Sire × ecological region interaction in Bonsmara cattle

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The possible interaction between sire and four ecological regions in which Bosmara cattle are mainly found in South Africa was investigated. Birth and weaning weight records of 43 628 registered Bonsmara calves born between 1976 and 1997 from 18 herds were available. Restricted Maximum Likelihood (REML) procedures were used in the analyses. Genetic correlations and expected correlated response to selection were estimated assuming the same trait (e.g. weaning weight) to be a different trait when measured in each of four different regions. The results indicate that for the purpose of genetic evaluation, the three bushveld regions need not be separated, but that it would be advisable to consider the highveld region as a separate environment. Selection of bulls bred on the Highveld for the purpose of genetic improvement in the bushveld regions is likely to be less effective than selection of bulls bred anywhere in the bushveld and conversely. The results have also, once again, confirmed that the interaction between sire and contemporary group (HYS) is usually more important than between sire and any designated region.

Die moontlike interaksie tussen vaar en vier ekologiese streke waarin Bonsmara beeste in Suid-Afrika hoofsaaklik voorkom is ondersoek. Geboorte en speen-rekords van 43 628 geregistreerde kalwers wat gebore is tussen 1976 en 1997 in 18 kuddes was beskikbaar. Beperkte maksimum aanneemlikheid (REML) prose-dures is gebruik in die ontleding. Genetiese korrelasies en verwagte genetiese vor-dering as gevolg van seleksie is beraam deur dieselfde eienskap (bv speenmassa) as verskillende eienskappe in elk van die vier streke te beskou. Die resultate toon dat vir genetiese evaluasie die drie bosveldstreke as een omgewing beskou kan word. Dit sal egter beter wees om die hoëveldstreek as 'n aparte omgewing te han-teer. Die seleksie van bulle wat op die Hoëveld geteel is met die doel om genetiese verbetering in die Bosveld te bewerkstellig behoort minder effektief wees as die seleksie van bulle wat enige plek in die Bosveld geteel is en andersom. Die resultate bevestig ook weereens dat vaar × kontemporêre groep (HYS) interaksie gewoonlik belangriker is as die interaksie tussen vaar en enige vasgestelde streek.

Keywords: Genotype x environment interaction, Bonsmara cattle

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Introduction

One of the main principles governing animal breeding is that an animal's phenotype (P) is the result of its genotype (G) inherited from its parents, and the environment (E) in which it was raised (P = G

+ E). Modern methodology, mainly initiated and inspired by the work of C.R. Henderson, has not only enabled scientists to separate these two causal components of performance or desireability, but to quantify any possible interaction between them (P = G + E + GE). If an animal changes rank in performance or breeding value across environments, it indicates the presence of a genotype × environment interaction, suggesting that individuals selected in one environment may not retain their full genetic superiority when transferred to other environments. Selection would be less effective, and response in one environment with selection conducted in another would be less than anticipated (Dickerson, 1962; Yamada, 1962; Tess *et al.*, 1979; Frisch, 1981; Bertrand *et al.*, 1985, Neser *et al.* 1998).

Sires reared and selected in one region often produce progeny in other regions and are capable, with artificial insemination, of siring progeny throughout the country and even the world. Of concern in genetic evaluations, is to what extent animals rank the same across these different environments. This has become an extremely important issue with the increasing development and use of artificial accelerated breeding techniques such as AI.

The purpose of this study was to investigate possible re-ranking (and resulting differences in correlated and direct genetic response) of sires in four different ecological regions in which Bonsmara beef cattle are mainly found. The locally developed synthetic Bonsmara is one of the most important beef breeds in South Africa.

Material and methods

Animals

A total of 43 628 birth and weaning weight records with 54 543 pedigree records for Bonsmara calves born from 1976 to 1997 were extracted from the database of the National Beef Cattle Performance and Progeny Testing Scheme. These records were from 18 herds located in four regions (environments) that according to Acocks (1988) differ in ecological and climatic conditions. Only herds that use artificial insemination (AI) were selected in an effort to increase the genetic links between the herds in the different ecological regions. Thus herds were genetically tied to one another through the common use of connecting sires. Basic edits excluded all animals with missing date of birth or missing age of dam and animals born after embryo transfer or in multiple births. In addition, all records with non-matching breeder and member numbers were excluded to insure that progeny were born and weaned in the same herd. The final edited data set consisted of 36 597 birth weight records and 29 251 weaning weight records with 127 connecting sires which were defined as sires with progeny in two or more herds. Of the connecting sires, 38 had progeny in two or more herds located in the same region, 43 had progeny in two different regions, 25 had progeny in three different regions and 21 had progeny in all four regions.

