Quantifying herd-year-season × sire interaction in Bonsmara cattle

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In an effort to quantify herd-year-season × sire interaction in Bonsmara cattle, four different models were fitted to the data used in Neser *et al.* (1996). The herds were also divided into two (bushveld and sour grassveld) regions in order to estimate the effect of region × sire interaction. Heritability estimates from herd-year-season × sire and year-season × sire interaction models were more or less equal (0.138 vs 0.136), while estimates of heritability of herd × sire and region × sire models were considerably lower (0.080 and 0.060). The separate analysis of the regions yielded heritability estimates similar to those obtained with the model which included herd-year-season × sire interaction (0.142 and 0.166). The estimate of the interaction as a proportion of the total variance remained more or less constant in the models which included year-season × sire, herd × sire and region × sire interaction (0.064, 0.061 and 0.059). It was, however, slightly lower than the model which included herd-year-season × sire interaction (0.084). The product moment correlation between the breeding values of sires in the two different regions was only 4.59% in the separate analysis of the two regions compared to 32.74% when the two regions were analysed together. This low correlation would indicate that separate analyses of regions should be considered. Furthermore, testing of sires for stability of their progeny's performance across regions, should receive attention.

In 'n poging om die effek van kudde-jaar-seisoen × vaar-interaksie in Bonsmara beeste te kwantifiseer, is vier verskillende modelle op die data wat in Neser *et al.* (1996) gebruik is, gepas. Die kuddes is ook in twee (bosveld en suurgrasveld) streke verdeel om die effek van streek × vaar-interaksie te ondersoek. Die oorerflikheidsberamings waar kudde-jaar-seisoen × vaar- en jaar-seisoen × vaar-interaksie ingesluit is, is min of meer dieselfde (0.138 vs 0.136), terwyl die oorerflikheids- beraming van kudde × vaar- en streek × vaar-interaksie heelwat laer is (0.080 en 0.060). Die aparte ontleding van die streke het oorerflikheidsberamings opgelewer soortgelyk aan die wat gedoen is met die model wat kudde-jaar-seisoen × vaarinteraksie ingesluit het (0.142 en 0.166). Die beraming van die interaksie as 'n proporsie van die totale variansie het min of meer konstant gebly in die modelle wat jaar-seisoen × vaar-, kudde × vaar- en streek × vaar-interaksie (0.064, 0.061 en 0.059) ingesluit het. Dit was egter effens laer as in die model wat kudde-jaar-seisoen × vaar-interaksie (0.084) ingesluit het. Die korrelasie tussen die teelwaardes van die bulle in die twee streke was slegs 4.59% in die aparte ontleding van die twee streke. Dit is in teenstelling met die 32.74% as die twee streke saam ontleed word. Hierdie lae korrelasie dui aan dat aparte ontledings vir die twee streke oorweeg moet word. Verder is dit ook noodsaaklik dat daar aandag gegee word aan die toets van bulle vir die stabiliteit van hulle nageslag se prestasie oor streke heen.

Keywords: Bonsmara cattle, genotype × environmental interaction

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Introduction

A substantial herd-year-season × sire interaction in Bonsmara cattle in South Africa was reported by Neser *et al.* (1996). Herd-year-seasons can be divided into its different components such as herds and year-seasons, while herds can be grouped into different ecological regions. The aim of this study was to quantify the effect of these different possible environmental factors contributing to the interaction in an effort to investigate how the problem can best be handled in practice.

Material and methods

Data

The data consisted of weaning weight records of 24 758 Bonsmara calves, the progeny of 503 sires in 30 herds. Artificial insemination (AI) was used in all herds. A more complete data description is given by Neser *et al.* (1996).

The herds involved are found in two distinct regions according to the report by Acocks (1988). Twenty-five herds with a total of 22 042 weaning weight records, the progeny of 440 sires, are located in the bushveld region (Region 1). The remaining five herds with a total of 2 716 weaning weight records, the progeny of 88 sires, are in the sour grasveld (Region 2). This means that two completely diverse climate ecotypes and vegetation types exist. Twenty-five sires had progeny in both regions. Ten of these with the most progeny in both regions were selected to demonstrate the differences between the sires' predicted breeding values in different regions. The ten sires were the most favoured for use in AI programmes.

