nobre *et al*., (2002) evaluated growth in beef cattle using the random regression model. The data was collected by the Brazilian Zebu Breeders Association with weight records on Nellore animals that were under Brazilian pasture conditions. They used two models for data analyses being multi-trait model (MTM) and random regression model. They concluded that genetic evaluation for growth in large populations of beef cattle by RRM is technically possible. However, they also stated that genetic values by RRM can be poor because of poor numerical properties, poor estimates of parameters and that good parameters may be hard to obtain directly by estimation with RRM and may have to be constructed from estimates from MTM.

Other applications of random regression models on beef cattle were on body weight of mature cows. Meyer (2000) modeled phenotypic variation in monthly weights of Australian beef cows using random regression models. Only phenotypic random regressions for animal effects, ignoring relationships were considered. Estimate of covariances between regression coefficients and error variances were obtained by REML. Analyses identified a cyclic, seasonal pattern of variation, both between animals and for temporary environmental effects. Orthogonal polynomials also proved to be capable of modeling cyclic pattern of variation but required a high order of fit (meaning a large number of parameters).

Arango *et al*., (2004) used random regression models in analyses of cow weight in beef cattle using orthogonal Legendre polynomials of age in months. Random parts of the model fitted RRM coefficients for additive and permanent environmental effects and temporary environmental effects were assumed to have heterogeneous variance by age in years. Quadratic fixed regression was reported to have fitted population trajectory sufficiently. Linear and quartic random regression coefficients were fitted for the additive genetic and the permanent environment, respectively. Results suggested that although cow weights do not fit a repeatability model with constant variances as well as covariance function-random regression model, a repeatability model might be an approximation for prediction of additive genetic effects.

Nephawe (2004) analyzed mature weights data of Bonsmara cows using random regression models using orthogonal Legendre polynomials on age in months. Fixed regressions were fitted to age in months and for contemporary group effects. The model also included the

RRM coefficients for additive and permanent environmental effects, while residual effects were modeled to account for heterogeneity of variance by age in years. The resulting covariance functions were used for estimation of breeding values along the trajectory for each animal. The results suggested that cow weights did not change much and that selection for cow weight could be effective. However, it was concluded that for practical purposes, simple repeatability models might be approximate for prediction of breeding values.

RRM were used in analysis of growth in pigs by Anderson and Peterson (1996) where pigs were weighed twice a week from 30 to 115 kg live weight. Weight gains were modelled as function of time, but were also modelled as function of feed intake from which a measure of efficiency was derived (i.e. the genetic merit for growth was a function of the amount of feed intake). The fixed curves of the model were a fourth order polynomial of days on test, while the order of random regressions was two. Growth rate was fairly linear between 30 and 50 days on test, and further decreased between 50 and 80 days on test, for both gilts and castrated males. Rather than model weights against feed intake, a multiple trait RRM model having both weight and feed intake traits against time on test would be a better way to examine feed efficiency without reducing the genetic variation in weight. A multiple trait RRM would simultaneously account for the changes in genetic and residual variation in each trait while allowing both traits to vary together with time. The general concept would be not to model trait against another if they are genetically correlated (Schaeffer, 2004)

Huisman *et al.*, (2002b) estimated genetic parameters for live weight of pigs using random regression models. The computer program SelAction was used to calculate the accuracy of selection on various indices. RRM performed better in the description of weight data of growing pigs and gave better estimates compared to multivariate model. When weight was fitted as a function of age in the random regression model, the fact that not all animals were weighed at the same age was taken into account. Daily feed intake (DFI) increased from the start of the growing period. Total variance of DFI increased over test, while genetic variance was fairly constant. Heritability estimates therefore decreased over test. The advantages were found to be (1) a higher accuracy of selection, (2) the use of information of the course of traits, and (3) the possibility to change the course of traits through selection.

In the study, “a genetic evaluation of growth in sheep using random regression model”, by Lewis and Brotherstone (2002), random regression models were compared to the Gompertz approach. The Gompertz approach uses a function with properties that describes growth as a comparatively simple equation. It has three parameters, of which the important ones are mature size and rate parameter (Emmans and Kyriazakis, 1997). Lewis *et al*., (2002) describes the Gompertz function as one of the growth functions that, when the environment (e.g. feeds, housing) is non-limiting, provides a useful description of growth as a comparatively simple, single equation. Analyses using random regression models yielded estimates of covariance functions that can be evaluated to provide estimates of genetic and environmental (co) variance components for every age (in days) on test. The conclusion was that, despite potential limitations, random regression has better properties for genetic evaluation and solutions for genetic and environmental effects are obtained simultaneously for all animals allowing family information to be used in the estimation. This was not the case in the two-step process used in the Gompertz approach. The RRM method offered a more powerful and flexible means than the Gompertz approach for evaluation of repeated live weight information to determine genetic merit.

McKay *et al*., (2002) analyzed growth curves in rainbow trout using random regression model. Heritability estimates for rainbow trout were reported to change with age and selection response might be maximized if selection is applied when heritability was the highest. After applying the RRM they concluded that RRM were useful in evaluating individual growth data for rainbow trout population and the technique allowed characterization of age trends for heritability and comparison of growth curves for different sexual maturity group categories.

The literature shows that RRMs are the most preferred models in analyzing longitudinal data or repeated records on individual individuals over time.

CHAPTER 2

ANALYSIS OF FEED INTAKE OF INDIVIDUALLY FED BEEF BULLS USING RANDOM REGRESSION MODELS

Abstract

The objective of the study was to estimate genetic parameters for weekly feed intake (FI) of beef bulls measured at centralized testing stations in South Africa using random regression models (RRM). Records of FI on Bonsmara bulls (n = 3 012) collected at various central performance testing stations in South Africa between 1999 and 2003 were analyzed. The model included the fixed linear regression of cumulative feed intake on third order orthogonal Legendre polynomials of the actual days on test (7, 14, 21, 28, 35, 42, 49, 56, 63, 70, 77 and 84 day) for starting age group and contemporary group effects. Random regressions on third order orthogonal Legendre polynomials were included for additional random effect of weaning-herd-year (WHY) effect and additive genetic effect of the animal and on fourth order for the additional random permanent environmental effect of the animal. The residual effects were assumed to be independently distributed with heterogeneous variance for each measurement period. Variance ratios for additive genetic, permanent environment and WHY for cumulative FI at different ages ranged from 0.07 to 0.10, 0.53 to 0.77 and 0.14 to 0.37, respectively. Estimates of genetic correlations among feed intake at different test days were high (>0.79) for any given pair of test days. The first additive genetic eigenfunction (with 95.6% additive genetic variance contribution) revealed that selection for decreased cumulative FI at any test day would tend to decrease cumulative feed intake throughout the test and vice versa. Random regression model could be used in genetic evaluation of cumulative feed intakes of individually fed beef bulls in South Africa.

1. Introduction

Animal feeds and feed intake measuring techniques are major expenses of bull central performance testing stations in beef production systems. Inclusion of feed intake information in selection decisions would ensure that genetic improvement of efficiency and profitability of beef cattle are facilitated (Archer *et al*., 1997). Several models such as the repeatability models have been used to analyze traits like feed intake that are measured repeatedly during a lifetime of an individual.

RRM were introduced in animal breeding by Henderson (1982) and Laird and Ware (1982). RRM can be used to calculate (co)variances between or at any age or time point. The covariance between two measurements at different ages is a function of the ages and some basic coefficients (Kirkpatrick *et al*., 1990). The advantages of RRM over multiple trait model (MTM) are that RRM require fewer parameters to describe longitudinal data and estimate (co)variances smoother and with less bias, allow for a theoretically more complete model, and have better properties for genetic evaluation and offer more powerful approach to evaluate repeated measures to determine genetic merit (Kirkpatrick and Heckman, 1989). Meyer and Hill (1997) considered the application of RRM to animal breeding data. In beef cattle, the method was outlined by Varona *et al*., (1997) and has been applied in many research studies (e.g. Meyer, 1999 and 2000; Arango *et al*., 2004). To feed intake data, most emphasis has been on pigs (Schnyder *et al*., 2001a; 2001b) and dairy cattle (Veerkamp and Thompson, 1999).

The objective of this study was to estimate the (co)variance components and variance ratios for feed intake of beef bulls at central performance testing stations in South Africa using random regression models.

