Direct and maternal additive and heterotic effects in crossbreeding Hereford, Simmentaler and Afrikaner cattle

S.J. Schoeman,* J.G.E. van Zyl[1] and Rensia de Wet
Department of Livestock Science, University of Pretoria, Pretoria, 0002 Republic of South Africa

Received 17 October 1991; accepted 14 August 1992

Data from purebred and crossbred cattle, consisting of the Hereford (H), Simmentaler (S) and Afrikaner (A) breeds, were analysed to estimate breed additive effects, individual heterotic effects, breed maternal, and average maternal heterotic effects. The traits studied were birth mass, weaning mass, and cow productivity and cow efficiency ratios. Among breed groups, crossbred calves showed higher values than purebred calves for most traits. Both two-breed and three-breed rotational systems outperformed purebred, F_1 crosses, and backcrosses. Simmentaler additive effects, expressed as a deviation from Afrikaner, were positive ($P \leq 0.001$) for all traits. Hereford additive effects were positive ($P \leq 0.05$) for weaning mass and cow efficiency only. Simmentaler maternal effects exceeded those of Afrikaner, while Hereford maternal effects were negative for weaning mass ($P \leq 0.001$) and cow efficiency ($P \leq 0.05$). Individual heterosis were in most cases positive but varied from –1.6% for birth mass (H × S) to 16.6% for cow productivity (H × S). Average maternal heterosis was positive ($P \leq 0.01$) for all traits and varied from 3.3% for birth mass to 39.4% for cow efficiency when expressed as a deviation from the purebred mean.

Data van suiwer- en kruisgeteelde beeste wat die Hereford (H), Simmentaler (S) en Afrikaner (A) insluit, is ontleed om direkte additiewe, individuele heterose, direkte materne en gemiddelde materne heterotiese effekte te beraam. Die eienskappe wat ingesluit is, is geboortemassa, speenmassa, koeiproduktiwiteits- en koeidoeltreffendheidsverhoudings. Kruisgeteelde kalwers het tussen rasgroepe hoër waardes as suiwerraskalwers vir meeste eienskappe getoon. Beide tweeras- en drieras-rotasiekruisteeltstelsels het beter as suiwer rasse, F_1-kruisings en terugkruisings presteer. Direkte additiewe effekte vir die Simmentaler, uitgedruk as afwyking van die Afrikaner, was vir alle eienskappe positief ($P \leq 0.001$). Additiewe effekte vir die Hereford was positief ($P \leq 0.05$) vir slegs speenmassa en koeidoeltreffendheid. Simmentaler materne effekte het dié van die Afrikaner oortref, terwyl Hereford materne effekte negatief vir speenmassa ($P \leq 0.001$) en koeidoeltreffendheid ($P \leq 0.05$) was Individuele heterose was in meeste gevalle positief maar het van –1.6% vir geboortemassa (H × S) tot 16.6% vir koeiproduktiwiteit (H × S) gevarieer. Gemiddelde materne heterose was positief ($P \leq 0.01$) vir alle eienskappe en het van 3.3% vir geboortemassa tot 39.4% vir koeidoeltreffendheid gevarieer, uitgedruk as afwyking vanaf die gemiddeld vir suiwer rasse.

Keywords: Beef cattle, breed additive, breed maternal, crossbreeding, heterosis.

---

* To whom correspondence should be addressed.

[1] Present address: P.O. Box 655, Bloemhof, 2660 Republic of South Africa.

Introduction

A large variety of breeds and crosses between these breeds make up the national beef cattle herd of South Africa. Since selection between breeds may result in more rapid improvement than can be achieved by selection within breeds (Cartwright, 1970), such variety suggests that it may be possibile to create certain breed combinations in crossbreds to increase productivity.

In commercial beef cattle production there is a need for the establishment of well-planned crossbreeding programmes which will enable the producer to select those systems and breeds that will maximize efficiency. Characterization of genetic and maternal effects attributable to breeds help producers to use these genetic resources effectively (Alenda *et al.*, 1980). Estimates obtained from crossbreeding studies are useful in the design of the most suitable crossbreeding system. To utilize this information effectively, it is necessary to partition these effects into those due to breeds (breed additive and breed maternal) and those due to heterosis (both individual and maternal).

