

Genetic variance components for residual feed intake and feed conversion ratio and their correlations with other production traits in beef bulls

R.R. van der Westhuizen[#], J. van der Westhuizen and S.J. Schoeman¹

ARC-Animal Improvement Institute, Private Bag X2, Irene 0062, South Africa

¹Department of Animal Sciences, University of Stellenbosch, Private Bag X1, Matieland 7602, South Africa

Abstract

Feeding costs of animals is a major determinant of profitability in livestock production enterprises. Genetic selection to improve feed efficiency aims to reduce feeding cost in beef cattle and thereby improve profitability. This study estimated genetic (co)variances between weaning weight and other production, reproduction and efficiency traits. Traits included residual feed intake (RFI), feed conversion ratio (FCR), growth (average daily gain (ADG), weaning weight (WW) and shoulder height (SHD)), reproductive (scrotum circumference (SCR)) and profitability traits measured in growth tests of young bulls. The only genetic correlations of significance with WW were those with SHD (0.50) and ADG (0.28). Weaning weight serves as no indication of an animal's production, owing to low genetic correlations with other traits (reproduction or feedlot post-weaning growth efficiency). The heritability estimated for FCR was 0.34 and for RFI 0.31 with a genetic correlation estimate of 0.75 between them. The estimated genetic correlation of profitability (Rand-value) with FCR and RFI were -0.92 and -0.59, respectively. The genetic correlations and expected correlated responses between RFI and FCR with Rand-value suggest that indirect selection for Rand-value through direct selection for FCR and/or RFI will result in slower genetic progress in Rand-value than direct selection. However, where the Rand-value cannot be calculated and/or direct selection for Rand-value is not possible, it would be better to select indirectly for Rand-value through the use of FCR rather than RFI.

Keywords: Beef cattle, feed conversion ratio, genetic (co)variances, profitability, residual feed intake

[#]Corresponding author. E-mail: bobbie@arc.agric.za

Introduction

High feeding costs are a major constraint in profitability in livestock production enterprises. Feed costs represent approximately one-half of the total cost of production for most classes of livestock. Therefore improvement of feed efficiency should be a major consideration in most breeding programs (Kennedy *et al.*, 1993). Genetic selection to improve feed efficiency aims to reduce the cost of feeding in beef cattle production and thereby improve profitability.

Traditionally, selection for growth rate has received considerable emphasis in most breed improvement schemes. The value of this strategy to the improvement of enterprise efficiency and profitability of ruminant production systems has, however, been questioned, since increased mature size is a direct consequence, resulting in an increased cost of maintaining females (Barlow, 1984; Scholtz & Roux, 1984). Thompson & Barlow (1986) showed that greater improvements in enterprise efficiency would result from an improvement in feed conversion efficiency of the growing animal and reduction in feed intake of the mature dam. Evidence of genetic variation in either of these traits was equivocal at the time. Koots *et al.* (1994b) reported highly negative weighted genetic correlations between feed conversion ratio (FCR) and growth rate and size. These correlations indicate that selection to reduce FCR and thus improve efficiency would be accompanied by an increase in growth rate, and an increase in mature cow size.

A second disadvantage of selection for FCR relates to problems inherent with selection on ratio measurements (Gunsett, 1986), involving two different traits (feed intake and growth) with different variances within them.

Considerable variation in feed intake, independent of size and growth rate, exists in beef cattle. This trait is defined as residual (or net) feed intake (RFI) (Archer *et al.*, 1997). There has been considerable interest in RFI as a measure of feed efficiency in animals. Much of that interest has been in quantifying the variability in RFI and determining how much of the variability is genetic (Kennedy *et al.*, 1993).

The main advantage of using RFI as an efficiency trait instead of FCR, as stated in the literature by Archer *et al.* (1997; 1998) and Herd & Bishop (2000), is the fact that RFI is not defined as a ratio trait and that selection to reduce RFI offers an opportunity to reduce feed intake, without compromising growth performance, and also without the possible correlated response in maturity type. These arguments therefore support reasoning that the inclusion of RFI will contribute towards both pre-weaning as well as post-weaning profitability in beef production.

