

Genetic parameters for reproductive traits in a beef cattle herd estimated using multitrait analysis

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Abstract

The object of this study was to estimate heritabilities and genetic correlations for reproductive traits in a composite multibreed beef cattle herd using multitrait analysis. A REML procedure fitting a multitrait animal model was used to analyse data. Heritabilities and genetic correlations for calving interval (CI), calving date (CD), calving date with a penalty score (CDP) and age at first calving (AFC) were estimated as traits of the dam. The estimated heritabilities for CI, CD, CDP and AFC obtained in this study were 0.01, 0.04, 0.06 and 0.40 respectively with a repeatability of 0.07, 0.12 and 0.13 for CI, CD and CDP. Genetic correlations between traits varied from low to moderate, except for high correlations between CD and CDP (0.98), CI and CD (0.75) and between CI and CDP (0.79). Heritabilities, genetic correlations and repeatabilities of CD and CDP obtained in this study suggest that CD and CDP are the same traits and that selection for CDP rather than for CD does not have any additional advantages. Due to the additional advantages of CD over CI and the fact that CD is a less biased measurement of the female reproductive complex, CD and AFC (because of its high heritability) may be considered as selection criteria for improvement of reproduction in beef cattle herds.

Keywords: beef cattle, breeding, genetics, heritability, reproduction

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Introduction

Reproduction is a complex trait with many components. Measures of reproductive performance used as selection criteria include calving interval (CI), calving rate, services per conception, age at first calving (AFC), days to calving and calving date (CD) (Meaker *et al.*, 1980; Bourdon & Brinks, 1983; Meyer *et al.*, 1990; Rege & Famula, 1993; Van der Merwe & Schoeman, 1995). Calving interval has traditionally been used as the preferred measure of reproduction, particularly in dairy cattle systems (Rege & Famula, 1993). However, because a relatively short breeding season is usually employed in beef cattle systems, CI has limited value as a selection criterion. For this reason, calving date is considered to be more suitable (Bourdon & Brinks, 1983).

In South Africa, the National Beef Cattle Improvement Scheme processes production data collected from farmers for use by the farmers for selection. Age at first calving and CI are most frequently used to evaluate reproductive performance. However, beef cattle are mostly mated during a limited breeding season. Bourdon & Brinks (1983), Marshall *et al.* (1990) and MacGregor (1995) have found CI to be a biased measure of reproductive performance due to its negative association with previous calving date (PCD), as cows that calve early in the season have the longest subsequent CI. For various reasons, Bourdon & Brinks (1983), Buddenberg *et al.* (1990), López de Torre & Brinks (1990), Marshall *et al.* (1990) and MacGregor (1995) suggested that CD should be used as the preferred measurement of reproduction for restricted breeding seasons. These reasons include lower birth weights, reduced incidence of dystocia, higher weaning and yearling weights and higher reconception rates.

Reducing the age at first calving is one way of improving lifetime efficiency in the beef cow (Van der Merwe & Schoeman, 1995). In general, beef heifers are managed to calve for the first time at three years of age. However, first-year mating of heifers has been advocated (Fahmy *et al.*, 1971; Meaker *et al.*, 1980; Nunez-Dominguez *et al.*, 1991) and applied in many herds, including the one under investigation. The advantage of mating heifers one year earlier lies in the potential increase in lifetime production of an extra calf (Meaker *et al.*, 1980). Most published heritabilities for age at first calving are low (Toelle & Robison 1985; Smith *et al.*, 1989; Frazier *et al.*, 1999) and indicate that age at first calving depends on nutrition and management. Most of these estimates were obtained by using univariate analysis. The objectives of this study

were to assess and to estimate heritabilities for and genetic correlations between CI, CD and AFC in a multibreed beef cattle herd using multitrait analysis, and to evaluate a penalty effect for CD.

