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Asian Journal of Animal and Veterinary Advances



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Genetic Analysis of Age at First Calving and Calving Interval in South African Holstein Cattle

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Abstract: This study was carried out to estimate genetic parameters for Age at First Calving (AFC) and first, second, third and fourth and later calving intervals (CI₁, CI₂, CI₃ and CI₄, respectively) in South African Holstein cattle. These parameters were subsequently used to Estimate Breeding Values (EBVs) for each trait. Mean phenotypic values and EBVs for AFC and CI were plotted against year of birth, to determine phenotypic and genetic trends for each trait. Data consisted of performance records of 20420 South African Holstein cows in 502 milk-recorded herds. Genetic parameters and EBVs were estimated by REML and BLUP procedures, respectively, using a multi-trait animal model. Heritability estimates were low for calving interval (0.03±0.01, 0.04±0.01, 0.04±0.01 and 0.03±0.01, respectively for CI₁, CI₂, CI₃ and CI₄) and moderate for AFC (0.26±0.02). Genetic correlations among calving intervals in different lactations were high (average of 0.78) indicating that these may be treated as the same trait. Phenotypically, AFC decreased at an average rate of 0.2 months per year, while CI increased by 1.9 days per year, for the period 1982-1998. On the other hand, average EBVs for AFC decreased by 0.06 months per year and increased by an average of 0.27 days per year for CI, in the same period. Thus, there was an increased genetic merit for heifers to attain early sexual maturity (reduced AFC) but post partum reproductive performance (indicated by calving interval) deteriorated. The consistently declining trend in genetic merit for CI underscores the need to include post partum female fertility in the breeding objective for South African Holstein cattle.

Key words: Female fertility, additive variances, phenotypic trends, genetic trends

INTRODUCTION

Female fertility is one of the most economically important traits in dairy cattle. Economic losses from impaired fertility are mainly due to lost production as a result of prolonged calving intervals (Van Arendonk *et al.*, 1989; Boichard *et al.*, 1997; Olori *et al.*, 2002), increased insemination costs, reduced returns from calves born and higher replacement costs (Bagnato and Oltenacu, 1994). In France, culling for low reproduction rate was reported by Colleau and Moureaux (1999) to account for 25% of disposal reasons. Esselmont and Kossaibati (1997) showed that the primary reason for culling in UK dairy cattle was due to failure to conceive, which accounted for 44% of culls in first lactation animals. Depending on the level of production, increasing calving interval by one-day costs the breeder about 1.8 US dollars in Ireland, without accounting for the costs of higher culling due to poorer fertility (Esselmont *et al.*, 2001; Olori *et al.*, 2002; Veerkamp *et al.*, 2001).

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In spite of its outstanding importance in contributing to dairy herd profitability, female fertility has in the past been left out of selection programmes. The low heritability of fertility traits has largely discouraged efforts to improve them (Raheja *et al.*, 1989; Grosshans *et al.*, 1997; Pryce *et al.*, 1998; Kadermideen, 2004). However, the additive genetic variation of fertility is relatively high (Philipsson, 1981; Hermus *et al.*, 1987; Raheja *et al.*, 1989; Oltenacu, 1991; De Jong, 1998; Grosshans *et al.*, 1997) and therefore, increasing the amount of information available for use in genetic evaluation may facilitate their improvement through selection. Of major concern is the evident antagonistic association between fertility and milk yield (Van Arendonk *et al.*, 1989; Oltenacu, 1991; Bagnato and Oltenacu, 1994; Campos *et al.*, 1994; Hoekstra *et al.*, 1994; De Jong, 1998; Pryce *et al.*, 1997; Ojango and Pollot, 2001; Nilforooshan and Edriss, 2004; Pryce *et al.*, 2004; Kadermideen, 2004; VanRaden *et al.*, 2004). The continual genetic improvement in yield traits taking place in most dairy cattle populations around the world is therefore expected to cause deterioration in fertility.

To maintain or recover high fertility in modern dairy cows calls for a two-prolonged approach involving both inclusion of fertility in broader breeding goals and adjustment to management practices (Pryce *et al.*, 2004). Selection for productive life can slow the long term decline in fertility, but direct selection for fertility should be more profitable (Washburn *et al.*, 2002; VanRaden *et al.*, 2004). Kadermideen and Simm (2002) observed an increase in economic returns of up to 38% by adding calving interval to the UK total merit index (£PLI).