Unfortunately, limited work has been done on RFI and on the genetic correlations between RFI, FCR and other production and reproduction traits in beef cattle under South African production and economical environments. The aim of this study was to estimate genetic (co)-variances (and ratios) between weaning weight and other traits and to compare RFI and FCR with growth (average daily gain (ADG), weaning weight (WW) and shoulder height (SHD)), reproductive (scrotum circumference (SCR)) and profitability traits measured in growth tests of young bulls. These results will serve as a clear indication of the value of the inclusion of RFI and FCR in breeding objectives aimed at breeding more profitable feedlot cattle under South African production and economical environments.

Materials and Methods

The data analysed in this study was collected from the centralised growth test stations of South Africa's Agricultural Research Council (ARC). Records from Bonsmara bulls, tested in centralised growth tests between 1989 and 2001 were used. The data set consists of the individual feed intake and weights of 6 738 bulls.

Young bulls are sent to one of the ARC central testing stations where individual feed intake and body measurements are taken on a weekly basis. On arrival, bulls go through a four-week adaptation period so that they can gradually adapt to the diet as well as learn to eat from their own feeding trough. The centralised growth test length was originally 20 weeks long. In 1990 the test period was shortened to a 16-weeks and in 1999 to 12-weeks (see recommendations of Archer & Bergh, 2000).

Traits measured in a centralised growth test are, among others, feed intake, weight, scrotum circumference (SCR) and shoulder height (SHD). Individual feed intakes and weights enable the calculation of average daily gain (ADG), feed conversion ratio (FCR), residual (or net) feed intake (RFI) as well as a feedlot profitability value for each bull (or a post-wean growth monetary value). Feed conversion ratio is defined as the average quantity of feed consumed by the animal to gain one kilogram in body (live) weight. Residual (or net) feed intake is defined as the quantity of feed consumed by an animal less or more than what would be expected for weight gain of the animal and its maintenance requirements (metabolic body weight is used as an indicator of maintenance requirements).

More precisely, RFI is calculated as the error term (e) when fitting the equation:

$$\text{Feed intake} = \mu + (\beta_w \times \text{mean metabolic weight}) + (\beta_g \times \text{weight gain}) + e,$$

where:

Feed intake = the daily feed intake in kg;

μ = constant;

mean metabolic weight = mean (weight^{0.73}) of the animal for the feed intake test period;

weight gain = live weight gain (kg/day) over the feed intake test period

β_w and β_g = the regression coefficients for metabolic weight and weight gain

e = the RFI

A post-weaning growth monetary value, calculated in South African Rand for each bull was simulated as if the tested bull was fed under feedlot conditions and sold to an abattoir. The following equation was used to derive a profit value (Rand-value) for each bull at the completion of the test period:

$$\text{Rand-value} = [\text{Uwt} \times \text{CPr/kg}] - [(\text{BWt} \times \text{BWtPr/kg}) + (\text{FI} \times \text{FPr/kg}) + ((\text{BWt} \times \text{BWtPr/kg}) \times (\text{Br}/365) \times \text{TI}) + (\text{VC})] \quad (1)$$

Where:

Uwt	=	Slaughter weight (55% of final weight)
CPr/kg	=	Price per kilogram carcass weight
BWt	=	Body weight on commencement of the test.
BWtPr/kg	=	Live weight price per kilogram for weaners
FI	=	Feed intake
FPr/kg	=	Feed price per kilogram
Br	=	Bank interest rate
TL	=	Test length
VC	=	Veterinary costs

The following assumptions were made to simulate the profit value and to create a comparable basis for statistical analyses:

- Live weight weaner calf price at R 8.25 per kilogram (The weight at the start of the growth test is used)
- Carcass price of R 12.35 per kilogram (It is assumed that all bulls are classified as A3)
- Feed cost set at R 0.90 per kilogram.
- Interest rate on an overdraft account at 14% per annum.
- It is assumed that all slaughter costs are covered by the fifth quarter.
- Slaughter percentage of 55%. (55% of the weight of the bull on completion of growth test)
- Veterinary costs of R 3.50 per week (approximately R 60 for a 4 week adaptation period and 12 week test)

Variance components, heritabilities and genetic correlations for and between weaning weight (WW), ADG, SCR, SHD, FCR, RFI and Rand-value were estimated simultaneously by multitrait restricted maximum likelihood (REML) procedures using the VCE package developed by Groeneveld (1994). Three multitrait analyses were done. The first multitrait was a six trait with WW, ADG, SCR, SHD, FCR and Rand-value. The random maternal effect for all traits was ignored. Secondly, FCR was removed from the model and RFI was included in the model. The third and last multitrait analysis includes all seven traits. This was done to remove any co-linearity between FCR and RFI, if any.