2. Materials and methods

2.1. Data

Data on Bonsmara bulls extracted from the South African National Beef Cattle Improvement Scheme (NBCIS) database were used in this study. Data consisted of records for bulls (n = 3 012) that had 12 measurements of weekly feed intake each, collected at various performance testing stations (Phase C) between 1999 and 2003. Bulls were placed in pens with electronic gates, which allowed individual access to particular feeders, and feed intakes were recorded every week during the test period. Bulls were fed on a pelleted ration containing 13.0 MJ ME/kg dry matter and 13% protein. The ration composed of 39.8% maize, 11.9% wheat pollard, 7.5% cottonseed, 5% lucerne, 20.5% maize straws, 9% molasses, 0.5% urea, 3.4% hominy chop, 0.5% salt, 1.4% limestone ground, 0.3% monocalcium phosphate and 0.2% vitamin-mineral premix which included the rumen modifier rumensin (Archer and Bergh, 2000). The bulls were tested for 84 days following a pre-test adjustment period of 28 days, as recommended by Archer and Bergh (2000). The weekly feed intake data was transformed into cumulative feed intake data (i.e. cumulative feed intake for week 2 = feed intake for week 1 + feed intake for week 2, cumulative feed intake for week 3 = feed intake for week 1 + feed intake for week 2 + feed intake for week 3, etc.).

A summary of the data analyzed in this study is given in Table 1. There were 194 contemporary groups, defined as the concatenation of test year, test number and the testing center where the bulls were tested. There were also 14 starting-age classes of tens (i.e. from

181 to 190 = starting-age class 2, from 191 to 200 = starting-age class 3, etc.). However, starting-age class 1 had the highest range of starting age, i.e. from 161 to 180, because of the few number of animals that fell under that starting-age range.

Table 1. Summary of the weekly cumulative feed intake data set

Feature	Number
Number of bulls	3 012
Weekly feed intake records per bull	12
Total number of records	36 144
Pedigree	12 441
Mean starting age	254
Range of starting ages	161-308
Starting-age classes	14
Weaning-herd-year group	253
Contemporary groups	194
Mean initial feed intake (kg)	58.66
Mean final feed intake (kg)	850.95

2.2. Statistical analysis

Cumulative feed intake for bulls were analyzed using random regression model. Following Arango *et al.*, (2004), several models were analyzed with different orders of fit for the orthogonal Legendre polynomials to find the best model of fit that would describe the data adequately with moderate number of parameters. The maximum of logarithm of likelihood estimates together with the eigenvalues were compared to select the best model to fit the random effects of the additive genetic and permanent environment of the animal. Prior assumptions about the shape of the trajectory to be modeled are not required when regressing on orthogonal polynomials (Meyer, 1998a). Initially, the same orders of fit were fitted for both the additive genetic and permanent environmental covariance functions, then later, each was allowed to have a different order of fit. The orders were kept constant for the fixed effects and the effect of the weaning-herd-year (WHY). The residuals for all models were assumed to be independently distributed with heterogeneous variance for each measurement period on test (i.e. variance for day 7, 14, 21, 28, 35, 42, 49, 56, 63, 70, 77 and 84 on test).

The general random regression model could then be represented as:

$$FI_{ij} = \sum_{p=0}^{n-1} b_p \varphi_p(d_{ij}) + \sum_{p=0}^{n\ -1} \alpha_p \varphi_p(d_{ij}) + \sum_{r=1}^{3} \ \sum_{p=0}^{n\ -1} \gamma_{r_p} \varphi_p(d_{ij}) + e_{ij}$$

where FI_{ij} is the j^{th} measurement of weekly cumulative feed intake on the i^{th} bull, b_p represents the fixed regression coefficients for the contemporary group (the concatenation of test year, test number and the test centre), α_p represents the fixed regression coefficients for the starting age class, γ_{rp} represents the random regression coefficients for the r^{th} random effect (i.e. WHY, additive genetic or permanent environment), d_{ij} represents the standardized actual days on test at recording for which Legendre polynomials are defined and $\varphi(d_{ij})$ were the respective p^{th} Legendre polynomials. The order of fit was denoted by n. The e_{ij} represented the residuals or the random residual effect.

In matrix notation the random regression model can be presented as follows:

$$\mathbf{y = Xb + Za + Z_c^{*}c + Z_q^{*}q + e}$$

y is a vector of observations on animals.

where **b** represents a vector containing fixed effects,

a are random regression coefficients for each animal representing the additive genetic contribution to the trait,

c are random regression coefficient for each animal representing the permanent environmental coefficient,

q are random regression coefficient for each animal representing the weaning-herd-year coefficient,

e is a vector of temporary environmental effects peculiar to each observation independent of age and animal,

X is the design matrix relating observations to the fixed effects,

Z is a matrix of standardized age covariates associated with each record and linked to all animals,

$\mathbf{Z_c}^{*}$ and $\mathbf{Z_p}^{*}$ are parts of **Z** corresponding to only those bulls with records, and

The first and second moments are:

$$\mathbf{E(y) = Xb}$$

$$\mathbf{Var}\begin{bmatrix} \boldsymbol{a} \\ \boldsymbol{c} \\ \boldsymbol{q} \\ \boldsymbol{e} \end{bmatrix} = \begin{bmatrix} \boldsymbol{Z(A \otimes K_A)Z'} & \boldsymbol{0} & \boldsymbol{0} & \boldsymbol{0} \\ \boldsymbol{0} & \boldsymbol{Z_c^{*}(I_c \otimes K_c)Z_c^{*'}} & \boldsymbol{0} & \boldsymbol{0} \\ \boldsymbol{0} & \boldsymbol{0} & \boldsymbol{Z_q^{*}(I_q \otimes K_q)Z_q^{*'}} & \boldsymbol{0} \\ \boldsymbol{0} & \boldsymbol{0} & \boldsymbol{0} & \boldsymbol{R} \end{bmatrix}$$

where $\boldsymbol{A}$, $\boldsymbol{I_c}$ and $\boldsymbol{I_q}$ are the numerator relationship matrix, an identity matrix for permanent environment and identity matrix for weaning herd-year, respectively. The $\boldsymbol{K_A}$, $\boldsymbol{K_c}$ and $\boldsymbol{K_q}$ are matrices for coefficients of the covariance functions (CFs) of genetic, permanent environmental and weaning herd-year (co)variances, respectively, with dimensions equals to order of fit of the CFs in the analysis; $\otimes$ is the direct matrix product and $\boldsymbol{R}$ is a matrix of the variance of the temporary environmental effects, which is a diagonal matrix allowing for heterogeneous variances by age in days on test.

DXMRR, a program for estimating genetic parameters for longitudinal data (Meyer, 1998b), was used to estimate (co)variance components. The matrices for coefficients $\boldsymbol{K_G}$, $\boldsymbol{K_c}$ and $\boldsymbol{K_q}$, and of the elements of $\boldsymbol{R}$ were estimated directly from the data by REML (Meyer and Hill, 1997). Average information-restricted maximum likelihood (AI-REML) procedure was chosen to maximise the likelihood function. The convergence of the covariance components was visually inspected by repeatedly fitting the estimated coefficients matrices values over iterations as starting values for estimation of (co)variance components. The convergence was declared when the variance of the log likelihood was less than 10^{-8}. The estimates of variance components converged within 38 rounds of iteration.

The effect of weaning-herd-year (WHY) on the post-weaning traits was investigated in previous studies (e.g. Tong *et al*., 1986; Amal and Crow, 1987; Schenkel *et al*., 2004; Nephawe *et al*., 2006). It has been shown that the weaning-herd-year should be included in the model to analyze post-weaning traits for bulls at central performance testing stations. In the current study, WHY was included as random in the model to determine its proportion ofvariance in weekly phenotypic measurements of feed intake.

3. Results and discussion

The mean and standard deviations for feed intake on each test day and are presented in Table 2. The mean values for weekly feed intakes gradually increased throughout the test and so did their respective standard deviations.

Table 2. Means for feed intake and standard deviations from all bulls for each test day of measurement

Test day	Mean (kg)	Standard deviation (kg)
7	58.66	15.45
14	122.91	26.62
21	188.30	36.87
28	255.78	46.86
35	325.58	57.27
42	398.48	66.20
49	471.31	75.96
56	546.17	84.75
63	622.73	92.29
70	699.63	101.01
77	775.20	108.61
84	850.95	116.90

3.1. Log likelihoods and eigenvalues

The fixed and random regressions on third order orthogonal Legendre polynomials were fitted for the fixed effects (contemporary groups and age-class-groups) and the effect of the weaning-herd-year in all models, respectively. The orders of fit were either different or similar for the additive genetic and the permanent environment.