In South Africa, breeding programmes for dairy cattle have been based primarily on increased milk production and to a lesser extent, on improved type. Barely any attention has been paid to traits relating to cow fertility. The average genetic merit for production traits over the past twenty years increased remarkably in the major dairy cattle breeds in South Africa (Banga and Rautenbach, 1999). These trends are probably due to the fact that yield is the main selection criterion for most South African producers. Du Plessis and Roux (1999) showed that South African milk price systems promote an increase in milk yield. Unfortunately these results may have a negative effect on cow fertility.

The primary objective of this study was to estimate genetic parameters for fertility traits in order to compute breeding values for these traits. This will make it possible to identify animals with high genetic merit for reproductive performance and hence facilitate the genetic improvement of fertility through selection. The secondary objective was to determine genetic trends for fertility traits over the past few years.

MATERIALS AND METHODS

The original data set consisted of performance records of 200 319 Holstein cows calving between 1980 and 2005 and pedigree information of 885567 animals. All data were obtained from the Integrated Registration and Genetic Information System of South Africa.

Basic edits to the original data set included deletion of records with unknown birth and calving dates. Age at calving within each lactation was restricted, to remove outliers, as shown in Table 1. These ranges were determined for the South African Holstein cattle population by Mostert *et al.* (2006). Records with CI less than 300 days or greater than 600 days were also discarded.

This editing resulted in a data set containing performance records on 150497 cows, sired by 3920 different sires in 2067 herds. Two calving seasons were defined as summer (October-March) and winter (April-September) (Mostert *et al.*, 2006). Each CI and AFC observation was assigned to a calving herd-year-season contemporary group. Only cows that had first CI were included in the analysis, to take into account the selection of cows which made subsequent records and to avoid selection bias. Contemporary groups with less than 5 animals or less than 2 sires were excluded.

Table 1: The limitations of calving age in different lactation numbers

Lactation No.	Calving age range (months)
1	20-42
2	30-54
3	40-67
4	50-79
5	60-91
6	70-103
7	80-115
8	90-127
9	100-139
10	110-151
11	120-163
12	130-175
13	140-187
14	150-199
15	160-211
16	170-223
17	170-223
18	190-247

Due to limitations in computing resources for analysing large data files, a random subset of data was extracted, based on contemporary group. The random data set comprised of AFC and first, second, third and fourth and later calving interval records (CI₁, CI₂, CI₃ and CI₄, respectively). First, second and third calving intervals were analysed as different traits while fourth and later calving intervals were analysed as the same repeated trait. A pedigree file containing all animals in the data set, going back five generations, was constructed. The pedigree file contained 65819 cows, daughters of 3189 sires and 43223 dams.

The Variance Component Estimation-Restricted Maximum Likelihood (VCE-REML) version 5.0 programs of Groeneveld *et al.* (2003) were used to estimate variance and covariance components. Variance components for AFC were estimated in a unitrait analysis. Covariance component estimates for calving intervals were obtained in a multitrait analysis. The general model equations for AFC, CI₁, CI₂ and CI₃ (Eq. 1) and CI₄ (Eq. 2), in matrix notation, were as follows:

$$y = Xb + Zu + e \quad (1)$$

$$y = Xb + Zu + Wp + e \quad (2)$$

Where:

- y = The vector of observations
- b = The vector of fixed effects consisting of calving herd-year-season and calving age (only for CI)
- u = The random vector associated with additive genetic effects of the animal
- X and Z = Incidence matrices relating observations to fixed environmental and random animal effects, respectively
- W = Incidence matrix relating observations to permanent animal environmental effects
- p = The vector of random permanent animal environmental effects to account for multiple CI records and e is the vector of unknown residual effects

Genetic correlations among calving intervals in different lactations were high, indicating that CI in different lactations may be treated as the same trait. Therefore, for estimation of breeding values,

CI in different lactations was regarded as the same repeated trait. Breeding values were estimated by Best Linear Unbiased Prediction (BLUP) procedures with an animal model using the prediction and estimation software (PEST) of Groeneveld *et al.* (2001). Phenotypic measurements and estimated breeding values were then averaged within birth year and phenotypic and genetic trends for the period 1982-1998 were determined for AFC and CI.