Environments (regions)

Different environments were identified in terms of regions or veld types as depicted by Acocks (1988), from which herds used in the analysis were extracted. In general, these environments differ in location, rainfall, temperatures, quality and quantity of natural pastures for grazing.

(i) Region 1: Sweet bushveld

This region is located in the area around Thabazimbi and Pietersburg in the Northern Province. The rainfall ranges from 350–500 mm per annum and temperature from 5–40°C (Bonsma, 1976). The dominant trees and shrubs include: *Grewia flaxa* (Maretwa), *Acacia* spp, *Boscia albitrunca* (Matlopi), *Combretum* spp and *Colophospermum mupane*. The most abundant grasses are: *Eragrostis*

spp, *Aristida* spp (Steek-grass), *Panicum maximum*, *Schidmidtia pappophoroides* and *Urochloa* spp (Acocks, 1988). This veld type is by definition "sweetveld", which is palatable year round and also able to maintain animals in good condition throughout the year. Unlike the sour veld, it does not possess an inherent protective mechanism of low palatability in the mature growth stage (Tainton, 1981).

(ii) Region 2: Sour-mixed bushveld

This area covers the western and eastern slopes and valleys of the Waterberg in the Northern Province. It is generally an open savanna with *Acacia caffra* the dominant tree, in a fairly tall and dense grassveld dominated by *Cymbopogon plurinodis*, *Themeda triandra*, *Elionurus muticus* and *Hyperrhenia* spp. Soils are sandy loam and the rainfall ranges from 350–650mm per annum (Acocks, 1988). The temperature varies from a minimum average of 2°C in winter to a maximum average of 40°C in summer (Bonsma, 1976). Generally, this region is predominantly a sour-mixed veld, because of the large variety of unpalatable species, which may dominate the sward under bad management

(iii) Region 3: Sweet-mixed bushveld

This region covers most of Griqualand West and much of the southern part of the Vryburg and Kuruman divisions. The rainfall, occurring in summer, ranges from 250 mm in the south to 450 mm in the north, but is very erratic. The temperature varies from a minimum average of 0°C in winter to a maximum average of 32°C in summer (Van den Berg, 1999, pers. comm.). The underlying rock is dolomite. The grass is by nature tall, dominated by *Themeda triandra* and *Cymbopogon plurinodis*, with much *Aristida diffusa*, *Stipagrostis uniplumis*, *Eragrotis lehmanniana*, *Heteropogon contortus*, *Digitaria eriatha*, *Chrysopogon serrulatis* and *Eutachys* spp. The most common shrub is *Tarchonanthus camphoratus*, associated with the following (and other) species: *Olea europaea*, *Grewia flaxa* and *Acacia karoo* (Acocks, 1988). This ecological region is in a mixed type of veld, which is predominately sweet. The major part of this type of veld is used for cattle ranching. Fodder produced in this veld type for domestic livestock comprises grazeable material from the herbaceous grass layer and browseable material from the woody and shrub layers (Meissner, 1998; pers. comm.).

(iv) Region 4: Highveld

The Highveld region covers the area of Kroonstad, Frankfort, Vrede, Ventersdorp and Koppies. This is an extremely dense *Themeda* veld, with no other species playing an important role. The indicator tree is *Leucosidea sericea*. This veld type occurs at high rainfall regions greater than 650 mm per annum (Acocks, 1988). The grass is sour and only palatable to livestock at an early growing stage. It is suited to mixed farming, with emphasis on crop production. The rainfall in this region is confined to summer months, and the growing season normally extends from September to April. The winter is too dry and cold for vegetation growth. The temperature varies from a minimum average of –1°C in winter to a maximum average of 26°C in summer (Van den Berg, 1999, pers. comm.). Cultivated pastures and hay could be used. *Digitaria eriantha* (Smuts finger) towards the west and *Eragrotis curvula* towards the east, are well-known examples (Meissner, 1998; pers. comm.). Unlike the other three regions generally accepted to be more suited to indigenous breeds owing to high temperatures, this region is believed to be suited to both indigenous and exotic breeds.