Firstly, the second order polynomials were fitted for both the additive genetic and the permanent environment, and then later the orders were increased by one for each effect until both were modeled by the fourth order. The log likelihood values increased each time when the order of fit and number of parameters were increased for both the additive genetic and the permanent environmental random regression parts of the model, with the exception of the last model (model 3-4-4-3) where the log likelihood was essentially the same as the previously analyzed model (model 3-3-4-3). The model that included the third order for the additive genetic and the fourth order for permanent environment had the largest log likelihood value (-93,003.04), meaning that model 3-3-4-3 provided the “best” fit of the data among all the models investigated. The different models with the different orders of fit, number of parameters estimated per model and maximum of logarithm of likelihood estimates are presented in Table 3.

Table 3. Number of parameters estimated and their respective maximum logarithm likelihood for each model used in the analysis

Model[a]	**Number of parameters**	**Log likelihood**
3-2-2-3	12	-115,575.88
3-2-3-3	15	-111,057.19
3-2-4-3	19	-103,740.09
3-3-3-3	18	-111,049.64
3-3-4-3	22	-93,003.04
3-4-4-3	26	-93,008.22

[a] First digit = order of fit for fixed effects, second digit = order for additive genetic, third digit = order of fit for permanent environment, fourth digit = order of fit for the weaning-herd-year

The eigenvalues, their proportions (in percentages) and the variance matrix for the residuals are represented in Table 4. The eigenvalues suggested that the second order would be sufficient to model the regression polynomials for the additive genetic effects, but orders of fit were further increased to three and four as the increase in the order of fit resulted in the increase in the log likelihood for the model which fitted order three for the additive genetic effects. The increase in number of parameter and orders of fit to four for the permanent environment also decreased the error residual variances at each test day, indicating that the greater estimates of error variances for other models tended to pick-up variation due to insufficient order of fit (Meyer, 1999). This suggests that higher orders of fit greater than four for the permanent environment would fit the data even better.

The model that fitted the data adequately was found to be model 3-3-4-3; i.e. fitting fixed regression orthogonal Legendre polynomials on order three for all fixed effects and random regression on order three for the weaning-herd-year and additive genetic and order four for the permanent environment. Model 3-3-4-3 was chosen on the basis that (1) the model had the highest log likelihood; (2) the eigenvalues proportion looked sufficient to fit the effects better; and (3) the model was amongst those that provided the lowest estimates of the residual variances. Therefore, model 3-3-4-3 was used in subsequent analyses.

Table 4. Covariance function’s eigenvalues (ξ) and total variability proportions (**%**) for additive genetic (**G**), permanent environment (**PE**) animal effects and the weaning-herd-year (**WHY**) effect and the error variances for each model analyzed

Effect[a]	**Model**[b]											
	3-2-2-3		**3-2-3-3**		**3-2-4-3**		**3-3-3-3**		**3-3-4-3**		**3-4-4-3**	
	ξ	**(%)**	ξ	**(%)**	ξ	**(%)**	ξ	**(%)**	ξ	**(%)**	ξ	**(%)**
G												
0	2003.97	**(99.90)**	2006.74	**(99.85)**	729.97	**(99.53)**	1977.57	**(98.19)**	814.60	**(95.60)**	2106.09	**(95.56)**
1	1.93	**(0.01)**	2.99	**(0.15)**	3.46	**(0.47)**	35.24	**(1.75)**	36.57	**(4.29)**	63.41	**(2.91)**
2							1.12	**(0.06)**	0.95	**(0.11)**	10.75	**(0.49)**
3											0.45	**(0.02)**
PE												
0	4547.96	**(98.28)**	4530.93	**(95.77)**	7157.97	**(95.09)**	4551.55	**(96.39)**	8399.52	**(94.75)**	7312.01	**(97.48)**
1	79.55	**(1.72)**	192.14	**(4.06)**	287.90	**(3.82)**	162.77	**(3.44)**	290.28	**(3.31)**	152.85	**(2.04)**
2			8.07	**(0.17)**	68.21	**(0.91)**	7.93	**(0.17)**	69.56	**(0.79)**	32.25	**(0.43)**
3					19.41	**(0.26)**			12.99	**(0.15)**	3.53	**(0.05)**
WHY												
0	3163.28	**(97.51)**	3588.34	**(98.33)**	2113.77	**(98.84)**	3606.50	**(98.41)**	2155.38	**(96.42)**	4147.28	**(95.69)**
1	76.64	**(2.36)**	59.13	**(1.62)**	23.81	**(1.11)**	56.49	**(1.54)**	79.09	**(3.54)**	185.87	**(4.29)**
2	4.00	**(0.12)**	1.86	**(0.05)**	0.95	**(0.04)**	1.80	**(0.05)**	0.95	**(0.04)**	0.90	**(0.02)**
σ_e^2												
7	125.36		26.14		0.01		26.00		0.01		0.01	
14	35.95		55.21		48.58		55.28		48.59		49.57	
21	60.90		94.82		46.53		94.89		45.99		47.83	
28	110.95		107.46		44.48		107.48		43.70		44.49	
35	141.89		78.69		61.03		78.69		59.60		59.84	
42	147.80		57.31		73.99		57.25		72.59		73.59	
49	119.53		65.69		63.37		65.69		60.94		64.54	
56	73.62		83.00		38.28		83.04		36.38		39.81	
63	45.91		90.45		43.38		90.45		44.30		42.23	
70	90.24		76.11		58.75		76.08		58.98		58.00	
77	250.70		38.98		30.87		39.08		22.90		32.90	
84	588.08		198.44		139.50		198.61		161.36		126.24	

[a] 0 = intercept, 1 = linear, 2 = quadratic, 3 = cubic. [b] First digit = order of fit for fixed effects, second digit = order for additive genetic, third digit = order of fit for permanent environment, fourth digit = order of fit for the weaning-herd-year

To evaluate the eigenfunctions for each test day, the eigenfunctions were multiplied by the vector of Legendre polynomial coefficients for each test day and the results are presented in Figure 1. The first eigenvalue of the additive genetic covariance functions contributed about 95.6% of the total variance indicating that selection towards its direction (i.e. selection for increase or decrease in cumulative feed intake) would produce rapid changes. The first eigenfunction (95.6%) exhibited a positive linear pattern which indicates positive additive genetic correlations across test days as bulls' performance test days increased. This means that selection for decreased cumulative feed intake at any test day would tend to decrease cumulative feed intake throughout the test and vice versa. The second and third eigenfunctions explained less than 5% of the total variation of additive genetic effects. Schenkel *et al*., (2002a) found the first, second and third eigenfuntions to contribute about 75%, 24% and 0.8% in genetic variation for daily feed intake, respectively.