Several crossbreeding studies have been carried out in South Africa (Mentz *et al.*, 1975; Mentz, 1977; Mentz *et al.*, 1979; Els, 1988), most of which were aimed at the utilization of the Afrikaner dam as basis. However, none of these authors have made any attempt to partition crossbreeding effects.

The aim of this study therefore was to partition crossbreeding effects in a crossbreeding experiment in which the Afrikaner dam was used as a purebred and as a crossbred with Hereford and Simmentaler sires. This was subsequently followed by two- and three-breed rotational crossbreeding.

Procedure

Experimental material

Data were obtained from a crossbreeding experiment conducted between 1972 and 1984 at the Mara Research Station in the northern Transvaal. The three pure breeds involved in the study were Afrikaner, Hereford and Simmentaler. Hereford and Simmentaler sires were initially mated to Afrikaner dams to produce the F_1. Owing to lack of space, no reciprocal crosses could be made. Back-crossing and both two- and three-breed rotational crossbreeding were subsequently carried out with the three breeds.

Multi-sire matings at five per cent males were used. Neither individual sire identities nor the exact number of sires used were recorded. All sires were replaced annually to minimize individual sire effects.

Management of the herd and replacement and selection procedures were described in more detail by Van Zyl (1991) and Van Zyl *et al.* (1992a; 1992b). Breeding took place from the beginning of January through February each year. Calving date was recorded from 1 to 100 with September 1st being 1 and December 9th being 100. Birth mass and sex of calves were recorded within 24 h *post partum.* Calves as well as cows were weighed every 28 days while calves were weaned on the first Wednesday, 196 days after birth. Since weaning ages therefore differed by a maximum of 8 days only, it was considered unnecessary to correct for this factor.

Weaning mass was recorded for each calf, and cow productivity and efficiency were calculated for each dam, as follows:

$$\text{Cow productivity} = \text{weaning mass x } ^{365}/\text{calving interval of calf}$$

$$\text{Cow efficiency} = \frac{\text{weaning mass of calf}}{(\text{body mass of cow at calving})^{0.75}} \times {}^{365}/\text{calving interval}$$

$$= \text{cow productivity}/(\text{body mass of cow at calving})^{0.75}$$

The entire data set included 3 076 calves of which 1 495 were purebred and 1 581 were crossbred. The number of records by year of birth for each breed group is presented in Table 1.

Although the dataset was highly unbalanced and the range of breed genotypes (and reciprocal crosses) was not fully represented, it was considered sufficiently connected to allow estimation of crossbreeding parameters.

Statistical analysis

The data were analysed by the method of least squares for unequal subclass numbers. Two analyses were performed. For each of the four traits, viz. birth mass, weaning mass, cow productivity and cow efficiency, the data were initially analysed with the following model:

$$Y_{ijklmn} = \mu + T_i + A_j + S_k + D_l + (BS)_{mn} + e_{ijklmn}$$

where μ = least-squares means,
T_i = the effect owing to year,
A_j = effect owing to the age of the dam,
S_k = effect owing to the sex of the calf,
D_l = effect of day of birth within year,
$(BS)_{mn}$ = effect owing to breed group within mating system,
e_{ijklmn} = random error.

The influence of first-order interactions between fixed effects was not included since it was of little importance (Van Zyl *et al.*, 1992a; 1992b).

A multiple regression model, suggested by Koger *et al.* (1975) and used by several authors (Dillard *et al.*, 1980; Peacock *et al.*, 1981; Robison *et al.*, 1981; Koch *et al.*, 1985; and others), was subsequently used to estimate the contributions of genetic crossbreeding effects (breed additive genetic, direct individual heterosis, breed maternal and average maternal heterosis). Because only a few breed groups were available, only average maternal heterosis could be estimated.