Table 1 Summary for the different models used for the respective traits

Factor	Effect	Levels	WW	ADG	SCR	SHD	FCR	RFI	Rand-value
Weaning age	C		X						
Weaning age ²	C		X						
Weaning contemporary	F	1 246	X						
Age	C				X	X	X	X	X
Age ²	C				X	X			
Dam age	C		X	X	X	X	X	X	X
Dam age ²	C		X						
Growth-test contemporary	F	514		X	X	X	X	X	X

WW = Weaning weight; ADG = Average daily gain; SCR = Scrotum circumference; SHD = Shoulder height; FCR = Feed conversion ratio; RFI = Residual feed intake; Age = Age of the animal at the end of the growth test; Dam age = Age of the dam at end of test; Weaning age = Age of the animal at weaning; C = Covariate; F = Fixed effect; Growth-test contemporary (test centre, test year, test phase and test number); Wean contemporary (herd, wean date, index code for treatment and sex)

The importance of non-genetic sources of variation on the traits was determined by the PROC GLM procedure of SAS (2000). Non-genetic sources that were included in the models for WW were the linear and quadratic regression of the age of the dam, the linear and quadratic regression of the age of the animal at weaning and the contemporary group for weaning weights (herd, weaning date, treatment code and sex) as fixed effects (1 246 levels). For ADG only the linear regression of the age of the dam and the contemporary group fixed effect for the growth test (which include test centre, test year, test phase and test number) were included in the model (514 levels). For SCR and SHD the linear and quadratic regression of the age of the animal at the end of the growth test, the linear regression of the age of the dam and the contemporary group fixed effect for the growth test were included as non-genetic sources. For FCR, RFI and Rand-value the linear regression of the age of the animal at the end of the growth test and age of the dam were included and the contemporary group effect as a fixed effect. These non-genetic sources were significant ($P < 0.001$) and were therefore included in the models for FCR, RFI and Rand-value. Table 1 provides a summary of the different models used for each trait.

To compare the effectiveness of response in Rand-value based on selection for RFI or FCR, expected correlated responses were estimated. Selection intensities for both traits were assumed to be equal and were therefore cancelled out of the equation of Falconer & Mackay (1996):

$$R_{2,1} / R_2 = r_A (h_1 / h_2)$$

- where: $R_{2,1}$ = Correlated response in trait 2 when selecting for trait 1
 R_2 = Direct response in trait 2 under selection for trait 2
 r_A = Genetic correlation between trait 1 and 2
 h_1 and h_2 = Square root of the heritability of trait 1 and trait 2, respectively.

Indirect selection will be better than direct selection if $R_{2,1}$ is greater than R_2 , therefore ($r_A \times h_1$) must be greater than h_2 . Indirect selection can therefore not be expected to be greater unless the secondary character has a substantially higher heritability and the genetic correlation is high.

Results and Discussion

Table 2 presents the descriptive statistics for the different traits and covariates included in the different models.

Table 2 General statistics for the different traits and covariances in models

Trait/Covariance	Min.	Max.	Mean	Std. Dev.
WW (kg)	125	375	234	30.6
ADG (kg)	857	2680	1654	237.6
SCR (mm)	210	470	342	27.7
SHD (mm)	1060	1580	1195	35.1
FCR (kg)	3.67	9.74	6.44	0.81
RFI	-3.73	3.56	0.11	0.91
Rand-value (R)	-824.78	494.36	-224	141
Age (days)	272	410	358	26.6
Dam age (days)	669	6032	2195	1008
Weaning age (days)	150	269	205	23.3

WW = Weaning weight; ADG = Average daily gain; SCR = Scrotum circumference;
 SHD = Shoulder height; FCR = Feed conversion ratio; RFI = Residual feed intake;
 Age = Age of the animal at the end of the growth test; Dam age = Age of the dam at the end of test;
 Weaning age = age of the animal at weaning