Materials and Methods

Data used in this study were obtained from the multibreed beef cattle herd of the Johannesburg Metropolitan Council. The animals were kept on two farms in an intensive management system (Paterson, 1981; MacGregor, 1997). The herd was established in 1962 when several crossbreeding experiments were initiated involving Hereford, Angus, Simmentaler, Charolais, Sussex, Brahman, Bonsmara, Afrikaner and Holstein sires that were mainly used on Afrikaner, Hereford and Bonsmara cows. These crossbred groups were subsequently pooled. The breed genotype of these animals is complicated (Paterson, 1981; MacGregor, 1997) and 352 breed genotypes have been identified. Females were bred using AI mainly during two restricted breeding seasons of approximately three to four months each, although a few cows also calved out of season. They were normally inseminated between September and December to calve between June and September of the following year. Animals that did not conceive during this breeding period were inseminated for a second time between May and July. Most (92%) of the females calved between June and September, 2% calved between October and January, while 6% calved in the second calving season between February and May.

Eighty one percent of all females that gave birth during the second calving season were first-calving heifers. Heifers that did not conceive during the first AI season were re-bred and calved at two and a half years of age. Because of this, only cow records were used in the analysis of calving interval, calving date and calving date with a penalty score. Month of calving varied from June to October. The data set contained 32691 observations from 13 049 females. There were 25 684 animals in the pedigree file.

Calving interval (CI) was calculated as the interval between successive calving dates. The mean CI from 22 799 records was 390.7 (\pm 71.72) days. In this study calving date (CD) was used in preference to days to calving (DC), as the date of first joining for each female was unknown. Calving date was recorded as the number of days from the onset of the first calving season (1 June) until the dam calved. Previous calving dates (PCD) were also recorded. The mean CD was 79.3 (\pm 20.31) days, which indicates that the majority of cows calved fairly early in calving season. The number of CD records was 22 465. Since a number of cows failed to calve each year, a penalty score was assigned to those females. The cow having the highest CD value in a specific year was identified and 21 days were then added to her CD value. Penalty score values assigned to non-calvers varied between years from zero in 1984, when all cows calved, to 336 days in 1979 to 1981. The mean calving date value with the penalty score added (CDP) was 88.3 (\pm 31.12) days with 25 440 calving dates recorded.

Mean age at first calving (AFC) of 7 251 heifer records was 781.8 (\pm 119.60) days. Most of those which failed to calve for the first time at approximately 2 years were culled, while some were retained in the herd and were rebred in the following breeding season.

A linear regression procedure of CI on CD, CD on PCD and CI on PCD was performed using the PROC REG procedure of SAS (1993) because CI is negatively associated with previous calving date (PCD) (Bourdon & Brinks, 1983; Buddenberg *et al.*, 1990; L6pez de Torre & Brinks, 1990; Marshal *et al.*, 1990; MacGregor, 1995). For the estimation of (co)variance components for AFC, CD, CDP and CI, a restricted maximum likelihood procedure fitting a multitrait animal model (using the REML VCE 4.2.5 package of Groeneveld, 1998) was used to analyse the data. Traits were considered as traits of the dam, and a repeatability model was fitted due to the repeatable nature of these traits. To determine the importance of possible non-genetic sources of variation on CI, CD, CDP and AFC, the following fixed effects were fitted into the initial model using the PROC GLM procedure of SAS (1993): the herd-birth year concatenation (HY) (46 levels), production year of the dam (14 levels) and genotype (352 levels), while the age of the cow was included as a covariate. Mean age of dams was 5.3 (\pm 2.78) years. Genotypes of the females were obtained from Skrypzeck *et al.* (2000). The following model was used for analysis:

$$\mathbf{y} = \mathbf{Xb} + \mathbf{Za} + \mathbf{e},$$

- y** = a vector of observations for the i^{th} trait,
b = a vector of fixed effects of the i^{th} trait,
a = a vector of random animal effects of i^{th} trait,
e = a vector of random residual effects of the i^{th} trait and
X and Z = incidence matrixes relating records of the i^{th} trait to fixed and random animal effects, respectively.

Model specifications for the four traits AFC, CI, CD and CDP in the initial models are presented in Table 1. For the operational models those effects having no influence ($P < 0.05$) on the traits were subsequently removed.