Table 1 Number of calves born by year for each breed group within mating type

Breed group	1972	1973	1974	1975	1976	1977	1978	1979	1980	1981	1982	1983	1984	Total
Pure breeds														
Hereford (H)	48	59	33	31	34	31	31	31	26	33	34	35	36	462
Simmentaler (S)	71	66	37	32	38	32	38	29	32	33	37	46	38	529
Afrikaner (A)	64	65	32	33	32	35	31	35	27	36	32	40	32	504
Two-breed crosses (F_1)														
H × A	21	22	0	0	0	0	0	0	0	0	0	0	0	43
S × A	45	45	0	0	0	0	0	0	0	0	0	0	0	90
Backcross from F_1														
A × HA	36	41	24	16	11	9	7	6	0	3	2	1	0	156
A × SA	42	40	24	22	15	11	10	6	4	3	2	0	0	179
S × SA	0	0	1	28	0	0	0	0	0	0	0	0	0	29
Two-breed rotational														
H × (AHA)	2	7	16	19	20	21	19	10	14	17	19	25	0	189
A × (HAH)	0	0	0	1	3	7	8	15	18	18	15	16	0	101
S × (ASA)	3	7	11	16	18	16	12	13	13	17	17	19	17	179
A × (SAS)	0	0	0	0	2	7	15	17	17	17	17	19	18	129
Three-breed rotational														
H × (SAH)	43	36	27	22	15	11	9	6	7	9	12	17	15	229
S × (HAS)	0	0	0	1	3	3	7	9	13	18	16	14	14	98
A × (HSA)	3	7	9	13	17	21	18	19	16	11	9	7	9	159

Note: Breed of sire given first.

The traits were analysed with the following model:

$$Y_{ijklm} = \mu + T_i + A_j + S_k + D_l + b_1\alpha_1 + b_2\alpha_2 + b_3\alpha_3 + b_4\beta_{12} + b_5\beta_{13} + b_6\beta_{23} + b_7\delta_1 + b_8\delta_2 + b_9\delta_3 + b_{10}h_m + e_{ijklm}$$

where μ, T_i, A_j, S_k, D_l, and e_{ijklm} are as previously defined, and

b_1, b_2, b_3 = breed additive effects for breeds 1, 2, and 3, respectively,

$\alpha_1, \alpha_2, \alpha_3$ = percentage of genes contributed by breeds 1, 2, and 3, respectively,

b_4, b_5, b_6 = heterosis effects from breeds 1 and 2, 1 and 3, and 2 and 3, respectively,

$\beta_{12}, \beta_{13}, \beta_{23}$ = percentage of loci occupied by genes from breeds 1 and 2, 1 and 3, and 2 and 3, respectively,

b_7, b_8, b_9 = direct breed maternal effects for breeds 1, 2, and 3, respectively,

$\delta_1, \delta_2, \delta_3$ = percentage of genes in the dam from breeds 1, 2, and 3, respectively,

b_{10} = average maternal heterosis effect,

h_m = percentage of loci in the dam with one gene from one breed and the other gene from a different breed,

1, 2, 3 = Hereford, Simmentaler, and Afrikaner, respectively.

The crossbreeding coefficients used were expressed as fractions based on the expected proportions of genes contributed by each breed for additive genetic, heterozygous loci and maternal effects (Dickerson, 1969; 1973). The variables, α_1 through h_m, are linearly dependent. Therefore, not all b_i (b_1 through b_{10}) are estimable. This was resolved by picking a set of estimable linear combinations of the regression coefficients (b_i) in which all effects were estimated as deviations from the Afrikaner.

As the breed genotype means were affected by finite sire representation, standard errors of breed genotype means and crossbreeding components were adjusted using prior estimates of heritability:

σ^2 sires/number of sires + σ^2 within sires/number of dams with σ^2 sires = $0.25 \times h^2 \times \sigma^2 p$.

Estimates of heritabilities were taken to be 0.35 and 0.25 for birth mass and weaning mass, respectively (Lasley, 1981). Heritability estimates for cow productivity and cow efficiency were assumed to be negligible and these standard errors were consequently not adjusted. Since some sires were used across breed groups, it was furthermore assumed that progeny of sires were equally represented across these groups. Covariance of sire effects were not accounted for and were ignored. Although the exact number of sires used was not recorded, an approximate number was derived from the calving rate and five per cent sires used.

Statistical analysis was carried out according to the procedures of the Statistical Analysis System (SAS, 1990).