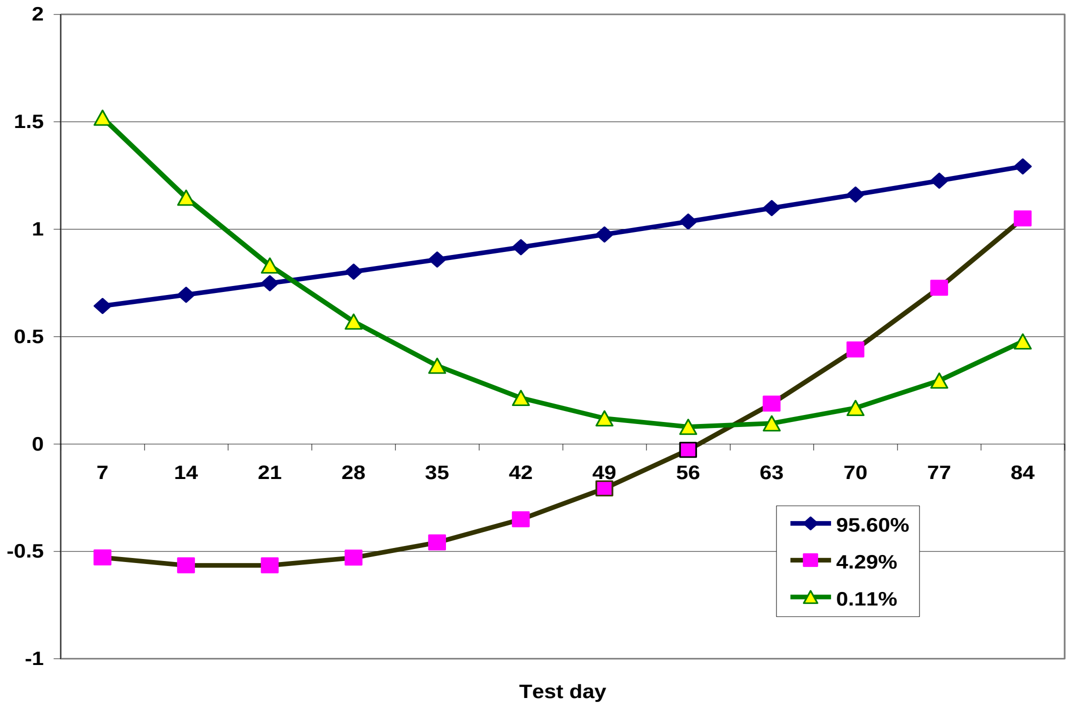

Figure 1. First, second and third eigenfuntions for cumulative feed intake at each test day for model 3-3-4-3 (eigenvalues, in contribution percentage, are presented in the legend)

3.2. Estimates of variance components

Estimates of variances for additive genetic, permanent environmental, weaning-herd-year and residuals, and their respective ratios for the range of days on test are shown in Table 5. The genetic variance estimates increased with increase in number of days on test from 83.51 kg^2 (at day 7) to 1084.64 kg^2 (at day 84). The heritability estimates slightly decreased with increase in number of days on test. The estimates ranged from 10% at the beginning of the test and declined to 7% at day 84. These heritability estimates exhibited a different pattern from that observed by Schenkel *et al*., (2002a) were the estimates increased as days on test increased.

The permanent environment ratio estimates started high (0.53) from the beginning of the test then increased to 0.77 at the end of the test. The permanent environment ratio estimates ranging from 0.13 (day 7) to 0.65 (at the end of the test) were observed by Schenkel *et al*., (2002a). The residual variance estimates fluctuated throughout the test and their respective ratio estimates started very low (< 0.00) at day 7 then rose to 0.04 at day 14 and decreased to 2% at the end of the test.

In general, the heritability estimates for feed intake at different test days were lower than both the estimated ratios for the permanent environment and the weaning-herd-year. The weaning-herd-year ratio estimates decreased from 0.37 at day 7 to 0.14 at the end of the performance tests. The weaning-herd-year had an important effect on the variation of cumulative feed intake, especially on the early days of the tests. Nephawe *et al*., (2006) analyzed post-weaning traits of Bonsmara bulls at central performance testing stations using a multiple trait model and found that the weaning-herd-year contribute about 10% to the phenotypic variation of daily feed intake.

Table 5. Estimates of variances for additive genetic ($\boldsymbol{\sigma_a^2}$), permanent environment ($\boldsymbol{\sigma_c^2}$), weaning-herd-year ($\boldsymbol{\sigma_q^2}$) and for the residual ($\boldsymbol{\sigma_e^2}$), and their respective ratios ($\mathbf{h^2}$, $\mathbf{c^2}$, $\mathbf{q^2}$, $\mathbf{e^2}$, respectively) for feed intake at different days on test.

Test day	$\boldsymbol{\sigma_a^2}$	$\mathbf{h^2}$	$\boldsymbol{\sigma_c^2}$	$\mathbf{c^2}$	$\boldsymbol{\sigma_q^2}$	$\mathbf{q^2}$	$\boldsymbol{\sigma_e^2}$	$\mathbf{e^2}$
7	83.51	0.10	455.51	0.53	324.78	0.37	0.01	0.00
14	118.90	0.10	594.01	0.51	409.71	0.35	48.59	0.04
21	162.69	0.10	874.58	0.55	521.07	0.32	45.99	0.03
28	212.29	0.10	1312.23	0.59	654.66	0.29	43.70	0.02
35	266.83	0.09	1958.83	0.63	806.63	0.26	59.61	0.02
42	327.25	0.08	2857.09	0.68	973.57	0.23	72.59	0.01
49	396.19	0.07	4012.73	0.71	1152.41	0.21	60.96	0.01
56	478.07	0.07	5385.01	0.74	1340.55	0.18	36.38	0.01
63	579.05	0.06	6895.44	0.76	1535.71	0.17	44.30	0.01
70	707.07	0.07	8454.88	0.77	1736.05	0.16	58.98	0.00
77	871.79	0.07	10008.81	0.78	1940.11	0.15	22.90	0.00
84	1084.64	0.07	11600.94	0.77	2146.82	0.14	161.36	0.02

3.3. Covariance estimates

The additive genetic, permanent environmental, the weaning-herd-year and phenotypic covariances between weekly cumulative feed intakes at different test days are presented in Figures 2 through 5. The additive genetic covariances estimates exhibited an increasing pattern with the increase in the difference between test days. The covariance estimates for the permanent environment and the weaning-herd-year also increased with increase in the difference between test days. In general, the additive genetic covariance estimates were lower than the covariance estimates for the other effects.

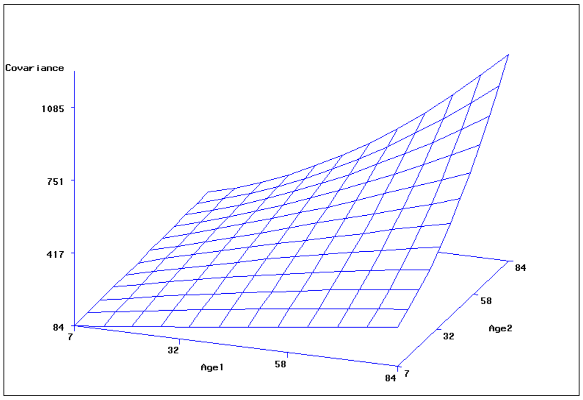

Figure 2. Additive genetic covariances between weekly feed intakes at different test days

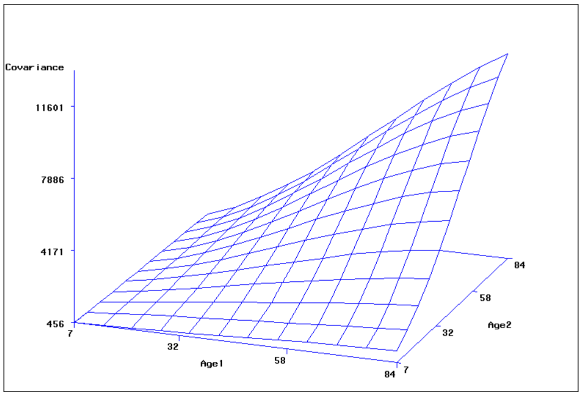

Figure 3. Permanent environmental covariances between weekly feed intakes at different test days

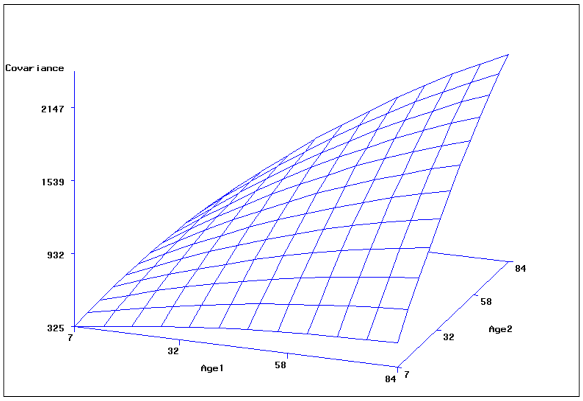

Figure 4. Weaning-herd-year covariances between weekly feed intakes at different test days

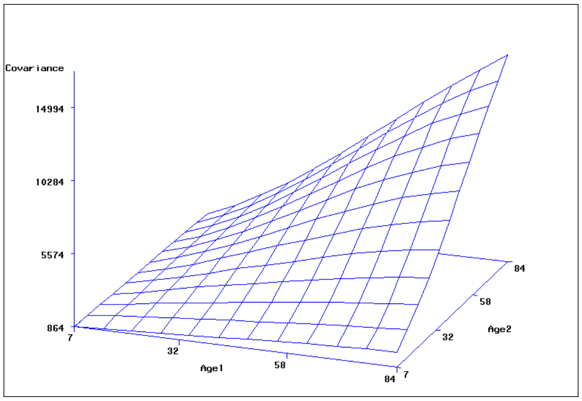

Figure 5. Phenotypic covariances between weekly feed intakes at different test days

3.4. Correlation estimates

In general, all correlation estimates decreased as the difference in days on test increased. The estimates of additive genetic, permanent environmental, WHY and phenotypic correlations between weekly feed intakes at different ages on test are presented in Figure 6 to Figure 9, respectively. Estimates of additive genetic correlation tended to decline as the difference in days increased, but were always higher than the correlation estimates for the permanent and the WHY effects, ranging from 0.80 at day 7 to 1.00 at the end of the test. Maximum correlation estimates closer to 1.00 between test days for permanent environment, WHY and phenotypic effects were observed and the minimum values were 0.46, 0.62 and 0.51 for the permanent environment, WHY and phenotypic effects, respectively.