Statistical analyses

The study was divided into two sections. In the first, bivariate analyses of the four regions were undertaken excluding the possible effect of a HYS × S (herd-year-season by sire) interaction. This was done because of computational constraints posed by the size of the dataset. In the second section, HYS × S interaction was included, but permanent maternal environment was excluded, for the same reason. All the analyses were done using the REML VCE package of Groeneveld (1996). Cameron (1993) reported that the genetic variance and covariance components estimated using bivariate REML methodology results in unbiased estimates of the genetic correlation, which is a measure of the genotype × environment interaction, since they allow the fitting of more realistic models.

In the first section the most comprehensive model (model 6) was fitted to estimate (co)variance components for weaning weight in different regions. This model can be described in matrix notation as follows:

$$Y = Xb + Z_1a + Z_2m + Z_3c + e$$

Where
Y = a vector of calf records for weaning weight
X = a known incidence matrix relating observations to fixed effects
b = a vector of fixed effects consisting of HYS, sex, age of dam (linear and quadratic regressions) and age at weaning (linear and quadratic regressions)
Z = a known incidence matrix relating observations to random effects
a = random vector of the additive genetic effects of the animal
m = random vector of the maternal genetic effects
c = random vector of the permanent maternal environmental effects
e = a random vector associated with residual error

The above model for weaning weight in each region is similar to the model for birth weight in each region, except for age at weaning.

As pointed out by Bertrand et al. (1987), Bradfield et al. (1997) and Neser et al. (1998), genotype × environment interactions of the type observed, may be caused, in part, by changes in the ranking of sires amongst contemporary groups, rather than changes in the ranking of sires across different regions. This hypothesis was examined in the second section of the study. In this section, two different models were fitted. The first model (limited model) included the additive maternal effect as well as the additive genetic effect and a correlation between direct and maternal effects. The second model (extensive model) included a S × HYS contemporary group interaction as an additional random effect in the model, while the rest of the effects were the same as in the limited model. Even though the available software (REML VCE of Groeneveld, 1996) allows consideration of additional random effects, both models in this analysis excluded the permanent maternal environment, a computing limitation imposed by the size of the data set.

Bivariate animal models were again used in the second section to estimate the genetic correlations between two traits (the same trait in two different regions) at a time. This analysis only considered combinations of regions that presented a significant sire × ecological region interaction in the previous analysis (i.e., Region 4 vs the three bushveld regions, respectively). This procedure was necessary only for these combinations of regions to investigate the importance of a genotype × environment interaction. This study focused on weaning weight because it is considered more important than birth weight in selection programs, and because genotype × environment interaction was proved to be less important for birth weight in the first section.

The correlated response relative to the response that would be obtained by selecting directly in environment Y is:

$$\frac{CR_Y}{R_Y} = \frac{r_g\, i_X\, h_X}{i_Y\, h_Y}$$

(Falconer, 1981)

where i = intensity of selection, h_X and h_Y are the square-roots of the heritabilities of the two traits respectively, r_g is the genetic correlation between the two traits and σ_{PY} is the phenotypic standard deviation of trait Y.

In this study, this ratio was used to show how much gain could be expected by carrying out the selection in environments other than the one in which the improved population is required to live. If this ratio is low, a genotype × environment interaction is most likely present and should be taken into account.

Results and discussion

(Co)Variance components

The estimates of the (co)variance components and genetic parameters for birth weight in each region are presented in Table 1.