Table 1 Effects and covariable included in initial statistical models for AFC, CI, CD and CDP

Effect	*Type	Number of levels	Trait			
			AFC	CI	CD	CDP
Herd	F	2	x			
Herd – year of birth	F	45-47		x	x	x
Production year	F	14	x	x	x	x
Genotype	F	256-352	x	x	x	x
Dam age	C	7	x	x	x	x

*F – fixed, C – covariable

Results and Discussion

Analyses of variance for the effects included in the operational models are presented in Table 2 (AFC and CI) and Table 3 (CD and CDP). The R^2 value was very low for CI but much higher for AFC, where the model fits the data fairly well. The low R^2 values for reproductive traits could be due to the composite nature of the female reproductive traits or to the large influence of unidentified environmental effects on reproductive performance.

Table 2 Analyses of variance for AFC and CI

Non-genetic source	Age at first calving			Calving Interval		
	df	Mean Square	Pr>F	df	Mean Square	Pr>F
HY						
Production year	13	527 241.69	0.0001	46	19 275.32	0.0001
Genotype	255	2 854.36	0.0001	13	80 546.30	0.0001
R^2		0.79			0.10	

Table 3 Analyses of variance for CD and CDP

Non-genetic source	Calving Date			Calving date (penalty score)		
	df	Mean Square	Pr>F	df	Mean Square	Pr>F
HY	44	49 061.51	0.0001	44	50 248.96	0.0001
Production year	13	2 195.49	0.0001	13	32 905.96	0.0001
Genotype	351	404.22	0.0001	348	893.51	0.0001
R^2		0.36			0.21	

In the cases of all four traits production year had an effect ($P \leq 0.0001$) and explained a large percentage of the total variance. The same applied to the herd-birth year (HY) concatenation. Although three of the four traits were also influenced by genotype ($P \leq 0.0001$), only a small proportion of the total variance was accounted for (0.10, 0.05 and 0.07 % for AFC, CD and CDP, respectively). Because of the large number of genotypes (256, 352 and 349 for AFC, CD and CDP, respectively) the least-squares means are not presented or discussed in this paper.

Regression equations and descriptive statistics for the reproductive traits are presented in Table 4. Although there is strong evidence ($P \leq 0.0001$) of a relationship between the different traits, r^2 values were fairly small, indicating relatively poor fit.

Table 4 Regression equations and descriptive statistics for reproductive traits

Dependent variable	Traits		Equation	*n	Significance	r ²
	Independent variable					
CI	CD		$y = 326.2 + 0.58 x$	22465	$P \leq 0.0001$	0.10
CD	PCD		$y = 47.0 + 0.43 x$	22465	$P \leq 0.0001$	0.19
CI	PCD		$y = 405.7 - 0.45 x$	20714	$P \leq 0.0001$	0.12

*number of observations

Cows that calved late in a year also tend to calve late in the subsequent year. In this study CD was delayed by 0.43 days for each day delay in the PCD. In most other comparable studies lower estimates in the order of 0.11 to 0.18 days were obtained (Bourdon & Brinks, 1983; Morris & Cullen, 1988; MacGregor, 1995). It was also shown that cows that calved earlier in a year had longer calving intervals in the subsequent year. Calving interval was reduced by 0.45 days for each one-day delay in previous calving date. It is well known that CI is a biased measure of reproductive performance in a restricted breeding season due to its negative association with previous calving date (PCD) (Bourdon & Brinks, 1983; Marshall *et al.*, 1990; MacGregor, 1995). Direct selection for a shorter CI could therefore result in indirect selection for later calving, since cows with the shortest CI are often those that calved late in the previous calving season. In several other studies (Bourdon & Brinks, 1983; Lishman *et al.*, 1984; Morris, 1984; Marshall *et al.*, 1990; Rege & Formula, 1993), a decrease in CI was also reported for each day delay in the previous calving date. Bourdon & Brinks (1983) found that calving interval was reduced by 0.86 days for each one-day delay in previous calving date. Likewise, Morris (1984) found regression coefficients of 0.70 for Angus and 0.54 days for Hereford cattle.

The effect of previous calving date on calving interval was greater than the effect of previous calving date on present calving date. This is to be expected, since calving interval is essentially a function of previous calving date. This suggests that CD is a more preferable trait than CI for restricted calving seasons.