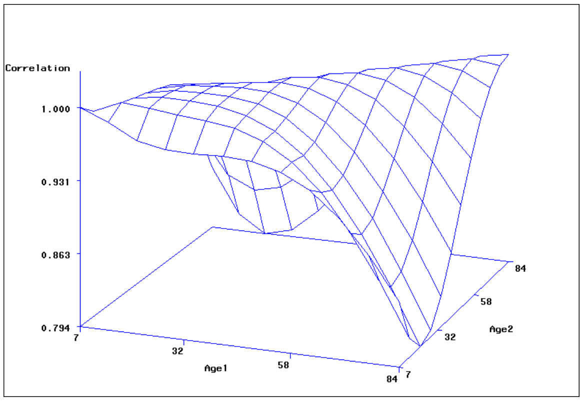

Figure 6. Additive genetic correlations between weekly feed intakes at different test days

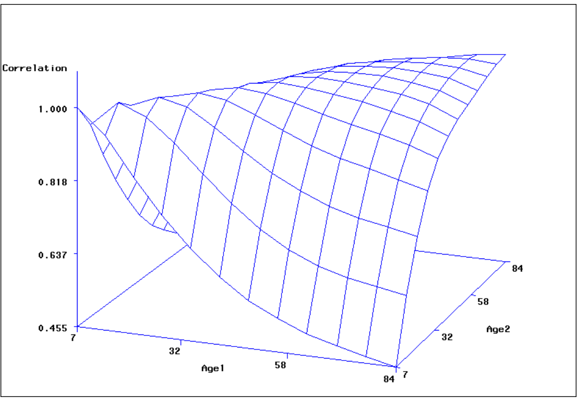

Figure 7. Permanent environmental correlations between weekly feed intakes at different test days

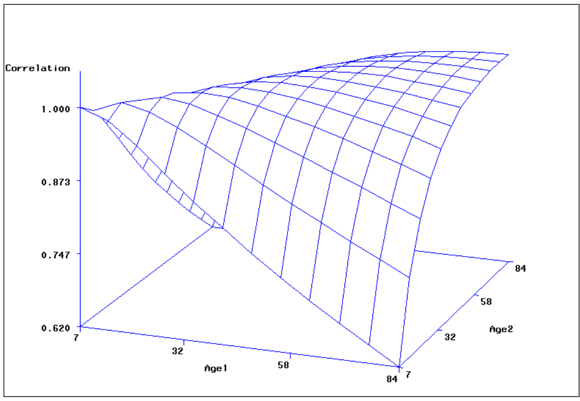

Figure 8. Weaning-herd-year correlations between weekly feed intakes at different test days

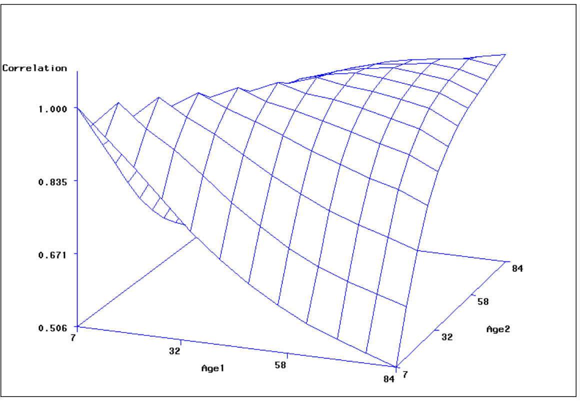

Figure 9. Phenotypic correlations between weekly feed intakes at different test days

4. Conclusions

Random regression models were used to analyze cumulative feed intakes of Bonsmara bulls at central performance testing stations in South Africa. The results suggest that fitting random regression orthogonal Legendre polynomials on third order for the additive genetic and order three for the permanent environment of the animal would suffice when modeling cumulative feed intake on test. The heritability estimates were lower than the estimated ratios for the permanent environment. The effect of the weaning-herd-year was more evident earlier in the test than later days on test. These results suggest that random regression models could be useful for the National Genetic Evaluation of cumulative feed intake of Bonsmara bulls participating in centralized performance tests. It is however not clear why the estimates of heritability observed in the current study are considerably lower than literature estimates. More research in this area is thus needed.

CHAPTER 3

RANDOM REGRESSION MODELS IN THE ANALYSIS OF BODY WEIGHTS OF INDIVIDUALLY FED BEEF BULLS IN SOUTH AFRICA

Abstract

The objective of the study was to estimate genetic parameters for body weights (BWT) of beef bulls measured at centralized testing stations in South Africa using random regression models (RRM). Weekly body weights of Bonsmara bulls (n = 2 919) tested between 1999 and 2003 were available for the analyses. The model included the fixed linear regression of the body weights on fourth order orthogonal Legendre polynomials of the actual days on test (7, 14, 21, 28, 35, 42, 49, 56, 63, 70, 77 and 84 day) for starting age group and contemporary group effects. Random regressions on fourth order orthogonal Legendre polynomials were included for additive genetic effects and additional uncorrelated random effects of the weaning-herd-year (WHY) and the permanent environment of the animal. The random residual effects were assumed to be independently distributed with heterogeneous variance for each test day. Variance ratios for additive genetic, permanent environment and WHY for weekly body weights at different ages ranged from 0.26 to 0.29, 0.37 to 0.43 and 0.26 to 0.34, respectively. Genetic correlations amongst body weights at different test days ranged from 0.89 to 1.00. Despite the 28-day adjustment period, WHY had a significant effect in variation of body weights of the bulls at the performance testing station. Random regression model could be used in genetic evaluation of body weights of individually fed beef bulls in South Africa.

1. Introduction

The South African National Beef Cattle Improvement Scheme (NBCIS) administered by the Agricultural Research Council (ARC), record measurements of feed intake, body weight and other traits (such as scrotum circumference, body measurements, functional appearance and condition scoring) during the central performance testing of beef bulls (Phase C). Traits such as feed intake and body weight that are measured repeatedly over a test period (e.g. during Phase C) are called longitudinal data. In animal breeding, the interest lies on genetic parameters that explains the shape of curves that describe such traits as those parameters might give information on whether and how desirable changes in the course of such trait can be achieved (Meyer, 1998c). Genetic parameters that describe the performance pattern for bulls at central performance testing stations under South African conditions are not available.

Traditionally, multiple-trait models (MTM) have been used to analyze such traits thus correcting observations towards certain landmark ages (e.g. beginning and final body weight). The adjustments are only for means but not for variances (Nobre *et al*., 2002). Optionally, the trait observations may be averaged to a single value (e.g. average daily gain), which might be essential in explaining the individual variation throughout the test. Meyer (1998c) reported that a better way of dealing with traits that are measured repeatedly over a lifetime of an individual is by using random regression models (RRM), thus fitting a set of random regression coefficients of time of measurements for each individual to allow for individual variation in the course of the trajectory. Kirkpatrick *et al*., (1990) showed that variance components for longitudinal data could be modeled using covariance functions (CF). RRM can be used to estimate covariance functions directly from the data by Restricted Maximum Likelihood (REML) procedures (Meyer, 1998a).