The results indicate that birth weight is a highly heritable trait in all regions, with the corresponding estimates of h^2 varying from 0.26 to 0.44. Maternal (m^2) estimates vary between 0.05 (Region 1) and 0.09 (Region 4). These estimates are comparable with the estimates of h^2 and m^2 for birth

Table 1 Estimates of (co)variance components (in kg²) and genetic parameters for birth weight in each region (using model 6)

Parameter	Region 1	Region 2	Region 3	Region 4
σ^2_a	3.794	2.143	7.088	4.868
σ^2_m	0.593	0.721	1.273	1.424
σ_{am}	−0.492	−0.505	0.891	−0.695
σ^2_c	`0.511	0.208	0.674	0.495
σ^2_e	7.975	5.221	7.224	9.424
σ^2_p	12.381 `	7.788	15.368	15.514
h^2	0.295 ± 0.032	0.258 ± 0.035	0.436 ± 0.058	0.300 ± 0.033
m^2	0.046 ± 0.017	0.087 ± 0.019	0.078 ± 0.017	0.088 ± 0.010
C_{am}	−0.040 ± 0.028	−0.065 ± 0.030	−0.058 ± 0.023	−0.074 ± 0.025
r_{am}	−0.328	−0.406	−0.297	−0.264
c^2	0.040 ± 0.009	0.025 ± 0.004	0.042 ± 0.022	0.031 ± 0.008
h^2_T	0.271	0.224	0.416	0.292
Log L	73433.944	73712.622	72883.841	74992.593

σ^2_a, direct additive genetic variance; σ^2_m, maternal additive genetic variance; σ_{am}, direct-maternal genetic covariance; σ^2_c, maternal environmental variance; σ^2_p, phenotypic variance; h^2, direct heritability; m^2, maternal heritability; C_{am} : σ_{am} / σ^2_p ; r_{am}, direct-maternal genetic correlation; c^2 : σ^2_c / σ^2_p ; h^2_T, total heritability; Log L, log likelihood; (Region 1 = sweet bushveld, Region 2 = sour-mixed bushveld, Region 3 = sweet-mixed bushveld, Region 4 = highveld).

Table 2 Estimates of (co)variance components (in kg^2) and genetic parameters for weaning weight in four regions

Parameter	Region 1	Region 2	Region 3	Region 4
σ^2_a	102.378	142.742	150.450	165.811
σ^2_m	78.213	52.490	117.183	56.809
σ_{am}	−18.056	−57.171	−61.675	−46.107
σ^2_c	44.874	29.623	36.431	71.011
σ^2_e	248.649	172.842	229.083	266.070
σ^2_p	456.057	340.527	471.473	513.584
h^2	0.216 ± 0.022	0.359 ± 0.025	0.282 ± 0.042	0.296 ± 0.039
m^2	0.165 ± 0.010	0.132 ± 0.015	0.220 ± 0.021	0.102 ± 0.026
C_{am}	−0.040 ± 0.012	−0.168 ± 0.017	−0.131 ± 0.019	−0.090 ± 0.015
r_{am}	−0.202	−0.661	−0.465	−0.475
c^2	0.095 ± 0.009	0.075 ± 0.013	0.069 ± 0.010	0.127 ± 0.020
h^2_T	0.251	0.244	0.247	0.244
Log L	47991.10	48598.01	48023.20	48846.88

See Table 1 for abbreviations.

weight obtained from Meyer (1992) and Van der Weshuizen (1997). Koots *et al.* (1994a) reported the weighted mean value of 0.31 for h^2 and 0.14 for m^2 from 23 different studies. The estimates of c^2 are slightly higher than the 0.021 reported by Van der Weshuizen (1997). The negative estimate for the covariance between direct and maternal genetic effects (expressed as a proportion of the phenotypic variance or as a genetic correlation) is comparable with most of the published results (Meyer, 1992).

The estimates of h^2 range from 0.22 to 0.36, depending on the ecological region (Table 2). Since the heritabiliy estimates across the four environments are much the same, similar rates of genetic improvement are expected in all environments. These results are similar to those of Baker (1980) and Mrode & Thompson (1990), who reported heritabilities for weaning weight of 0.30 and 0.32. Bradfield *et al.* (1997) and Neser *et al.* (1996) reported estimates of 0.26 for Santa Getrudis cattle and 0.28 for Bonsmara cattle, respectively. In a literature review, Koots *et al.* (1994a) reported a mean h^2 estimate of 0.24, the estimates being pooled over a number of studies with weights inversely proportional to an estimated variance adjusted to a constant heritability. The estimates of maternal heritability (m^2) ranged from 0.10 (Region 4) to 0.22 (Region 3) in the present analysis which are comparable to the results of Neser *et al.* (1996) who reported a maternal heritability of 0.17 for weaning weight in Bonsmara calves. Koots *et al.* (1994a) reported a weighted mean heritability for maternal effects of 0.13 for weaning weight. With the exception of Region 4, the maternal additive effect was more important than the permanent maternal environmental effect. The correlation between direct genetic and maternal effects (ram) were negative across all four (4) regions, which is comparable to the results of Meyer (1992) and Robinson (1996) who reported a ram of − 0.59 and −0.45. Koots *et al.* (1994b) reported a pooled ram literature value of −0.30 from 23 studies. It is interesting to note that the "total" heritability was consistent across regions.