Table 5 shows the heritabilities (h^2) for and genetic correlations (r_g) between CI, CD, CDP and AFC. Heritability estimates are presented on the diagonal (bold) while genetic correlations are above the diagonal. With the exception of AFC, heritabilities for the other traits were very low.

Table 5 Heritabilities and genetic correlations for reproductive traits

Trait	CI	CD	CDP	AFC
CI	0.01	0.75	0.79	-0.03
CD		0.04	0.98	0.09
CDP			0.06	0.08
AFC				0.40

The heritability for CI corresponds with those found in the literature. Koots *et al.* (1994) also reported a mean h^2 of 0.01 for CI (based on three estimates), while López de Torre & Brinks (1990) found a h^2 of 0.02 for CI. The h^2 estimates of 0.04 for CD also correspond with those found in the literature. Koots *et al.* (1994) reported a mean h^2 of 0.08 for CD (based on seven estimates), while Meacham & Notter (1987), López de Torre & Brinks (1990) and Rege & Famula (1993) obtained higher h^2 estimates of 0.16, 0.17 and 0.16, respectively.

Notter (1988), Meyer *et al.* (1990), Ponzoni & Gifford (1994) and Johnson & Bunter (1996) emphasised the need to include all cows in the analysis, including cows that failed to calve during a restricted breeding season (non-calvers) for valid genetic evaluation of CD and variance component estimation. Biased estimates are obtained if data on open cows are omitted, as the results will not include the most genetically inferior and, therefore, potentially most informative animals (Notter, 1988). Heritability estimates obtained when open cows are excluded are expected to be biased downwards, thus suggesting that useful amounts of genetic variation for female fertility may exist (Notter, 1988). This requires that all non-calvers be assigned a penalty score value, which would allow their inclusion in the analysis. However, penalty values must be calculated in such a way that they will not bias cows which did calve (MacGregor, 1997). The procedure proposed by Notter (1988) and applied by both Buddenberg *et al.* (1990) and Meyer *et al.* (1990) used threshold theory to calculate penalty values of non-calvers. Ponzoni & Gifford (1994) applied the procedure

of Meyer *et al.* (1990). They found that the projected penalty values fell within the calving period, and consequently assigned the same value of 390 days to all non-calvers. Johnson & Bunter (1996) found that this method produced a penalty value that was lower than 8% of all cows that calved in a specific year. Johnson & Bunter (1996) concluded that this result was unsatisfactory, as some calvers would be unfairly compared with non-calvers. Since few cows are concurrently at the same stages of their reproductive cycles, and since the breeding season may not start at the same time each year, a single penalty value for all non-calvers may be undesirable as it would fail to simulate the actual herd situation. Most cows would eventually mate and calve if a restricted breeding period was not enforced (MacGregor, 1997).

Three methods for assigning a predicted value to non-calvers were also investigated by Johnston & Bunter (1996). The first method (P360) assigned a value of 360 days to all non-calvers, and was described by Schneeberger *et al.* (1991). Johnston & Bunter (1996) showed that P360 did not produce a satisfactory predicted value for non-calvers because there were cows that calved with a CD higher than 360 days. The other two methods identify a projected value that is assigned to each non-calver within a joining management group (i.e. the last calver within the group), and a constant number of days were added to this record to generate the projected value for all non-calvers. The two constants tested were plus 21 (P21) and 42 days (P42). MacGregor (1997) investigated two methods for assigning a predicted value to non-calvers. The first method involved establishing the relationship between present calving date and previous calving date by means of regression analysis. This was done by estimating the regression coefficient of present calving date on previous calving date, excluding all non-calvers. Each non-calver was then assigned a present calving date value based on an own previous calving date. In order to ensure that non-calvers received the longest calving days, 21 or 42 days were added to the value calculated from the regression. The second procedure was the P21 method that was described by Johnston & Bunter (1996). Johnston & Bunter (1996) and MacGregor (1997) suggested the P21 method because this method of adding a fixed number of days to the last calving date of calvers to calculate a penalty-calving-date value for non-calvers was successful in assigning a meaningful value to non-calvers. Therefore, P21 was also used in this study.