RESULTS

The structure and descriptive statistics of the data used in the genetic analysis of AFC and CI are shown in Table 2. The covariance estimates among calving intervals in different lactations are shown in Table 3. The additive genetic variances were 1.96 months for AFC and 103.5, 131.5, 136.3 and 82.78 days, respectively for CI₁, CI₂, CI₃ and CI₄. Additive variances were higher for CI₂ and CI₃ than for CI₁ and CI₄. Heritability estimates for AFC and calving intervals and genetic and residual correlations among calving intervals are shown in Table 4. AFC had a moderate heritability (0.26) while estimates for CI were low (0.03 for CI₁ and CI₄ and 0.04 for CI₂ and CI₃). Genetic correlations were high (greater than 0.70) except for that between CI₁ and CI₄ (0.61). The highest correlations were between adjacent calving intervals and estimates generally decreased as calving intervals got further apart. Residual correlations among calving intervals shown in Table 4 were mostly zero, the highest being that between CI₁ and CI₃ (0.02) and CI₂ and CI₃ (0.02). The phenotypic and genetic trends for AFC and CI between 1982 and 1998 are shown in Fig. 1 and 2, respectively. Phenotypically, AFC decreased at an average rate of 0.2 months per year while CI increased by 1.9 days per year. Mean breeding value for AFC decreased by 0.06 months per year and increased by an average of 0.27 days per year for CI.

Table 2: The structure of the data used for analysis

Traits	No. of records	HYS	Sires	Herds	Min	Max	Mean	σ_p
AFC	20419	1110	1214	293	20	42	28	3.7
CI ₁	20419	1110	1214	293	300	600	392	58.0
CI ₂	18589	1244	1184	270	300	600	395	59.0
CI ₃	10681	1325	887	241	300	600	395	58.0
CI ₄	15529	1600	759	465	300	600	397	57.0

HYS: Herd-year-season, Min: Minimum value, Max: Maximum value, σ_p : Standard deviation

Table 3: Estimates of additive variance for all traits (σ^2 , on diagonal) and covariance among calving interval traits (off diagonal)

Traits	AFC	CI ₁	CI ₂	CI ₃	CI ₄
AFC (months)	1.96±0.02	-	-	-	-
CI ₁ (days)	-	103.5±0.28	95.77±0.25	93.26±0.31	61.40±0.26
CI ₂ (days)	-	-	131.50±0.31	133.60±0.29	77.50±0.22
CI ₃ (days)	-	-	-	136.30±0.33	78.27±0.22
CI ₄ ^a (days)	-	-	-	-	82.78±0.26

^a: Permanent environment = 71.73±0.49

Table 4: Heritability estimates of fertility traits (on the diagonal), genetic correlations (above the diagonal) and residual correlations (below the diagonal) among calving intervals

Traits	AFC	CI ₁	CI ₂	CI ₃	CI ₄
AFC (months)	0.26±0.02	-	-	-	-
CI ₁ (days)	-	0.030±0.01	0.82±0.06	0.78±0.05	0.61±0.08
CI ₂ (days)	-	0.004±0.01	0.04±0.01	0.99±0.01	0.74±0.10
CI ₃ (days)	-	0.020±0.01	0.02±0.01	0.04±0.01	0.73±0.11
CI ₄ ^a (days)	-	0.000±0.00	0.00±0.00	0.00±0.00	0.03±0.01