Random regression models were introduced to the analysis of longitudinal data by Henderson (1982) as well as Laird and Ware (1982). Meyer and Hill (1997) considered the application of RRM to animal breeding data. In beef cattle, the method was outlined by Varona *et al*. (1997) and has been applied in many research studies (e.g. Meyer, 1999 and 2000). RRM have a number of advantages over the traditional model (MTM), which include (1) allowing calculation of (co)variances between or at any age or time point (Huisman *et al*., 2002a), (2) requiring fewer parameters to describe longitudinal data and estimate (co)variances smoother and with less bias as compared to multivariate model, (3) allowing for a theoretically more complete model and, (4) having better properties for genetic evaluation and offering more powerful approach to evaluate repeated live weight information to determine genetic merit (Kirkpatrick and Heckman, 1989).

The objective of this study was to estimate genetic parameters for weekly body weights (BWT) using random regression models (RRM) on data of beef bulls collected at centralized testing stations in South Africa.

2. Materials and methods

2.1 Data

Data on Bonsmara bulls were obtained from the National Beef Cattle Improvement Scheme (NBCIS) database. The data consisted of 2 919 records for bulls that had undergone Phase C of the NBCIS collected from 1999 to 2003. Body weights were collected weekly for 12 weeks (84 days. Before each weighing the animals were denied access to food and water overnight, following a pre-test adjustment period of 28 days (4 weeks). Bulls were placed in pens with electronic gates, which allowed individual access to particular feeders and were fed on a pelleted ration containing 13.0 MJ ME/kg dry matter and 13% protein. The ration composed of 39.8% maize, 11.9% wheat pollard, 7.5% cottonseed, 5% lucerne, 20.5% maize straws, 9% molasses, 0.5% urea, 3.4% hominy chop, 0.5% salt, 1.4% limestone ground, 0.3% monocalcium phosphate and 0.2% vitamin-mineral premix which included the rumen modifier rumensin (Archer and Bergh, 2000).

A summary of the data set is given in Table 1. The contemporary group was defined as the concatenation of test year, test number and the testing center where the bulls were tested. The starting ages were grouped into 14 classes of tens (i.e. from 181 to 190 = starting-age class 2, from 191 to 200 = starting-age class 3, etc.). However, starting-age class 1 had the highest range of starting age, i.e. from 161-180, because of the few number of animals that fell under that starting-age range.

Table 1. Summary of the weekly body weight data set

Feature	**Number**
Number of bulls	2 919
Number of records per bull	12
Total number of records	35 028
Number of animals in Pedigree	12 441
Mean starting age (days)	242
Starting age range (days)	161-308
Starting-age classes	14
Weaning-herd-year groups	211
Contemporary groups	135
Mean initial body weight (kg)	273
Mean final body weight (kg)	402

2.2. Statistical analysis

Random regression model was used to analyze weekly body weights of beef bulls. The model was similar to that of Schenkel *et al*., (2002b), fitted for consecutive body weights of bulls tested in central evaluation stations in Ontario (Canada), with the exception that only one breed was used in the current analysis. The model included the fixed regression of body weights on fourth order (cubic) orthogonal Legendre polynomials of the actual days (7, 14, 21, 28, 35, 42, 49, 56, 63, 70, 77 and 84) on test for starting age group and contemporary group effects. Random regressions on fourth order orthogonal polynomials of the actual days on test were included for the additive genetic effect of the animal and additional uncorrelated random effects of the weaning-herd-year and the permanent environment of the animal.

The effect of WHY on the post-weaning traits was investigated in several studies (Tong *et al.*, 1986; Amal and Crow, 1987; Schenkel *et al.*, 2004; Nephawe *et al.*, 2006). The recommendation from these studies was that WHY must be included in the model for post-weaning traits of bulls at central performance testing stations. Although a more traditional approach would be to fit the WHY as a fixed effect, the WHY on post-weaning weight was fitted as random in order to estimate its variance (Schenkel *et al.*, 2002b; Nephawe *et al.*, 2006).

The model can then be represented as:

$$w_{ij} = \sum_{p=0}^{n-1} b_p \varphi_p(d_{ij}) + \sum_{p=0}^{n-1} \alpha_p \varphi_p(d_{ij}) + \sum_{r=1}^{3} \sum_{p=0}^{n-1} \gamma_{r_p} \varphi_p(d_{ij}) + \varepsilon_{ij}$$

where w_{ij} is the j^{th} measurement of weekly body weight on the i^{th} bull, b_p are the fixed regression coefficients for the contemporary group (the concatenation of test year, test number and the test centre), α_p are the fixed regression coefficients for the starting age class, γ_{rp} are the random regression coefficients for the r^{th} random effect (i.e. WHY, additive genetic or permanent environment), d_{ij} are the standardized actual days on test at recording for which Legendre polynomials are defined and $\varphi(d_{ij})$ are the respective p^{th} Legendre polynomials. The n denotes the order of fit (in this study, order = 4) and e_{ij} represents the random residual effect that was assumed to be independently distributed with heterogeneous variance for each measurement period on test (i.e. variance for day 7, 14, 21, 28, 35, 42, 49, 56, 63, 70, 77 and 84 on test).

In matrix notation the random regression model can be presented as follows:

$$\mathbf{y} = \mathbf{Xb} + \mathbf{Za} + \mathbf{Z_c^*c} + \mathbf{Z_q^*q} + \mathbf{e}$$

y is a vector of observations on animals.

where **b** represents a vector of fixed effects,

a are random regression coefficients for each animal representing the additive genetic contribution to the trait,

c are random regression coefficient for each animal representing the permanent environmental coefficient,

q are random regression coefficient for each animal representing the weaning-herd-year coefficient,

e is a vector of temporary environmental effects peculiar to each observation independent of age and animal,

X is the design matrix relating observations to the fixed effects,

Z is a matrix of standardized age covariates associated with each record and linked to all animals, while

$\mathbf{Z_c^*}$ and $\mathbf{Z_q^*}$ are parts of **Z** corresponding to only those bulls with records, and

The first and second moments are:

$$\mathbf{E(y) = Xb}$$

$$\mathbf{Var}\begin{bmatrix} a \\ c \\ q \\ e \end{bmatrix} = \begin{bmatrix} Z(A \otimes K_A)Z' & 0 & 0 & 0 \\ 0 & Z_c^{*}(I_c \otimes K_C)Z_c^{*'} & 0 & 0 \\ 0 & 0 & Z_q^{*}(I_q \otimes K_q)Z_q^{*'} & 0 \\ 0 & 0 & 0 & R \end{bmatrix}$$

where $\boldsymbol{A}$, $\boldsymbol{I_c}$ and $\boldsymbol{I_q}$ are the numerator relationship matrix, an identity matrix for permanent environment and identity matrix for weaning herd-year, respectively. The $\boldsymbol{K_A}$, $\boldsymbol{K_c}$ and $\boldsymbol{K_q}$ are matrices for coefficients of the covariance functions (CFs) of the additive genetic, permanent environmental and weaning herd-year (co)variances, respectively, with dimensions equals to order of fit of the CFs in the analysis; $\otimes$ is the direct matrix product notation and $\boldsymbol{R}$ is the variance of the temporary environmental effects, which is a diagonal matrix allowing for different variances by age in days on test.

(Co)variance components were estimated using DXMRR program of Meyer (1998b). The matrices for coefficients $\boldsymbol{K_G}$, $\boldsymbol{K_c}$, $\boldsymbol{K_q}$ and of the elements of $\boldsymbol{R}$ were estimated directly from the data by REML (Meyer & Hill, 1997) as covariance matrices of the corresponding random regression. The convergence of the covariance components was visually inspected by repeatedly fitting the estimated coefficients matrices values over iterations as starting values for estimation of (co)variance components.

2. Results and discussion

The mean and standard deviations for body weights at each test day were calculated and are presented in Table 2. The mean values for weekly body weights gradually increased throughout the test and so did their respective standard deviations. This pattern was expected, as when the number of days on test increases, their mean body weights are also expected to increase.

Table 2. Means and their respective standard deviations for body weights for each test day of measurement

Test day	Mean (kg)	Standard deviation (kg)
7	273	37.26
14	284	38.50
21	298	39.86
28	309	41.36
35	321	42.92
42	333	43.71
49	345	44.71
56	357	45.72
63	369	45.97
70	380	46.81
77	391	47.30
84	402	48.62

3.1. Covariance functions

The estimated coefficient matrices (**K**) of the covariance functions, the eigenvalues, percentages for additive genetic, permanent environment and WHY effects are presented in Table 3. The first eigenvalue in all coefficient matrices dominated, thus indicating that much variation is explained by the first eigenvalue.