The (co)variance components and the genetic parameters for weaning weights in the four different regions obtained in the second section using the limited alternative and the extensive models are presented in Table 3 and 4, respectively.

In the second section the log likelihood values obtained under the two different models tested

Table 3 Estimates of (co)variance components (in kg^2) and genetic parameters for weaning weight in four regions fitting a limited model (excluding a sire $\times$ HYS interaction)

Parameter	Region 1	Region 2	Region 3	Region 4
σ^2_a	155.817	150.255	95.358	136.803
σ^2_m	127.717	159.120	129.560	85.513
σ_{am}	-46.113	-69.234	-16.519	-61.761
$\sigma^2_{sire \times HYS}$	–	–	–	–
σ^2_e	287.394	237.221	259.433	184.355
σ^2_p	524.815	477.362	467.832	344.91
h^2	0.273 ± 0.022	0.275 ± 0.019	0.197 ± 0.033	0.336 ± 0.028
m^2	0.224 ± 0.019	0.291 ± 0.010	0.268 ± 0.021	0.210 ± 0.030
C_{am}	-0.088 ± 0.011	-0.145 ± 0.017	-0.035 ± 0.019	-0.179 ± 0.022
r_{am}	-0.327	-0.448	-0.149	-0.571
Sire$\times$HYS	–	–	–	–
h^2_T	0.287	0.264	0.289	0.252
Log L	48898.972	48363.858	48014.368	48740.343

σ^2_a , direct additive genetic variance; σ^2_m , maternal additive genetic variance; σ_{am} , direct-maternal genetic covariance; $\sigma^2_{sire \times HYS}$, sire $\times$ HYS interaction variance; σ^2_p , phenotypic variance; h^2, direct heritability; m^2 , maternal heritability; C_{am} , σ_{am} / σ^2_p ; r_{am} , direct-maternal genetic correlation; sire$\times$HYS, $\sigma^2_{sire \times HYS}$ /σ^2_p ; h^2_T , total heritability; Log L, log likelihood. (Region 1 = sweet bushveld, Region 2 = sour-mixed bushveld, Region 3 = sweet-mixed bushveld and Region 4 = highveld).

Table 4 Estimates of (co)variance components (in kg^2) and genetic parameters for weaning weight in four regions fitting an extensive model (including a sire $\times$ HYS interaction)

Parameter	Region 1	Region 2	Region 3	Region 4
σ^2_a	45.859	38.559	31.821	57.882
σ^2_m	121.589	61.355	114.331	93.423
σ_{am}	3.902	-9.686	5.558	8.399
$\sigma^2_{sire \times HYS}$	29.326	39.944	65.962	47.718
σ^2_e	268.630	207.768	266.949	314.465
σ^2_p	469.306	337.940	484.621	521.887
h^2	0.099 ± 0.034	0.111 ± 0.025	0.066 ± 0.058	0.113 ± 0.036
m^2	0.261 ± 0.021	0.177 ± 0.019	0.239 ± 0.026	0.182 ± 0.030
C_{am}	0.008 ± 0.024	-0.029 ± 0.021	0.012 ± 0.019	0.016 ± 0.029
r_{am}	0.052	-0.199	0.0921	0.114
Sire$\times$HYS	0.063 ± 0.011	0.115 ± 0.009	0.138 ± 0.018	0.093 ± 0.010
h^2_T	0.240	0.162	0.201	0.225
Log L	47902.267	48033.782	47863.387	48621.067

See Table 3 for abbreviations.

across regions indicated that the model including a S × HYS interaction effect was most suitable.