^a: Permanent environment = 0.02±0.01

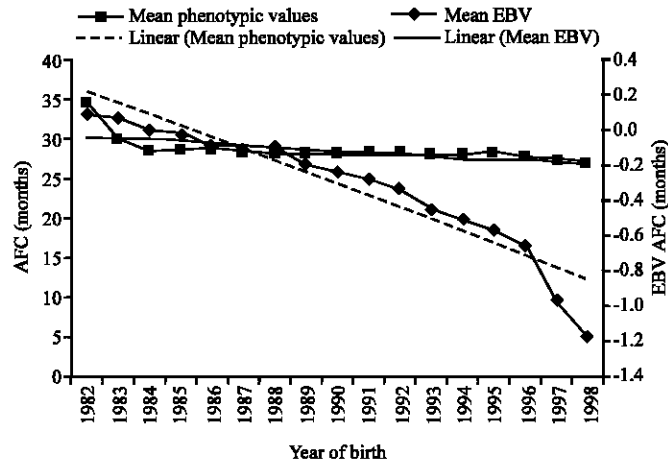


Fig. 1: The phenotypic and genetic trends for AFC. Regression equation for phenotypic value AFC (y) on the year of birth (x): $y = -0.2267x + 30.648$; $R^2 = 0.4669$. Regression equation for breeding value of AFC (y) on the year of birth (x): $y = -0.0667x + 0.2798$; $R^2 = 0.8848$

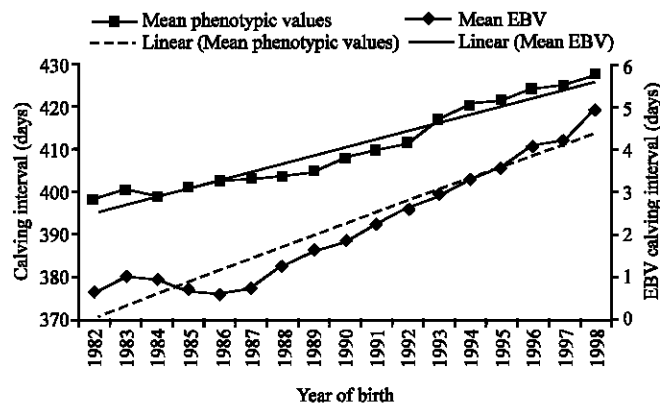


Fig. 2: The phenotypic and genetic trends for CI. Regression equation for phenotypic value CI (y) on the year of birth (x): $y = 1.94x + 392.7$; $R^2 = 0.95$. Regression equation for breeding value of CI (y) on the year of birth (x): $y = 0.2699x - 30.648$; $R^2 = 0.9204$

DISCUSSION

The heritability of AFC was higher than estimates obtained for Holstein-Friesian cattle (Seykora and MacDaniel, 1983) (0.05) and Guernsey cattle (Hermus *et al.*, 1987) (0.12) in the USA. Rege (1991) (0.47) and Ojango and Pollot (2001) (0.38) however, reported higher heritability estimates in Kenyan Holstein-Friesian cattle. The discrepancies could be due to differences in genetic variation among the populations, differences in statistical models used for analysis or varying reactions of the same breed to different environmental conditions. The moderate estimate of heritability for AFC observed in this study indicates that there is potential for improvement of this trait through selection. AFC is economically important because it determines when an animal commences its productive life and hence could influence lifetime productivity. In a seasonal calving production system, the early

attainment of puberty is particularly important in avoiding a shift in first calving to the following calving season. The limitation however, is that AFC is subject to management biases and furthermore, excludes heifers which fail to conceive.

The low heritability estimate of CI is in agreement with many other studies on Holstein-Friesian cattle (Hoekstra *et al.*, 1994; Veerkamp *et al.*, 2001; Olori *et al.*, 2002; Wall *et al.*, 2003, 2004) and Guernsey cattle (Hermus *et al.*, 1987). Higher estimates were however reported for Holstein-Friesian cattle in Kenya (Rege, 1991; Ojango and Pollot, 2001) and Florida, USA (Campos *et al.*, 1994). The low heritability of CI in the current study indicates that this trait is mainly influenced by environmental factors such as management decisions taken by the farmer. Calving interval is a trait of high economic importance and a reduction in CI could be described as one of the outcomes of improved fertility. Calving Interval can be considered a good indicator of cow fertility because of the high correlation between CI and several direct measures of fertility (Campos *et al.*, 1994; Grosshans *et al.*, 1997; Pryce *et al.*, 1997, 1998; Olori *et al.*, 2002). Analysing CI as a measure of fertility, however, presents a problem because CI requires a record of consecutive calving dates. Therefore, relying on CI alone would delay selection decisions. In addition, CI excludes records of cows that are culled due to failure to conceive, which may result in biased estimates of breeding values.