Results and Discussion

Breed group differences

The analysis of variance for the four traits according to the first model is presented in Table 2. All effects in the model were significant sources of variation. The influence of the fixed effects, viz. year, dam age, sex, and date of birth, and their first-order interactions was discussed by Van Zyl *et al.* (1992a).

Breed group effects were also significant ($P \leq 0.001$) for all traits considered, accounting for 17.3, 39.9, 24.6, and 15.8% of the variation in birth mass, weaning mass, cow productivity, and cow efficiency, respectively. Least-squares means for the mating types and breed groups are presented in Table 3.

The values differed widely among the mating types. Birth mass was significantly ($P \leq 0.01$) heavier in the two-breed crosses than in the other breed groups and was therefore adversely affected. Two-breed and three-breed rotational crosses exceeded the other breed groups in weaning mass, cow productivity and cow efficiency. The three-breed rotational crosses exceeded the purebred means by 12.9, 16.1, and 12.6%, and the two-breed rotational crosses by 3.6, 6.5, and 4.8% in weaning mass, cow productivity, and cow efficiency, respectively. In general, the results are consistent with those reported in most studies (Peacock *et al.*, 1981; Urich *et al.*, 1986; and others).

Table 2 *F* values, error mean squares and test of significance of variances for birth mass, weaning mass, cow productivity and cow efficiency

	Traits (kg)			
Source	Birth mass	Weaning mass	Cow productivity	Cow efficiency
Years	11.43***	42.55***	9.74***	7.03***
Dam age	44.58***	122.80***	5.06**	3.95**
Sex	306.10***	739.54***	119.21***	98.31***
Date of birth	100.24***	59.88***	40.12***	40.31***
Mating type (Breed group)	51.88***	189.90***	44.93***	27.29***
Error mean square	20.48	394.00	1185.28	0.119
Mean ± *SD*	36.28 ± 4.53	216.53 ± 19.85	214.00 ± 34.43	1.97 ± 0.34
R^2 model (%)	32.48	64.08	36.61	26.84

** $P \leq 0.01$.

*** $P \leq 0.001$.

Table 3 Least-squares means (± *SE*) of birth mass, weaning mass, cow productivity and cow efficiency for breed groups within mating types

	Traits (kg)			
Breed groups[1]	Birth mass	Weaning mass	Cow productivity	Cow efficiency
Pure breeds	35.7 ± 0.25^{a}	204.9 ± 1.34^{a}	186.6 ± 9.80^{a}	1.75 ± 0.091^{a}
Hereford (H)	34.1 ± 0.37	187.4 ± 1.52	177.2 ± 8.82	1.68 ± 0.093
Simmentaler (S)	40.2 ± 0.35	241.9 ± 1.60	227.8 ± 8.97	2.02 ± 0.096
Afrikaner (A)	33.3 ± 0.35	193.9 ± 1.55	174.7 ± 8.95	1.68 ± 0.090
Two-breed crosses				
(F_1)	38.0 ± 0.74^{b}	219.1 ± 4.60^{b}	199.3 ± 11.91^{ab}	1.86 ± 0.111^{abd}
H × A	37.5 ± 0.89	220.7 ± 7.59	199.0 ± 12.95	1.95 ± 0.129
S × A	38.2 ± 1.15	220.4 ± 3.88	204.3 ± 11.14	1.87 ± 0.108
Backcross from F_1	35.9 ± 0.47^{a}	220.2 ± 2.44^{bc}	203.6 ± 10.16^{b}	1.83 ± 0.103^{bc}
A × HA	35.6 ± 0.59	217.3 ± 2.69	205.4 ± 9.05	1.81 ± 0.096
A × SA	36.1 ± 0.55	224.9 ± 2.43	213.5 ± 9.36	1.94 ± 0.093
S × SA	38.1 ± 1.40	234.8 ± 5.70	209.6 ± 11.97	1.94 ± 0.119
Two-breed rotational	36.3 ± 0.38^{a}	223.5 ± 2.06^{c}	203.4 ± 10.01^{b}	1.88 ± 0.104^{c}
H × (AHA)	35.8 ± 0.58	223.8 ± 2.53	203.1 ± 9.37	1.87 ± 0.093
A × (HAH)	35.4 ± 0.74	206.0 ± 3.27	195.4 ± 9.99	1.77 ± 0.104
S × (ASA)	38.5 ± 0.59	235.5 ± 1.87	221.1 ± 9.34	2.08 ± 0.092
A × (SAS)	36.0 ± 0.64	225.8 ± 2.74	210.7 ± 9.63	1.87 ± 0.103
Three-breed rotational	36.7 ± 0.40^{a}	231.5 ± 2.08^{d}	216.7 ± 10.01^{c}	1.97 ± 0.098^{d}
H × (SAH)	36.9 ± 0.51	241.0 ± 2.17	232.0 ± 9.20	2.08 ± 0.094
S × (HAS)	38.3 ± 0.78	242.8 ± 3.18	231.3 ± 9.80	2.14 ± 0.099
A × (HSA)	36.2 ± 0.61	215.9 ± 2.55	205.2 ± 9.32	1.84 ± 0.094