It can be seen from Table 2 that the least profitable animal in the growth tests has resulted in a loss of R 824.78 while the most profitable animal resulted in a profit of R 494.36 based upon these assumptions. The average Rand-value was a loss of R 223.93 with a standard deviation of R 141.28. This accentuates the necessary of selecting the most suitable animals for feedlotting in order to make a profit. The mean FCR (6.44 ± 0.81) corresponds with the mean FCR of 6.5 ± 0.9 obtained by Arthur *et al.* (2001). The range of RFI of -3.73 to 3.56 correlates well with the range estimated for Bonsmara cattle by Archer & Bergh (2000) of between -3.76 and 3.72 . The mean RFI of 0.11 ± 0.91 , however, differs from the mean of 0.00 ± 0.67 presented by Archer & Bergh (2000) as well as the zero means obtained by both Herd & Bishop (2000) and Arthur *et al.* (2001). The reason for the difference in the mean of this study is the result of the way the regression coefficients for metabolic weight and gain were applied in the calculations of RFI. These coefficients were obtained from an initial extended data file (11 839 records) before it was reduced to 6 738 records to be able to estimate genetic variance components. Figure 1 presents the frequency distribution for RFI. The skewness statistic for this distribution is -0.0429 , while the standard error of skewness is 0.0298 . Since two times the standard error of skewness is greater than the absolute value for the skewness statistic the distribution is not significantly skewed. The data is leptokurtic ("taller" than a normally distributed population) due to a positive (0.475 ± 0.119) kurtosis statistic.

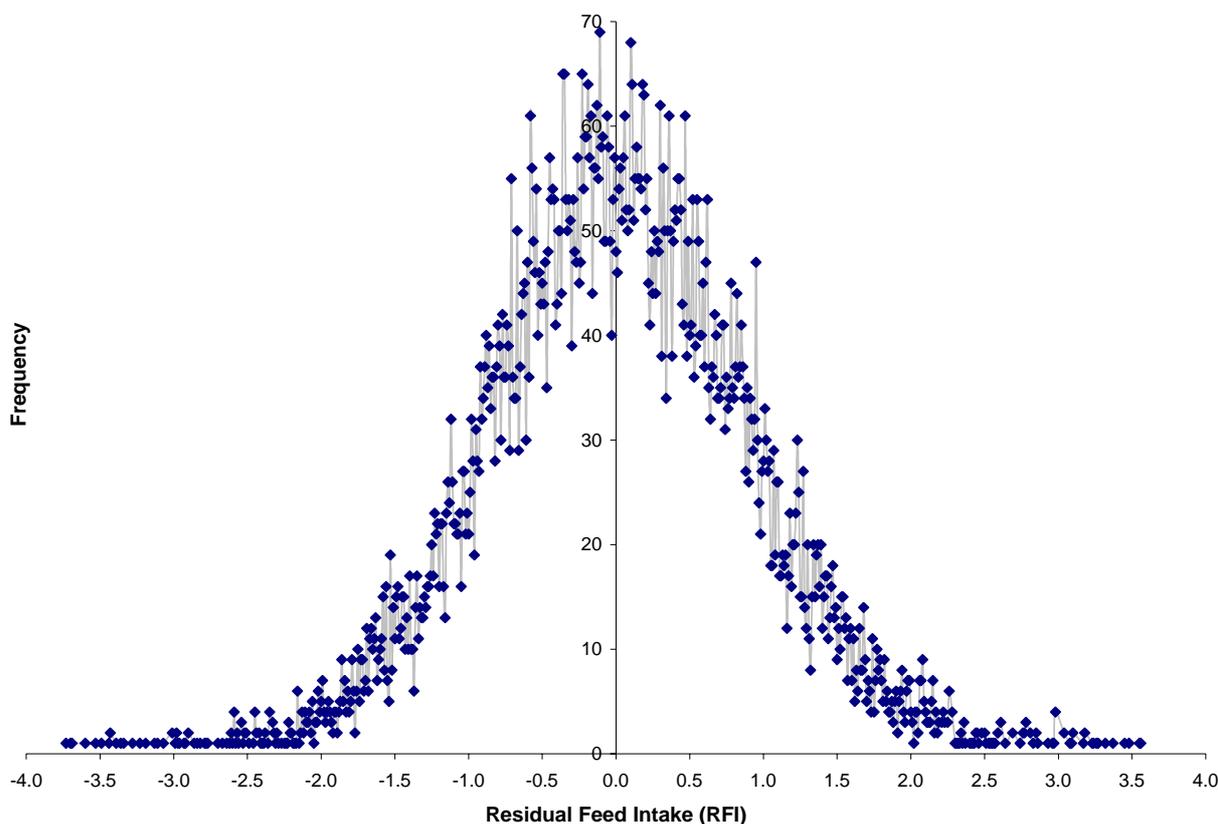


Figure 1 Frequency distribution of residual feed intake (RFI)