Due to the low heritability of measures of reproductive performance, selection for improved fertility in dairy cattle was, in the past, considered not worthwhile (Raheja *et al.*, 1989; Grosshans *et al.*, 1997; Pryce *et al.*, 1998; Kadermideen, 2004). The relatively high additive genetic variation reported for fertility traits (Phillipsson, 1981; Hermus *et al.*, 1987; Raheja *et al.*, 1989; Oltenu, 1991; De Jong, 1998) however, suggests that there is potential to improve them genetically through selection. This could be achieved by increasing the amount of information used in their genetic evaluation (e.g., using information on correlated traits). The Scandinavian countries were the first ones to broaden their breeding objectives to include fertility and this has been both feasible and beneficial (Phillipsson, 1981; Phillipsson and Lindhe, 2003). Fertility traits are generally correlated with traits that are either well recorded or more heritable. Traits such as body condition scoring, linear type, milk progesterone and milk urea nitrogen have been shown to be genetically correlated with improved fertility (Dadati *et al.*, 1986; Darwash *et al.*, 1999; Melendez *et al.*, 2000; Pryce *et al.*, 2000; Dechow *et al.*, 2001; Godden *et al.*, 2001; Veerkamp *et al.*, 2001; Gutierrez *et al.*, 2002; Royal *et al.*, 2000, 2002; Wall *et al.*, 2003, 2005; Berry *et al.*, 2003; Haile-Mariam *et al.*, 2004; Kadermideen, 2004). Thus, incorporation of traditional measures of fertility and all these measures that improve fertility, directly and indirectly could be used to improve the accuracy of genetic predictions for fertility.

The high genetic correlations observed among calving intervals in different lactations were in agreement with estimates reported in Sweden which ranged from 0.65 between first CI and third CI to 0.99 between first CI and second CI (Haile-Mariam and Kassa-Mersha, 1994) and suggest that CI in different lactations may be treated as the same repeated trait. A decrease in the genetic correlation among CI was observed as the distance between lactations increased. Haile-Mariam and Kassa-Mersha (1994) also reported higher correlations for adjacent calving intervals, which decreased as calving intervals got further apart.

The decreasing trend observed for AFC indicates an improvement in the genetic merit of this trait. This may be, in part, a correlated response to selection for increased yield. However, the increasing trend for CI in the past two decades, suggests that the genetic merit for post-partum fertility in South African Holstein cattle has been deteriorating. A possible cause of this undesirable trend is intense selection for increased yield, without much attention on fertility.

CONCLUSIONS

Cow fertility is a trait of outstanding importance in dairy cattle and is increasingly being incorporated in national dairy cattle breeding objectives worldwide. In South Africa, the genetic

improvement of this trait in dairy cattle is hampered by the lack of breeding values for any measures of reproductive performance. Variance component estimates for Age at First Calving (AFC) and Calving Interval (CI) obtained in the current study form the basis for routine genetic evaluation of cow fertility in South African Holstein cattle. The observed decline in genetic merit for CI in the South African Holstein cattle population, underscores the need to include female fertility in the breeding objective for South African Holstein cattle.

Despite the fact that they are not the best fertility traits, AFC and CI are the only direct measures of reproductive performance available on the South African National Milk Recording Scheme database. In the absence of suitable data to enable genetic evaluations of measures derived from service data, these traits could be used to improve female fertility. Efforts are however needed to record other fertility traits that are not open to management biases, such as calving rate, days to first service, non-return rates, inseminations per conception, etc. Artificial Insemination (AI) data could be used to compute such traits.

The low heritability of fertility traits is an impediment to genetic improvement through selection. These traits however have relatively high additive genetic variance and therefore, increasing amount of information available for use in their genetic evaluation may facilitate their improvement through selection. Cow fertility traits are correlated with traits that are either well recorded or more heritable, such as body condition score, certain linear type traits, milk progesterone and milk urea nitrogen. Such traits could be used to supplement the prediction of genetic merit for fertility, thereby improving the accuracy of selection.

ACKNOWLEDGMENTS

The authors would like to thank the Integrated Registration and Genetic Information System for supplying the data and the Agricultural Research Council for computational resources.

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