[a—d] Least squares means between mating types with at least one common superscript, do not differ significantly ($P \leq 0.01$).

[1] Breed of sire is identified by first symbol in crosses.

Large variation in all four traits was evident within the different mating types, depending on the sire breed used. This was also illustrated by Alenda *et al.* (1980). The use of Afrikaner sires depressed most of the traits whereas Simmentaler sires had a pronounced improving effect thereon. Within the pure breeds, the Simmentaler was superior in weaning mass, cow productivity and cow efficiency. Simmentaler cows were found to be 20.2% more efficient than Hereford and Afrikaner cows.

The most important reasons for differences in performance among breed groups are breed additive, breed maternal, individual heterosis, and maternal heterosis components (Dillard *et al.*, 1980). These crossbreeding components, obtained from the second model, are presented in Table 4.

Breed additive effects

Breed additive genetic effects were positive for both Hereford and Simmentaler for all four traits. These values were significant ($P \leq 0.001$) and higher for the Simmentaler as compared to the Hereford in which case only weaning mass and cow efficiency were significant ($P \leq 0.05$). The additive contributions of the Simmentaler were positive by 21.9, 21.9, 21.6 and 22.6% for the four traits, respectively, over those of the Afrikaner.

These results therefore indicate that using the large-framed European Simmentaler as one parent in a crossbreeding system will increase both birth and weaning mass (as can be expected) but also cow productivity and cow efficiency, despite the fact that smaller cows are favoured.

Individual heterotic effects

Individual heterotic effects were significant ($P \leq 0.05$) and positive in 8 of the 12 estimates (Table 4). For birth mass only, the H × A cross showed a significant ($P \leq 0.001$) effect of 5.3% on midparent value. Those effects between H × S and S × A were not significant ($P > 0.05$).

Greater heterosis was obtained for weaning mass and cow productivity than for birth mass and cow efficiency. Heterotic effects on weaning mass were significant ($P \leq 0.01$) for all three breed combinations and were 11.0% for H × S, 10.1% for H × A, and only 3.1% for S ×A. For cow productivity, corresponding values were 16.6, 10.7, and 4.8% for H × S, H × A, and S × A, respectively. Although not carried out in practice and on account of estimates derived from the model, the highest heterosis values were predicted for weaning mass, cow productivity, and cow efficiency (15.1%) when crossing Hereford sires with Simmentaler dams. Therefore, taking into account all traits considered when exploiting individual heterosis in single crosses, the H × S combination seems to be more favourable than both the H × A and S × A combinations.

Table 4 Crossbreeding component estimates (± *SE*) for birth mass, weaning mass, cow productivity and cow efficiency