Table 3 presents the summary of the stepwise regression procedure that was fitted in order to determine to what extent FRC and RFI contributed to the variances of the Rand-value. Seventy four percent of the variance of Rand-value is explained by FCR while RFI only accounts for 36% of the variation in the Rand-value. This was expected because of FCR been a component of Rand-value. A greater improvement in Rand-value is therefore expected with an improvement in FCR than of RFI.

The heritabilities and genetic correlations for and between traits of the three different multi-trait models were the same up to two decimals. This shows that the co-linearity effect between FCR and RFI is insignificant. Therefore, only results of the seven-trait analysis (third model) will be presented.

Table 4 presents the heritabilities and genetic correlation estimates for and among the different traits investigated in this study as well as some estimates from the literature (Koots *et al.*, 1994a; b; Arthur *et al.*, 2001). Unfortunately, when RFI was included into the multi-trait analysis, the multi-trait converge with status 3 (Groeneveld, 1994) and therefore, the standard errors of the heritabilities were not meaningful.

Table 3 Summary of stepwise regression model to predict Rand-value

Summary of Stepwise Procedure to predict Rand-value when FCR was included						
Step	Variable Entered	Partial R-Square	Model R-Square	C(p)	F Value	Pr > F
1	FCR	0.7385	0.7385	1402.08	19022.80	< 0.0001
2	WW	0.0432	0.7817	61.00	1331.61	< 0.0001
3	ADG	0.0008	0.7824	39.12	23.75	< 0.0001
4	SHD	0.0009	0.7833	13.43	27.65	< 0.0001
5	SCR	0.0003	0.7836	6.00	9.43	0.0021
Summary of Stepwise Procedure to predict Rand-value when RFI was included						
Step	Variable Entered	Partial R-Square	Model R-Square	C(p)	F Value	Pr > F
1	RFI	0.3609	0.3609	8918.35	3804.57	< 0.0001
2	ADG	0.2211	0.5821	3504.33	3563.48	< 0.0001
3	WW	0.1303	0.7124	313.77	3052.15	< 0.0001
4	SHD	0.0104	0.7228	61.69	251.97	< 0.0001
5	SCR	0.0024	0.7251	6.00	57.69	< 0.0001

WW = Weaning weight; ADG = Average daily gain; SCR = Scrotum circumference; SHD = Shoulder height; FCR = Feed conversion ratio; RFI = Residual feed intake

Table 4 Heritability (on diagonal) and genetic correlation estimates (above diagonal) for and among traits

	WW	ADG	SCR	SHD	FCR	RFI	Rand-value
WW	0.32 0.24*	0.28	0.15	0.50	-0.03	-0.05	-0.24
ADG		0.37 0.31*	0.21	0.48	-0.69	-0.09	0.65
SCR			0.42 0.48*	0.09	-0.06	0.05	0.01
SHD				0.52 0.61*	-0.24	-0.02	0.10
FCR					0.34 0.32*	0.75	-0.92
RFI						0.31 0.32**	-0.59
Rand-value							0.36

WW = Weaning weight; ADG = Average daily gain; SCR = Scrotum circumference; SHD = Shoulder height; FCR = Feed conversion ratio; RFI = Residual feed intake

* Koots *et al.* (1994a); # Koots *et al.* (1994b); ** Arthur *et al.* (2001)

The heritabilities for and genetic correlation estimates between WW, ADG, SCR, SHD and FCR are of the same order as those obtained by Koots *et al.* (1994a; b), as shown in Table 4. The large difference in

heritability estimates for WW, compared to literature values can be ascribed to the exclusion of additive maternal effects in the current study (Koots *et al.*, 1994a; b). The only two genetic correlations between weaning weight and other traits that were in the same order than correlations obtained by Koots *et al.* (1994b) were the correlations between WW and SHD (0.50) and between WW and ADG (0.28). However, it should be keep in mind that the estimates reported by Koots *et al.* (1994b) were obtained from two trait analyses, compared to the seven trait analyses in this study. This could be a reason for the differences between the genetic correlations obtained in this study compared to the correlations obtained by Koots *et al.* (1994b).