Statistical analysis

Five analyses, using the derivative-free Restricted Maximum Likelihood programme (DFREML) developed by Meyer (1991, 1995), were performed. Four different models were fitted to the data, *viz:*

$y = X\beta + Z_1a + Z_2m + Z_3c_1 + Z_4c_5 + e$ (Model 1)
$y = X\beta + Z_1a + Z_2m + Z_3c_2 + Z_4c_5 + e$ (Model 2)
$y = X\beta + Z_1a + Z_2m + Z_3c_3 + Z_4c_5 + e$ (Model 3)
$y = X\beta + Z_1a + Z_2m + Z_3c_4 + Z_4c_5 + e$ (Model 4, used in the analyses of the two regions),

where y is an **nx1** vector of weaning weight records, **X** is an **nxp** incidence matrix that relates data to the unknown vector of location parameters β. The vector β contained herd-year-season and sex as fixed effects while age of dam and age at weaning were included as linear regressors. The incidence matrices $\mathbf{Z_1}$ and $\mathbf{Z_2}$ relate the unknown random vectors of direct breeding value **(a)** and maternal breeding value **(m)**, respectively, to **y**. The incidence matrices, $\mathbf{Z_3}$ and $\mathbf{Z_4}$, relate the unknown additional random vectors of herd × sire interaction (HXS) ($\mathbf{c_1}$), year-season × sire interaction (YSXS) ($\mathbf{c_2}$), region × sire interaction (RxS) ($\mathbf{c_3}$), herd-year-season × sire (HYSXS) ($\mathbf{c_4}$) and permanent maternal environment ($\mathbf{c_5}$), also to **y**. The unknown vector **e** contains the random residuals owing to environmental effects peculiar to individual records.

When the first three models were implemented, the data over all herds were utilized, while model 4 was used in the separate analyses of data from the two regions. Results obtained by Neser *et al.* (1996) were used to study the effect of years and seasons within a herd on the estimates of heritability and variances. In model 1, the effect of herds was evaluated. Model 2 was used to quantify the effect of year-season on the estimates of heritability and variances, while the effect of different regions was compared in model three. In models four and five, the breeding values of sires within each region were evaluated.

Fitting only a sire × herd interaction assumes that all progeny of a sire in a herd were subjected to the same environmental covariance, irrespective of time. Fitting a year-season × sire interaction implies that all the progeny of a sire at a certain time were subjected to the same environmental covariance, irrespective of place or managerial level. On the other hand, a herd-year-season × sire interaction implies that records of progeny of a sire in a specific herd-year-season were environmentally correlated, while records in the same herd but different herd-year-seasons were not (Meyer, 1987).

The data were adjusted for possible heterogeneous variance. Standardisation, however, had no effect on the results.

Results

The estimates of heritability and some variance component estimates obtained from analyses using the five models are presented in Table 1.

The interaction variance and direct heritability estimates in the combined analyses were the highest with the model which included herd-year-season × sire interaction. This was to be expected, since most of the variation should be explained by a concatenation of herds, years and seasons. Meyer (1987) and Dong & Mao (1990) found that estimated interaction effects were relatively higher for models with herd-year-season × sire interaction fitted, compared to models with only herd × sire interaction. Although the estimates of the interaction as proportion of the total variance are relatively low, their influence on the estimation of the direct heritability is quite substantial. Van Tassel & Berger (1994) reported that even with low levels of interaction, biases in sire variance and heritability estimates were substantial when interaction was ignored. They concluded that interaction should be included in the variance component model even if the interaction is present at relatively low levels.

It is interesting to note that estimates of maternal heritability remain fairly constant irrespective of the model fitted. This could possibly be explained by the fact that only the sire component was

Table 1 Heritability and some variance component estimates for weaning weight obtained in the five analyses

	Combined analyses				Separate analyses	
	HYSxS*	YSxS	HxS	RxS	Reg 1	Reg 2
Direct heritability	0.138	0.136	0.080	0.060	0.142	0.166
SE	0.000	0.026	0.030	0.000	0.024	0.079
Maternal heritability	0.136	0.129	0.138	0.108	0.135	0.238
SE	0.020	0.025	0.025	0.008	0.025	0.080
Interaction as proportion of total variance	0.084	0.064	0.061	0.059	0.080	0.108
SE	0.000	0.007	0.008	0.006	0.007	0.022
Direct additive variance	67.461	66.887	39.123	29.388	68.635	92.552
Maternal additive variance	66.831	63.474	67.478	52.895	65.219	132.433
Variance owing to interaction	41.393	31.181	29.642	28.767	38.430	60.248
Error variance	265.969	274.546	296.264	304.147	264.697	254.341
Phenotypic variance	490.743	491.151	488.998	489.638	481.930	556.274
Intraclass correlation	0.290	0.349	0.248	0.203	0.309	0.278

* Results obtained by Neser *et al.* (1996)

included in the interaction.