The estimates of direct heritability ranged from 0.21 to 0.29 using the model that omitted the effect of S × HYS interaction (Table 3). When a S × HYS interaction was fitted as an additional random effect (Table 4), the estimates of direct heritability ranged from 0.07 to 0.11 across the four regions. Omitting a S × HYS interaction thus leads to an overestimation of the direct additive genetic variance of weaning weight by more than 50%. This is in agreement with the results of Bertrand *et al.* (1987), Neser *et al.* (1996) and Bradfield *et al.* (1997).

It is evident from the above two tables that the inclusion of S × HYS interaction in the model does not have a pronounced effect on the additive maternal effects, since the additive maternal effects were generally consistent irrespective of the model. According to Neser *et al.* (1996), a possible explanation for this is that only the sire component was utilized in the interaction.

The estimates of S × HYS interaction ranged from six to 14% and are in agreement with Neser's (1996) estimates of six to 10%. These results are also comparable with the 13% of Bradfield *et al.*, (1997). The variance owing to S × HYS interaction was higher than the direct additive variance for Regions 2 and 3. This is in contrast to the estimates of several studies reported in the literature (Bertrand *et al.*, 1985; Notter *et al.*, 1992; Neser *et al.*, 1996).

It should, however, be mentioned that, even though the S × HYS interaction was significant, its estimate was generally small. This can be attributed to the fact that sires included after editing were generally those that had produced a large number of progeny in the 21 years of the study. They might therefore represent a selected group of sires.

Correlation

Genetic correlations (r_g) were estimated among the same trait in different regions to assess the relative magnitude of change in performance of sires among different environments (ecological regions). The estimated genetic correlations for birth and weaning weights among the different regions (both direct and maternal) are presented in Tables 5 and 6, respectively.

The results indicate that the direct genetic correlation estimates between birth weight across regions was not significantly different from one, suggesting no re-ranking of sires across regions, with the exception of the sweet bushveld (Region 1) vs the highveld (Region 4). The fact that sires generally did not interact with the environments (ecological regions), suggests that birth weight in the four ecological regions could be regarded as one trait under the same genetic control. These results suggest that the breeding value evaluations for birth weight conducted in one region would be valid across all regions represented in this study, except perhaps for the sweet bushveld vs the highveld. With the exception of the sweet bushveld vs the sour-mixed bushveld, sires did not interact with the environment for maternal effects.

These results are comparable with the results of Nunn *et al.* (1978), who reported the genetic cor-

Table 5 The estimated genetic correlations (± S.E.) among birth weight in the four ecological regions

	Region 1	Region 2	Region 3	Region 4
Region 1	–	0.88 ± 0.080	085 ± 0.094	0.50 ± 0.112
Region 2	0.53 ± 0.167	–	0.80 ± 0.059	0.83 ± 0.118
Region 3	1.00 ± 0.014	1.00 ± 0.055	–	0.97 ± 0.030
Region 4	1.00 ± 0.008	1.00 ± 0.071	1.00 ± 0.013	–

Note: Direct genetic correlations above the diagonal, maternal genetic correlations below the diagonal.

Table 6 The estimated genetic correlations (± S.E.) among weaning weights in the four ecological regions

	Region 1	Region 2	Region 3	Region 4
Region 1	–	0.89 ± 0.073	0.97 ± 0.056	0.50 ± 0.103
Region 2	0.53 ± 0.120	–	0.96 ± 0.084	0.32 ± 0.140
Region 3	0.79 ± 0.111	0.68 ± 0.090	–	0.38 ± 0.092
Region 4	0.52 ± 0.151	0.65 ± 0.133	0.69 ± 0.100	–

Note: Direct genetic correlations above the diagonal, maternal genetic correlations below the diagonal.

relation of sire's progeny performance among regions ranging from 0.86 to 1.00 for birth weight. Tess *et al.* (1984) reported the genetic correlations for sire progeny performance across environments of 0.83, suggesting little or no re-ranking of sires across environments for birth weight.

The results in Table 6 indicate that the genetic correlation estimates between weaning weights in the three bushveld regions (Regions 1, 2 and 3) were not significantly different from unity, suggesting that there was no interaction between the genotype and the environment for these ecological regions and that weaning weight across these regions should be under the same genetic control, as follows from Robertson (1959). Furthermore, the fact that sires did not interact with environments indicates that they would not change rank across the different bushveld regions.