Weaning weight, due to its low genetic correlation with other traits, is a poor predictor of an animal's feedlot post-weaning growth efficiency and profitability.

The heritability estimate of 0.34 for FCR corresponds well with the mean estimate reported by Koots *et al.* (1994a), as well as those obtained by Archer *et al.* (1999), Robinson *et al.* (1999) and Herd & Bishop (2000), but is slightly lower than the 0.42 obtained by Arthur *et al.* (2001). The heritability estimate of 0.31 for RFI corresponds to that of 0.32 estimated by Arthur *et al.* (2001).

The genetic correlation estimate between RFI and FCR of 0.75 is very close to the estimate of 0.74 in broilers, obtained by Van Bebber & Mercer (1994). The correlation estimates between RFI and the other traits were almost zero. This confirms that RFI is genetically independent of ADG and SHD. Selection for growth rate (ADG) has been repeatedly associated with an increase in mature cow size and its benefit to overall herd productivity has been seriously questioned (Barlow, 1984; Scholtz & Roux, 1984).

The biggest advantage in the use of RFI is therefore its independence of ADG and SHD. Therefore, genetic selection against RFI has the potential to improve feed efficiency in young animals without increasing cow size. FCR on the other hand is lowly correlated with SHD (-0.24). This indicates that selection for FCR will have a small effect on SHD and that it is possible to select animals with a low FCR without a drastic change in SHD, and therefore in maturity type.

A high genetic correlation estimate of -0.92 between FCR and Rand-value was obtained. This was expected because for each kg feed an animal consumes less in order to gain a kg in body weight, the more profitable the animal becomes (see equation 1). The genetic correlation between ADG and Rand-value of 0.65 also shows an increase in Rand-value with an increase in ADG. RFI is also genetically correlated with the Rand-value ($r_g = -0.59$), but to a much lesser degree than FCR.

Table 5 Expected correlated response in Rand-value through selection for FCR, RFI and direct selection for Rand-value

	Selection for FCR	Selection for RFI	Selection for Rand-value
Selection response on Rand-value	0.87	0.55	1.00
Improvement in Rand-value per generation, when 30% best bulls are selected	R 50.36	R 31.84	R 57.89

FCR = Feed conversion ratio; RFI = Residual feed intake

The expected correlated response in Rand-value through direct selection for FCR ($R_{FCR-Rand-value}/R_{Rand-value}$) was 0.87, while the expected correlated response in Rand-value through direct selection for RFI ($R_{RFI-Rand-value}/R_{Rand-value}$) was 0.55 (Table 5). This means that if the 30% most profitable sires were selected on profitability (Rand-value), to be use as parents for the next generation, the response to selection is R 57.89 (with a selection deferential of R 160.81). When 30% of bulls are selected direct for FCR, the correlated response of selection on Rand-value would be R 50.36. This is R 7.53 per generation less then for direct selection for Rand-value. When the best 30% of bulls are selected on RFI, the correlated response of selection in the next generation for Rand-value would only be R 31.84. This is R 26.05 per generation less than direct selection on Rand-value. These results suggest that it would be more efficient to select directly for Rand-value than through indirect selection for either FCR or RFI. Where the Rand-value cannot be

calculated and direct selection is not possible, it would be better to select indirectly for Rand-value through the use of FCR rather than RFI.

Conclusion

For Bonsmara cattle, under South African conditions, the genetic correlations between weaning weight and other traits contributing to feedlot profitability suggests that the indirect genetic response in these traits through the direct selection on weaning weight would be small, if any.

The partial R-square values, genetic correlations and expected correlated responses between RFI and FCR with Rand-value suggest that indirect selection for Rand-value through the selection for FCR and/or RFI would result in slower genetic gain in Rand-value than direct selection for Rand-value. However, where the Rand-value cannot be calculated and/or direct selection for Rand-value is not possible, it would be better to select indirectly for Rand-value through the use of FCR rather than RFI.