Although the interaction estimates are lower in the analyses which included herd × sire and region × sire interaction, the direct heritability estimate is also lower owing to both a decrease in the additive variance and an increase in residual variance. Since only 25 sires had progeny in both regions, the data structure could also play a role in the reduction in the direct heritability. Neser *et al.* (1998) showed how poor data structure can influence the estimation of variance components. A possible explanation for the increase in the residual variance in the analysis where herd × sire interaction is accounted for, is that herds were distributed over regions, since when region × sire interaction is fitted, it is even slightly higher.

The direct heritability estimate in the analysis which included year-season × sire interaction is roughly the same as in the analysis which included herd-year-season × sire interaction. The estimated interaction was, however, lower, owing to the exclusion of herd × sire interaction. The increase in the error variance could also be ascribed to the exclusion of herd × sire interaction, since this model implies that all the progeny of the sires were subjected to the same year-season effect.

The phenotypic and interaction variance estimates are higher in Region 2. The direct heritability estimate is also slightly higher owing to higher estimates of additive and lower residual variance. The coefficient of variation in both regions is, however, roughly equal (15.97 vs. 15.83). Region 1 is, however, slightly more favourable (aver: 215.26 ± 34.38 vs. 200.15 ± 31.68) for production.

Robertson (1959) suggests that if the genetic correlation between environments is less then 0.8, then the genotype × environment interaction is of biological importance. The respective genetic correlations, as measured by intraclass correlations, in all the different analyses fall below 0.35, with the correlation for region × sire interaction the lowest at 0.203. The lower intraclass correlation in the analysis of herd × sire interaction (0.248) could indicate that management levels play a slightly bigger role in the interaction than year-seasons (0.349).

The predicted breeding values for 10 of the more important AI sires, obtained in the analysis which includes region × sire interaction and the separate analyses of the two regions are presented in Table 2.

Table 2 Predicted breeding values for weaning weight obtained in the analyses which included region × sire interaction and the separate analyses of the two regions

			Combined analyses			Separate analyses		
Sire	n_1	n_2	Region 1	Region 2	Difference	Region 1	Region 2	Difference
A	300	49	−2.659*	−6.900	4.241	−1.592	−10.778	9.186
B	191	47	3.257*	−4.241	7.498	6.353	−7.931	14.284
C	558	28	0.785	−0.775	1.560	2.191	−2.486	4.677
D	428	21	−5.317*	4.233	9.550	−8.230	8.291	16.521
E	65	35	−1.589*	−9.936	8.347	2.333	−6.471	8.804
F	316	68	−0.172*	−4.236	4.064	0.530	−2.082	2.612
G	339	36	6.586*	−3.192	9.778	12.859	0.356	12.503
H	235	37	−7.119	−0.329*	6.790	−11.247	−1.476	9.771
I	191	23	9.034*	−0.537	9.571	10.019	−1.900	11.919
J	633	73	5.491	−1.944	7.435	11.523	4.076	7.447

where n_1 = progeny in Region 1 and n_2 = progeny in Region 2; * region in which it was bred.

The product moment correlation coefficients between breeding values in the different regions, where data from both regions were analysed together is 32.74%. This is in contrast to a correlation of 4.59% between the breeding values of the two regions in the separate analyses of the regions. The higher correlation estimate in the first case is due to the fact that BLUP utilises the ties that exist between regions through the relationship matrix. The correlation between the breeding values for Region 1 in the two analyses is 87.25% and those for Region 2, 84.12%. The high correlation estimates would indicate that more or less the same animals would be selected in the analysis where both regions were analysed together, if the interaction is considered, as when the regions are analysed separately.

The differences between the predicted breeding values for certain sires are, however, alarming as well as the fact that certain of these AI sires have negative breeding values for weaning weight in both regions.

All bulls listed were selected for growth and other traits from standardised growth tests and were functionally correct. According to Theron *et al.* (1994) the correlation between growth in intensive feeding performance trials and growth under field conditions is negligible. Breeding value predictions for some sires were positive in both regions. This indicates that some sires, although a small minority, produce superior progeny in both regions. In general, the sires performed the best in the region in which they were bred.

Conclusions

The results obtained in this study tempt one to suggest that herd-specific breeding values should be estimated and selection carried out within herds. This will not make provision for the year-season × sire interactions, thus not entirely solving the genotype × environment interaction problem. Also since stud herds in South Africa are relatively small averaging 46 females of two years and older (Bonsmara average 140 females), within-herd selection will restrict the scope of selection and increase inbreeding. The stud breeders' market would be restricted to customers in an identical environment and managerial level to their own.

Grouping herds into distinct regions and estimating both region-specific and general breeding values, seem a better alternative. Sires should then be used (tested) in many herds and across regions. A breeder can then either select a sire with a high region-specific breeding value or a stable breeding value. It is perhaps not too presumptuous to suggest that sires that are stable across regions, should also be more stable across herds and year-seasons. Selection for stability is a general practice in plant breeding.

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