It is interesting to note that the genetic correlation obtained between Region 1 and Region 2 is lower than that obtained between Region 1 and Region 3. It is also true for the maternal genetic correlation estimate. This could possibly be explained by the fact that the conditions in Regions 1 and 3 are very similar. These two regions are located in the sweet and sweet-mixed veld types dominated by similar grass species with relatively the same rainfall, temperatures and other climatic conditions. Region 2 is located in the sour type of veld, as explained earlier.

The genetic correlations of 0.50, 0.32 and 0.38 among weaning weights measured in Regions 4 vs 1, 2 and 3 respectively, are appreciably and significantly different from unity. These correlations demonstrate a significant genotype × environment interaction for weaning weight for Region 4 (Highveld) and the three bushveld regions. This suggests that some rank changes of sires would occur from the combinations of Region 4 to any of the other three ecological regions. However, it should be mentioned that the genetic correlations are not zero or negative, suggesting that there would be some overlapping of genes between Region 4 and the other regions. Selection carried out in Region 4 would only yield partial improvement in the other three regions and the converse is also true. Based on these results, it may be necessary to perform separate analyses for some regions to evaluate the breeding values of sires in regions where rank changes are likely to occur.

These results are comparable with other results in the literature. Nunn *et al.* (1978) reported genetic correlations of sires progeny performance among regions ranging from 0.73 to 0.78 for weaning weight in eight regions of the United States with Simmental cattle. Tess *et al.* (1979) reported the genetic correlation of 0.90, estimated between two regions. Bertrand *et al.* (1985) used variances from the across region analysis and calculated the genetic correlation of sire progeny performance for weaning weight of 0.64, indicating that some rank changes among sire progeny performance were occurring across regions. Bradfield *et al.* (1997) used the same approach and estimated the genetic correlation of sire progeny performance between two environments of 0.63.

The maternal genetic correlations are consistent across Regions 2, 3 and 4 (about 0.70), while the other correlations are much lower (Region 1 vs 2 & 4), indicating the possibility of rank changes for

maternal effects across some environments in this study.

In the second section of this study genetic correlations were estimated using the limited model (omitting a S × HYS interaction — Table 3) and also the extensive model (including a S × HYS interaction — Table 4). The estimated genetic correlations obtained from the two different models are compared to show the bias owing to the effect of S × HYS interaction in estimating the genetic correlation of the same trait as expressed in different regions, and the results are presented in Table 7.

Table 7 Genetic correlations (±S.E.) between Region 4 and Regions 1, 2 & 3

	Region 1	Region 2	Region 3
Region 4	0.54 ± 0.091	0.39 ± 0.128	0.41 ± 0.104
Region 4*	0.81 ± 0.077	0.85 ± 0.096	0.79 ± 0.085

(Region 4 = limited model, Region 4* = extensive model)

The genetic correlations ranged from 0.39 to 0.54 when omitting a S × HYS interaction, but increased to the range of 0.79 to 0.85, when the interaction between sire and HYS were included in the model. The estimates of genetic correlations obtained with the inclusion of S × HYS interaction are not appreciably different from unity, suggesting no drastic re-ranking of sires across regions and that the changes of ranking between contemporary groups are more important than changes across regions. Bradfield et al. (1997) and Neser et al. (1998), reported similar results for weaning weight in beef cattle. Their results indicated that inclusion of a sire × contemporary group interaction increased the genetic correlation between two traits from 0.63 to 0.83.

Correlated response

As the inclusion of a HYS × S interaction is, however, not suitable for the current genetic evaluations of beef sires in South Africa, owing to the lack of connecting sires across years, herds and regions, it might be necessary in practice to account for correlated responses when selecting animals in different regions.

A genetic correlation estimate provides a means of quantifying the interaction for the purpose of predicting response to selection. According to Falconer (1981) the improvement of performance in an environment different from the one in which selection was carried out can be predicted from the knowledge of the heritability of performance in each environment and the genetic correlation between the two performances in the different environments. The improvement expected from indirect solution in a different environment can then be compared to that expected if selection was directly for performance in the environment where improvement is required. This comparison, expressed as a ratio of local selection, is presented in Tables 8 and 9 for birth and weaning weight respectively.