References

- Archer, J.A., Arthur, P.F., Herd, R.M., Parnell, P.F. & Pitchford, W.S., 1997. Optimum post weaning test for measurement of growth rate, feed intake and feed efficiency in British breed cattle. *J. Anim. Sci.* 75, 2024-2032.
- Archer, J.A., Arthur, P.F., Herd, R.M. & Richardson, E.C., 1998. Genetic variation in feed efficiency and its component traits. *Proc. 6th Wrld. Congr. Genet. Appl. Livest. Prod.* 25, 81-84. (Armidale, Australia).
- Archer, J.A. & Bergh, L., 2000. Duration of performance tests for growth rate, feed intake and feed efficiency in four biological types of beef cattle. *Livest. Prod. Sci.* 65, 47-55.
- Archer, J.A., Richardson, E.C., Herd, R.M. & Arthur, P.R., 1999. Potential for selection to improve efficiency of feed use in beef cattle: a review. *Aust. J. Agric. Res.* 50, 147-161.
- Arthur, P.F., Renand, G. & Krauss, D., 2001. Genetic parameters for growth and feed efficiency in weaner versus yearling Charolais bulls. *Aust. J. Agric. Res.* 52, 471-476.
- Barlow, R., 1984. Selection for growth and size in ruminants: Is it time for a moratorium. Eds. Hofmeyr, J.H. & Meyer, E.H.H., *Proc. 2nd Wrld. Congr. Sheep Beef Cattle Breed*, Pretoria. pp. 421-432.
- Falconer, D.S. & Mackay, F.C., 1996. *Introduction to quantitative genetics*. Addison Wesley Longman Limited, Edinburgh Gate, Harlow, Essex CM20 2JE, England.
- Groeneveld, E., 1994. VCE-A multivariate multimodel REML (Co) variance component estimation package. *Proc. 5th Wrld. Congr. Genet. Appl. Livest. Prod.* 22, 47-48 (Guelph, Canada).
- Gunsett, F.C., 1986. Problems associated with selection for traits defined as a ration of two component traits. *Proc. 3rd Wrld. Congr. Genet. Appl. Livest. Prod.* 11, 437-442 (Lincoln, Nebraska, USA).
- Herd, R.M. & Bishop, S.C., 2000. Genetic variation in residual feed intake and its association with other production traits in British Hereford cattle. *Livest. Prod. Sci.* 63, 111-119.
- Kennedy, B.W., van der Werf, J.H.J. & Meuwissen, T.H.E., 1993. Genetic and statistical properties of residual feed intake. *J. Anim. Sci.* 71, 3239-3250.
- Koots, K.R., Gibson, J.P., Smith, C. & Wilton, J.W., 1994a. Analyses of published genetic parameter estimates for beef production traits. 1. Heritability. *Anim. Breed. Abstr.* 62, 311-338.
- Koots, K.R., Gibson, J.P. & Wilton, J.W., 1994b. Analyses of published genetic parameter estimates for beef production traits. 2. Phenotypic and genetic correlations. *Anim. Breed. Abstr.* 62, 825-853.
- Robinson, D.L., Oddy, V.H. & Smith, C., 1999. Preliminary genetic parameters for feed intake and efficiency on feedlot cattle. *Proc. Assoc. Advmt. Anim. Breed. Genet.* 13, 492-495.
- SAS, 2000. *SAS/STAT user's guide (Version 8.02)*. SAS Institute Inc., Cary, North Carolina, USA.
- Scholtz, M.M. & Roux, C.Z., 1984. Correlated response to selection for growth, size and efficiency. Eds. Hofmeyr, J.H. & Meyer, E.H.H., *Proc. 2nd Wrld. Congr. Sheep and Beef Cattle Breeding*, Pretoria. 433-443.
- Thompson, J.M. & Barlow, R., 1986. The relationship between feeding and growth parameters and biological efficiency in cattle and sheep. *Proc. 3rd Wrld. Congr. Appl. Livest. Prod.* 11, 271-282 (Lincoln, Nebraska, USA).
- Van Bebber, J. & Mercer, J.T., 1994. Selection for efficiency in broilers: A comparison of residual feed intake with feed conversion ratio. *Proc. 5th Wrld. Congr. Appl. Livest. Prod.* 13, 53-56 (Guelph, Canada).