	Traits (kg)			
Component	Birth mass	Weaning mass	Cow productivity	Cow efficiency
Purebred LSM	35.7 ± 0.25	204.9 ± 1.34	186.6 ± 9.80	1.75 ± 0.092
Afrikaner LSM	33.3 ± 0.35	193.9 ± 1.55	174.8 ± 8.93	1.68 ± 0.094
Additive genetic[a]				
Hereford (H)	0.74 ± 0.672	7.91 ± 3.622**	5.29 ± 6.657	0.15 ± 0.058*
Simmentaler (S)	7.29 ± 0.654***	42.55 ± 3.424***	37.69 ± 6.303***	0.38 ± 0.064***
Individual heterosis				
H × S	−0.60 ± 0.932	23.66 ± 4.943***	33.54 ± 9.079***	0.28 ± 0.093**
H × A	1.97 ± 0.493**	19.24 ± 2.678***	18.87 ± 5.032	0.06 ± 0.048
S × A	−0.02 ± 0.469	6.72 ± 2.543**	9.60 ± 4.864*	0.08 ± 0.052
Direct maternal[a]				
Hereford	0.05 ± 0.653	−13.56 ± 3.484***	−3.05 ± 6.453	−0.16 ± 0.064*
Simmentaler	−0.37 ± 0.628	6.16 ± 3.327	14.04 ± 6.188	−0.06 ± 0.058
Average maternal heterosis	1.18 ± 0.423***	12.73 ± 2.314***	13.44 ± 4.307	0.69 ± 0.044***

* $P \leq 0.05$; ** $P \leq 0.01$; *** $P \leq 0.001$.

[a] Regression coefficients for Afrikaner (A) additive genetic and direct maternal effects = 0.

Breed maternal effects

The breed maternal influence is strictly environmental as related to offspring traits, but it depends on the genotype of the dam and its associated environmental effects (Koch, 1972; Sellier, 1976). It therefore quantifies the 'maternal ability' of the dam.

Direct maternal effects were significant ($P \leq 0.05$) in 3 of the 8 estimates obtained (Table 4). It was non-significant ($P > 0.05$) for birth mass. For weaning mass, however, it was negative (7.0%) and significant ($P \leq 0.001$) for the Hereford and non-significant ($P > 0.05$) for the Simmentaler. This large negative Hereford maternal effect overrides the positive breed additive effect. Hence, purebred Herefords have low weaning masses (Table 3), probably associated with low milk production in Hereford dams (Reyneke & Bonsma, 1964). Similarly, the negative direct maternal effect on efficiency (9.5%) cancels the positive direct additive effect. The direct maternal effect of the Simmentaler was positive (8.0%) and significant ($P \leq 0.05$) for cow productivity, but non-significant ($P > 0.05$) for cow efficiency.

Simmentaler maternal ability therefore tends to exceed that of both Afrikaner and Hereford, while Afrikaner maternal ability was superior to that of the Hereford for weaning mass and cow efficiency. The Hereford should therefore not be considered as dams in crossbreeding systems.

Average maternal heterotic effects

Maternal heterotic effects are those related to the effect of the crossbred dam. This effect is probably the result of increased milk production and fertility of the crossbred cow.

Average maternal heterotic effects were positive and significant ($P \leq 0.01$) for all four traits (Table 4). It contributed 3.3, 6.2, 7.2, and 39.4% to the purebred means of the four traits, respectively, emphasizing the advantage to be gained in efficiency from the use of crossbred dams in commercial beef cattle production.

Conclusions

Despite limitations in the dataset, some valuable conclusions could be made. The study re-emphasizes firstly the value of crossbreeding for increased production and efficiency in commercial beef production. The superiority of two- and especially three-breed rotational crossbreeding systems became apparent.

On the basis of the magnitude of differences in breed additive, heterotic and breed maternal effects, it seems that introducing Simmentaler genes in crossbreeding systems in this region would tend to increase values of weaning mass, cow productivity and cow efficiency. It might furthermore be suggested that Hereford dams did not provide the needed maternal ability to maximize growth and productivity in Simmentaler crossbred calves.

Acknowledgements

The authors express their gratitude to the Transvaal Region of the Department of Agriculture for making the data available, as well as to all people who were involved in the project at any stage.

References

ALENDA, R., MARTIN, T.G., LASLEY, J.F. & ELLERSIECK, M.R., 1980. Estimation of genetic and maternal effects in crossbred cattle of Angus, Charolais and Hereford parentage. I. Birth and weaning weights. *J. Anim. Sci.* 50, 226.

CARTWRIGHT, T.C., 1970. Selection criteria for beef cattle for the future. *J. Anim. Sci.* 30, 706.

DICKERSON, G.E., 1969. Experimental approaches in utilizing breed resources. *Anim. Breed. Abstr.* 37, 191.