The results indicate that sires selected for birth weight in any ecological region should result in some improvement in all regions presented in this study (Table 8). It should be noted that, if selection were made in Region 3, better improvement could be expected in other regions, than direct selection in those regions. However, indirect selection from other environments other than Region 3, would not yield a correlated response higher than direct selection in those regions. As higher birth weights are cause for concern to many farmers, it could be extrapolated from this study that selection for either high or low birth weight could be done in any region with a corresponding high or low correlated response across all environments. High birth weight has an association with calv-

Table 8 Comparison between expected direct and indirect correlated response to selection for birth weight. Correlated response is expressed as a ratio from the direct expected response in a specific region

	Region 1	Region 2	Region 3	Region 4
Region 1	1	0.941	0.699	0.496
Region 2	0.823	1	0.615	0.770
Region 3	1.033	1.144	1	1.169
Region 4	0.504	0.895	0.805	1

Note: The column headings indicate the regions where selection is carried out, the row headings the regions in which the correlated response is predicted.

Table 9 Comparison between expected direct and indirect correlated response to selection for weaning weight. Correlated response is expressed as a ratio from the direct expected response in a specific region

	Region 1	Region 2	Region 3	Region 4
Region 1	1	0.690	0.849	0.427
Region 2	1.147	1	1.083	0.352
Region 3	1.108	0.851	1	0.371
Region 4	0.585	0.291	0.389	1

Note: The column headings indicate the regions where selection is carried out, the row headings the regions in which the correlated response is predicted.

ing difficulty (dystocia).

The results indicate that selection for weaning weight in Region 2 would result in correlated responses in Regions 1 and 3, slightly higher or as high as the direct selection response. Thus the best improvement could be attained in the bushveld regions by favouring superior sires that were progeny tested in Region 2. Also sires that were progeny tested in Region 3, would increase weaning weights in Region 1 better than direct selection. These results are, therefore, in agreement with Falconer (1960), who concluded that selection in the environment less favourable to the expression of the trait resulted in full potential genetic improvement for the trait in both favourable and unfavourable environments. Selection in the more favourable environment for the expression of the trait do not give similar results for both environments.

The results also suggest that farmers in Region 4 would make best improvements in weaning weight by using sires from their own region rather than selecting sires from other regions. The lowest estimated correlated responses were obtained between Region 4 vs the three bushveld regions, indicating that indirect selection from the bushveld regions would not yield response as high as direct selection. On the other hand selecting sires from Region 4 would result in noticeably lower correlated responses in the bushveld regions, than direct selection.

Conclusion

In general, it was found that sires do not interact significantly with environments for birth weight,

suggesting no evidence of re-ranking of sires for birth weight across four ecological regions. The results of the breeding value evaluations conducted in one ecological region would be valid across all regions presented in this study.

The results emanating from this study suggest that Bonsmara breeders in any of the bushveld regions (sweet bushveld, sour-mixed bushveld & sweet-mixed bushveld) can consider sires from any of the three regions to improve weaning weight in their herds. However, better improvement should be attained in the sweet bushveld and sweet-mixed bushveld regions by selecting sires from the sour-mixed bushveld, a more harsh but equally hot region.

The results also suggest that sires from the highveld region should not be utilized in the bushveld regions, and conversely. Highveld sires should be considered only in local breeding programs as follows from the evidence of a genotype × environment interaction for weaning weight between the highveld and all the bushveld regions. However, it should be noted that the estimates of the genetic correlations is positive indicating that best sires in the highveld would not necessarily be the worst sires in the bushveld regions. The method of evaluation dictates the properties of predicted breeding values. In the second section it was shown that changes in ranking of sires between different contemporary groups appears to be much more important than changes in ranking across different ecological regions. Inclusion of S × HYS interaction is, however, not suitable for the current genetic evaluations of beef sires in South Africa, because of the lack of connecting sires across years, herds and regions. This impracticality of the extensive model has led to the investigation of a limited (realistic) model, and its results suggest that it might be necessary in practice, to estimate region specific breeding values, except for the Bushveld regions. These results support the findings of Neser *et al.* (1998). Therefore, if a limited model is fitted, the breeding values obtained will be directly applicable only to certain regions. Differences not significantly different from unity for some genetic correlations suggest that combining the different bushveld regions should receive serious consideration.

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