Schenkel *et al*., (2002b) observed that fitting order three for the additive genetic effects for the weekly body weights of bulls tested at centralized performance testing stations would suffice. In the current study, the fourth order contributed only 0.01% of the total variability for additive genetic animal effects. Albuquerque and Meyer (2001) found that fitting fourth-order polynomial for the permanent environment effect of the animal, for growth from birth to 630d, was sufficient. In the current study, fitting the second-order for the permanent environment would have sufficed.

Table 3. Covariance function's estimated coefficient matrices (**K**), their corresponding eigenvalues (ξ) and total variability proportions (**%**) for additive genetic (**G**), permanent environment (**PE**) animal effects and the weaning-herd-year (**WHY**) effect.

Effect[a]	**K**

	0	**1**	**2**	**3**	**ξ**	**%**
G						
0	541.68	41.05	-7.18	5.37	545.01	98.17
1		12.45	-0.61	0.47	9.29	1.67
2			0.87	0.10	0.81	0.15
3				0.15	0.06	0.01
PE						
0	791.48	107.86	-25.73	-3.45	807.70	94.96
1		49.53	-3.76	-3.31	34.40	4.04
2			7.71	0.31	6.86	0.80
3				1.95	1.70	0.20
WHY						
0	550.22	40.90	-8.19	-1.99	553.50	96.01
1		21.18	-2.28	-1.39	18.31	3.81
2			4.21	0.46	3.92	0.68
3				0.87	0.74	0.13

[a] 0 = intercept, 1 = linear, 2 = quadratic, 3 = cubic

3.2. Estimates of variance components

Table 4 presents estimates of variances for additive genetic, permanent environmental, WHY and the residual for body weight, and their respective ratios at different days on test.

The additive genetic variances increased throughout the test, starting at 194.8 at the beginning of the test and rose to 361.8 at the end of the test. The heritability estimates ranged from 0.28 at day 7 to 0.26 at day 49 and remained constant until at the end of the test. These heritability estimates are comparable to estimates obtained by Amal and Crow (1987) on Angus-Hereford bulls. However, the estimates for Charolais-Simmental bulls were higher (i.e. ranging from 0.61 to 0.47 for starting weight and weight at 140 days, respectively). Schenkel *et al*., (2002b) reported higher estimates that ranged from 0.33 to 0.40 from day 0 to day 140, respectively. The heritability estimates have shown a different pattern (i.e. constant with time) as compared to estimates from Schenkel *et al*., (2002b) study that increased as the test progressed. Amal and Crow (1987) presented a similar pattern similar to what was observed in the current study using a sire model on data for both Angus-Hereford and Charolais-Simmental bulls. Nephawe *et al*., (2006) using Bonsmara data and fitting a multiple trait model, reported a slightly higher ADG heritability estimates (0.34) than observed in this study.

The estimated variances and ratios for the permanent environment increased over time, ranging from 259.5 to 587.4 and from 0.37 to 0.43, respectively. The ratios were similar to those of Schenkel *et al*., (2002b), which ranged from 0.36 at the beginning of the test to of 0.41 at the end of the test. Variance estimates for the WHY also increased over time (i.e. from 236.3 to 355.2), but their respective ratios decreased over time, starting at 0.34 at the beginning of the test and dropping to 0.26 at the end of the test. Amal and Crow (1987) found a similar (0.33) effect of the WHY and suggested that part of the variation due to WHY in bull body weights might have been due to age of dam. Simm *et al*., (1985) reported that 20% to 30% of the variation in bull weights between 200 and 400 days of age for bulls weaned at 168 days was due to the effect of the age of the dam. Meyer *et al*., (1993) reported that maternal effects might affect post-weaning weights during the test as a carry-over from weaning weight. Schenkel *et al*., (2002b) also observed a significant WHY effect (from 0.32 to 0.18 for the start and end of the test, respectively) on bulls' test body weights. However, Schenkel *et al*., (2002b) and Schenkel *et al*., (2004) observed about 8% WHY effect and indicated that the dam effect was not important in the analysis of post-weaning performance on test. Schenkel *et al*., (2004) also indicated that the WHY variation observed in their study was more likely to be due to real pre-weaning environmental effects than other sources of variation such as genetic and maternal effects. Nephawe *et al*., (2006) evaluated the importance of the dam effect (accounting for both maternal additive and permanent environmental effects) on both weaning and post-weaning traits and found that the dam effect did not contribute significantly to post-weaning traits. It can be suggested that the dominating effect of WHY in the current study throughout the test, might be due to other pre-weaning environmental effects other than maternal effects.

Table 4. Estimates of variances[1] for additive genetic, permanent environment, weaning-herd-year and for the residual, and their respective ratios[2] for weight at different days on test.

Test day	σ_a^2	h^2	σ_c^2	c^2	σ_q^2	q^2	σ_e^2	e^2
7	194.80	0.28	259.54	0.37	236.29	0.34	4.71	0.007
14	216.81	0.29	274.13	0.37	235.37	0.31	24.04	0.032

21	235.68	0.29	302.82	0.38	241.66	0.30	27.99	0.034
28	251.29	0.29	336.85	0.39	251.89	0.29	27.72	0.032
35	264.03	0.28	373.01	0.40	264.67	0.28	30.54	0.033
42	274.64	0.27	410.39	0.41	279.22	0.28	45.56	0.045
49	284.03	0.26	448.20	0.42	294.65	0.28	45.10	0.042
56	293.29	0.26	484.75	0.44	309.70	0.28	27.76	0.024
63	303.73	0.26	517.48	0.44	322.97	0.28	30.30	0.025
70	317.00	0.26	544.21	0.44	333.69	0.27	42.32	0.034
77	335.33	0.26	565.34	0.44	342.91	0.27	28.62	0.022
84	361.82	0.26	587.35	0.43	355.22	0.26	77.27	0.056

[1] $\boldsymbol{\sigma_a^2}$, $\boldsymbol{\sigma_c^2}$, $\boldsymbol{\sigma_q^2}$ and $\boldsymbol{\sigma_e^2}$ are estimates of variances for additive genetic, permanent environment, weaning-herd-year and for the residual, respectively

[2] $\mathbf{h^2}$, $\mathbf{c^2}$, $\mathbf{q^2}$ and $\mathbf{e^2}$ are ratios for additive genetic, permanent environment, weaning-herd-year and for the residual, respectively

In general, the heritability estimates were lower than the ratios for WHY effects, thus indicating the considerable influence of WHY on body weights throughout the test. Compared with Schenkel *et al*., (2002), estimates of variance for the temporary environmental effects were fluctuating throughout the test and their corresponding ratios were very low as they contributed less than 5% of the total variance of the weekly body weights of bulls on test.

3.3. Covariance estimates

The additive genetic, permanent environmental, WHY and phenotypic covariance estimates are presented in Figure 1, Figure 2, Figure 3 and Figure 4, respectively. The covariances due to the permanent environment were always higher than those due to additive and WHY effects. In general, the covariance estimates for all effects between adjacent days exhibited an increasing pattern as animals aged. The additive genetic, permanent environmental, WHY and phenotypic (co)variance estimates ranged from 195 to 362, 260 to 587, 230 to 355 and 695 to 1382, respectively. Nephawe (2004) and Arango *et al*., (2004) also reported an increasing pattern for genetic (co)variances when applying RRM to the genetic evaluation of cow weights in beef cattle.