DICKERSON, G.E., 1973. Inbreeding and heterosis in animals. In: Proc. Anim. Breed. Genet. Symp. in honor of J.L. Lush. ASAS, Champaign, p. 54.

DILLARD, E.U., RODRIQUES, O. & ROBISON, O.W., 1980. Estimation of additive and non-additive direct and maternal genetic effects from crossbreeding beef cattle. *J. Anim. Sci.* 50, 653.

ELS, D.L., 1988. Kruisteling vir vleisproduksie. Ph.D. thesis, Univ. of the Orange Free State, Bloemfontein.

KOCH, R.M., 1972. The role of maternal effects in animal breeding. VI. Maternal effects in beef cattle. *J. Anim. Sci.* 35, 1316.

KOCH, R.M., DICKERSON, G.E., CUNDIFF, L.V. & GREGORY, K.E., 1985. Heterosis retained in advanced generations of crosses among Angus and Hereford cattle. *J. Anim. Sci.* 60, 1117.

KOGER, M., PEACOCK, F.M., KIRK, W.G. & CROCKETT, J.R., 1975. Heterosis effects on weaning performance of Brahman-Shorthorn calves. *J. Anim. Sci.* 40, 826.

LASLEY, J.F., 1981. Beef cattle production. Prentice-Hall, New Jersey.

MENTZ, A.H., 1977. Produksiepotensiaal van verskillende eerste-kruising Afrikanerbeeste. Ph.D. thesis, Univ. of the Orange Free State, Bloemfontein.

MENTZ, A.H., COETZER, W.A. & ELS, D.L., 1975. Kruisteling met die Afrikanermoer as basis. I. Dragtigheidsduurte, geboortemassa en die voorkoms van distokie by die nageslag van verskillende rasse van vaars. *S. Afr. J. Anim. Sci.* 5, 53.

MENTZ, A.H., ELS, D.L. & COETZER, W.A., 1979. Crossbreeding with the Afrikaner dam as basis. II. Weaning performance of progeny of different sire breeds. *S. Afr. J. Anim. Sci.* 9, 205.

PEACOCK, F.M., KOGER, M., OLSON, T.A. & CROCKETT, J.R., 1981. Additive genetic and heterosis effects in crosses among cattle breeds of British, European and Zebu origin. *J. Anim. Sci.* 52, 1007.

REYNEKE, J. & BONSMA, J.C., 1964. Milk production studies with beef cattle in the subtropics. I. Milkfat and solids-non-fat production of cows with summer or winter calves. *Proc. S. Afr. Soc. Anim. Prod.* 3, 184.

ROBISON, O.W., MCDANIEL, B.T. & RINCON, E.J., 1981. Estimation of direct and maternal additive and heterotic effects from crossbreeding experiments in animals. *J. Anim. Sci.* 52, 44.

SAS, 1990. SAS Users Guide (6th edn.). Statistical Analysis System Institute, Inc., Cary, NC.

SELLIER, P., 1976. The basis of crossbreeding in pigs: a review. *Livest. Prod. Sci.* 3, 203.

URICH, J.J., PAHNISH, O.F., REYNOLDS, W.L. & KNAPP, B.W., 1986. Comparison of two- and three-way rotational crossing, beef × beef and beef × Brown Swiss composite breed production. *J. Anim. Sci.* 62, 344.

VAN ZYL, J.G.E., 1991. Studies on performance and efficiency of pure- and crossbred cattle in an arid bushveld environment. D.Sc.(Agric) thesis, Univ. of Pretoria, Pretoria.

VAN ZYL, J.G.E., SCHOEMAN, S.J. & COERTZE, R.J., 1992a. Sire breed and breed genotype of dam effects in crossbreeding beef cattle in the subtropics. I. Birth and weaning mass of calves. *S. Afr. J. Anim. Sci.* 22, 161.

VAN ZYL, J.G.E., SCHOEMAN, S.J. & COERTZE, R.J., 1992b. Sire breed and breed genotype of dam effects in crossbreeding beef cattle in the subtropics. II. Calving interval and cow productivity. *S. Afr. J. Anim. Sci.* 22, 166.