The h^2 estimate for CDP of 0.06 is somewhat lower than the heritabilities found in the literature. Buddenberg *et al.* (1990) assigned a penalty score for CD to all non-calvers and obtained a h^2 estimate for CD in first calvers of 0.39. The majority of h^2 estimates for these traits found in the literature were estimated using univariate analyses, and this could be the reason for the higher h^2 found in the literature, especially for CDP, compared to this study. Although the heritabilities obtained for CD and CDP are both low, CDP heritability was slightly higher than the heritability for CD. The heritability for CD would be expected to be biased downwards (Notter, 1988) because of the exclusion of all open cows. The assignment of a penalty score may be a way to increase the heritability of CD and to ensure a less biased measurement for reproductive performance.

The genetic correlation of 0.75 between CD and CI suggests that selection for an earlier CD would decrease CI. The high positive genetic correlation between CI and CD confirm the positive regression of CI on CD. The same applies to the correlation of 0.79 between CI and CDP. The high genetic correlation of 0.98 between CD and CDP suggests that these two traits are, in effect, the same trait. Although the h^2 for both CI and CD was low, CD is preferred to CI because of the high negative correlation between CI and PCD (previous calving date) and other disadvantages associated with CI as discussed by Bourdon & Brinks (1983), Buddenberg *et al.* (1990), López de Torre & Brinks (1990), Marshall *et al.* (1990) and MacGregor (1995).

The h^2 of 0.40 for AFC found in this study corresponds to most other estimates found in the literature. Kassab (1995), Singh *et al.* (1996) and Magana & Segura (1997) obtained h^2 values for AFC of 0.46, 0.36 and 0.46, respectively. It therefore seems to be possible to change age at first calving through selection. However, Koots *et al.* (1994) reported a mean h^2 of 0.06 for AFC. Singh *et al.* (1996) found a r_g of 0.68 between AFC and CI. The r_g values found in this study between AFC and CI, and between AFC and CDP were very low and were of limited genetic value.

Because of the repeatable nature of CI, CD and CDP, a repeatability model was fitted to these reproductive traits. Table 6 shows the repeatability estimates of the traits when traits were considered as traits of the dam.

Table 6 Repeatability of reproductive traits

Trait	Repeatability
Calving interval	0.07
Calving date	0.12
Calving date with penalty scores	0.13

The repeatabilities obtained for CI, CD and CDP correspond to those found in the literature. For CD, Harwin *et al.* (1969), Lesmeister *et al.* (1973), Baily *et al.* (1985) and Rege and Famula (1993) reported repeatabilities of 0.14, 0.10, 0.12 and 0.23, respectively. Lindley *et al.* (1958), Plasse *et al.* (1966), Schalles & Marlowe (1969) and Baily *et al.* (1985) obtained repeatability estimates for CI of 0.06, 0.03, 0.02 and -0.05, respectively. Repeatabilities for CD or CDP therefore seem to be higher than those for CI. These low repeatabilities were expected because of the low heritabilities that were obtained in this study. This suggests that if a dam calves early in a calving season it does not necessarily mean that she will calve early in the subsequent calving season, and suggests that environment plays a greater role in reproduction traits.

Conclusions

In general, the heritabilities for all reproductive traits with the exception of AFC were low. However, selection for AFC would probably lead to animals that would be sexually mature at a younger age, but would be predisposed to calving difficulties.

Although the h^2 estimates for both CI and CD were low, CD is preferred to CI because of the negative regression coefficient of CI on PCD. Heritabilities, genetic correlations and repeatabilities of CD and CDP obtained in this study suggest that CD and CDP are the same trait. Therefore, selection for CDP does not provide any additional advantage over selection for CD. No unfavourable genetic correlations were identified in this analysis and it seems that CD is a suitable indicator trait for reproductive performance. The use of multitrait analyses in reproductive traits should become a more applied practice. It should be an essential part of analysing reproductive data, especially where selection indices for genetic improvement of reproduction are relevant.

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