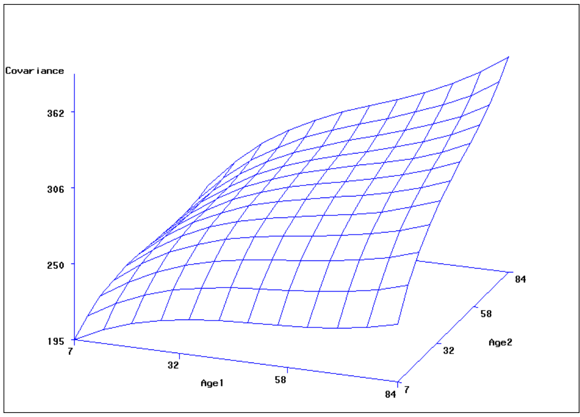

Figure 1. Additive genetic covariances between weekly body weights at different test days

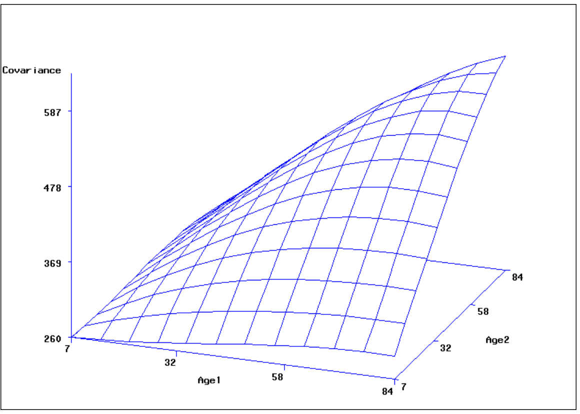

Figure 2. Permanent environmental covariances between weekly body weights at different test days

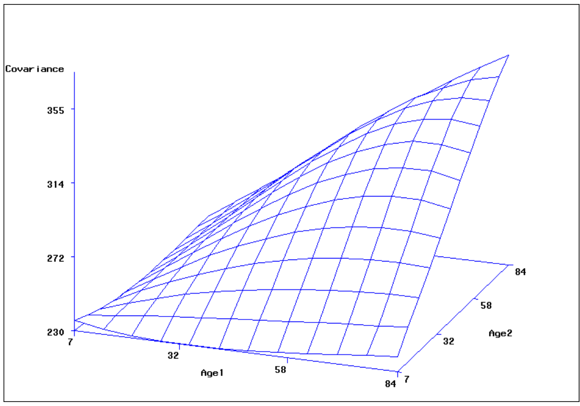

Figure 3. Weaning-herd-year covariances between weekly body weights at different test days

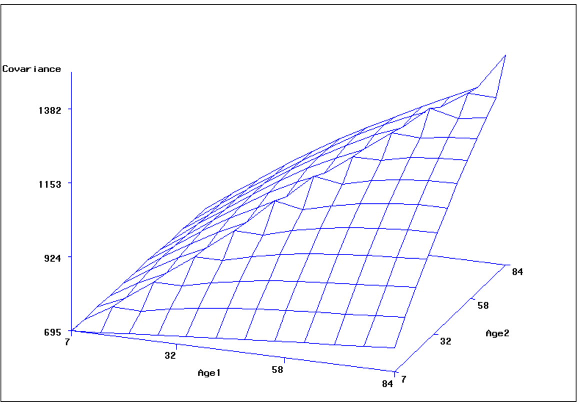

Figure 4. Phenotypic covariances between weekly body weights at different test days

3.4 Correlation estimates

The estimates of additive genetic, permanent environmental, WHY and phenotypic correlations between weekly body weights at different ages on test are presented in Figure 5, Figure 6, Figure 7 and Figure 8, respectively. Estimates of additive genetic correlation tended to decline as the difference in days increased. Additive genetic correlation estimates were always higher than the correlation estimates for the permanent and the WHY effects and were more than 0.88 for any pair of days on test. Maximum correlation estimates closer to 1.00 between ages for the permanent environment, WHY and phenotypic effects were observed and the minimum values were 0.76, 083 and 0.78 for the permanent environmental, WHY and phenotypic effects, respectively. In general, correlation estimates for all effects decreased as the interval between days on test increased.

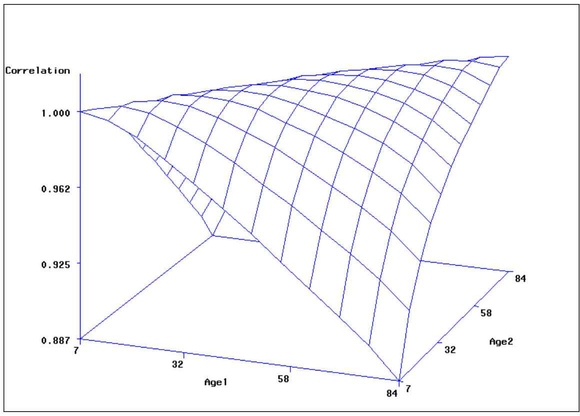

Figure 5. Additive genetic correlations between weekly body weights at different test days

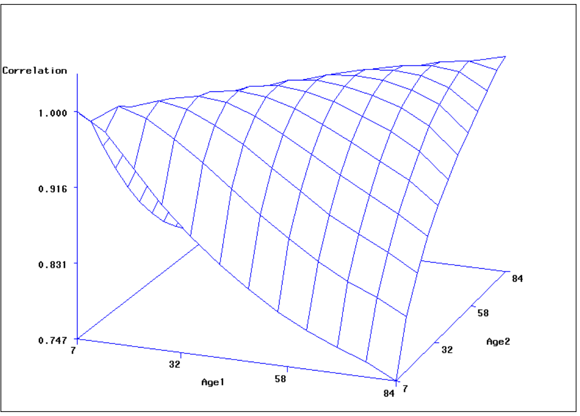

Figure 6. Permanent environmental correlations between weekly body weights at different test days

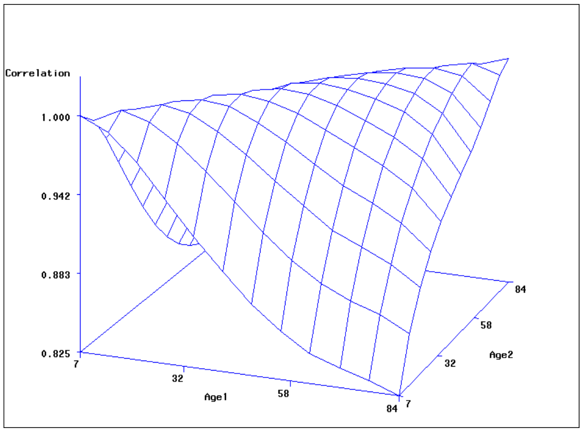

Figure 7. Weaning-herd-year correlations between weekly body weights at different test days

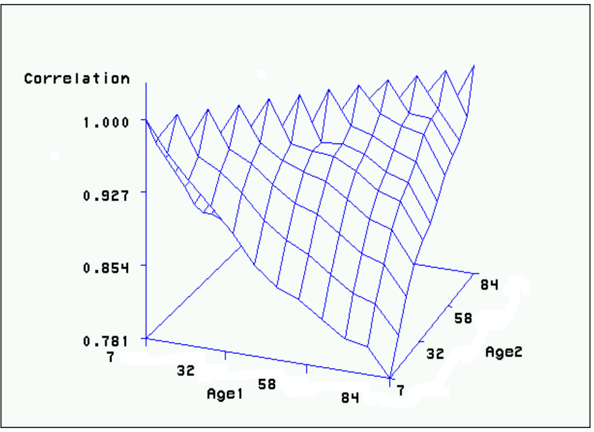

Figure 8. Phenotypic correlations between weekly body weights at different test days

4. Conclusions

Body weights of individually fed Bonsmara bulls were analyzed using random regression models. The model enabled the trajectory for both the genetic and environmental parameters over the test period to be studied. The total additive variance increased throughout the test but their respective heritability estimates were constant for several days on test. The heritability estimates for weekly weights were comparable to the literature estimates. The weaning-herd-year made a considerable contribution to the variation in weekly body weights of bulls undergoing performance tests, despite the 28-day pre-adjustment period. Random regression models could be useful for the National Genetic Evaluation of body weights of Bonsmara bulls.

CHAPTER 4

1. General conclusions

Random regression models were used in the analysis of weekly feed intake and weekly body weights of bulls at central performance testing stations and provided estimates of variation in both traits were obtained by fitting a set of random regression coefficient for each bull to allow for individual variation in the course of the trajectory. The results suggest that fitting random regression orthogonal Legendre polynomials on third order for the additive genetic and order three for the permanent environment of the animal would suffice in modeling cumulative feed intake. The heritability estimates for cumulative feed intake were low as compared to the estimated ratios for the permanent environment. The weaning-herd-year and the additive genetic correlations were high for any pair of test days. The effect of the weaning-herd-year was more evident at the beginning than final days on test.

The additive variance for weekly body weights also increased throughout the test but their respective heritability estimates were constant for several days on test. The heritability estimates for weekly weights were comparable to the literature estimates. The weaning-herd-year had a considerable contribution to the variation of weekly body weights of bulls undergoing performance tests, despite the 28-day pre-adjustment period. Random regression models could be useful in the National Genetic Evaluation of beef bulls at central performance testing stations.

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