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Analysis of environmental and genetic factors influencing reproductive traits and calf survival to weaning in Tswana cattle selected for early growth traits

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The objective of this study was to determine the environmental and genetic factors affecting reproductive traits and calf survival from birth to weaning in Tswana breed of cattle. Analyses of environmental and genetic effects for calf survival traits were done using 7223 records of animals which were born between 1996 and 2013 from 1659 dams and 188 sires in 54 contemporaries. Analyses of environmental and genetic effects for age at first calving were done using 818 records of animals born between 1998 and 2013 from 611 dams and 136 sires in 49 contemporaries, while calving interval analyses were done using 1804 records of cows born between 1999 and 2013 from 496 dams and 121 sires in 45 contemporaries. Reproductive traits analysed were age at first calving (AFC) and calving interval (CI). AFC was analysed using univariate animal model while CI was analysed using repeatability model. Calf survival to weaning (CS) was analysed as a binomial trait using generalised mixed linear logistic model with logit as link function in the ASREML program. Significant environmental effects for reproductive traits were selection line, calving year and season. CS was significantly influenced by calf sex, selection line, calf-birth weight and dam age. The estimated heritability values for reproductive traits were 0.07±0.02 for CI and 0.10±0.07 for AFC. Heritability estimate obtained for CS was 0.07±0.05.

Low genetic variability obtained in reproductive traits and calf survival to weaning trait indicates that improvement of these traits through genetic selection may prove to be slow.

Key words: heritability estimates, binomial trait, logistic model, repeatability model.

INTRODUCTION

Reproductive efficiency has been described as a fundamental goal in beef cattle production (Dickerson, 1970; Meacham and Notter, 1987; Van Doormaal, 2007; Robinson et al., 2017). Milagres et al. (1979) and Janson (1980) also reported variation in reproduction efficiency to be associated with variation in management and nutrition.

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They further noted that genetic variation of reproductive efficiency is very low and estimated heritability to vary between 0 and 10%. Although beef cattle improvement has traditionally focused on production traits, breeding programs should consider all traits of economic importance to optimise genetic gain (Phocas et al., 1998; Albera et al., 2004). Gutiérrez et al. (2007) reported that calving-interval is one of the major reproductive traits to be taken into consideration. Calving interval affects the efficiency of beef cattle production, if it is not well managed (Opsomer et al., 2000; Lamming and Royal, 2001; Lopez-Gatius et al., 2001). Prolonged calving interval is suggested to be either caused by failure of cyclic cows to show oestrous or by failure of the cows to recommence cycling after calving especially if the production management is not conducive and both pre- and postpartum nutritional requirements of the cows are not well met (Mwaanga and Janowski, 2000; Stevenson, 2001; De Rensis et al., 2008).

The American Simmental Association (Shanks et al., 2001) stated that the inclusion of reproductive competency measures in performance evaluation programs would allow producers to identify superior bulls with early conception and easy breeding characters. The practice of culling non-pregnant females has commonly been a recommended management approach to advance production efficiency in beef cattle (Azzam and Azzam, 1991; Dziuk and Bellows, 1993). Age at first calving is also described as a good indicator of cow fertility influencing the overall herd productivity (Gutierrez et al., 2002). Dams calving at a young age tend to be more resourceful in beef production system since a decrease in age of heifers at first calving increases the average number of calves weaned per cow during its entire production life hence improving the cow’s lifetime productivity (Yilmaz et al., 2004; Marshall et al., 1990).

However, harmonizing growth and reproductive performance in beef cattle managed in tropical regions is challenging (Luna-Nevarez et al., 2010), since the variations in body size and milk production in cattle results in varied nutrient requirements for growth, maintenance and reproduction (Arango and Van Vleck, 2002; MacNeil, 2005). Luna-Nevarez et al. (2010) observed opposing relationship between cow size and fertility in Brangus cattle and further suggested maturing rate index to be negatively correlated with both age at first calving and calving interval. Besides age at first calving and calving interval, calf survival also has a major impact on herd economic efficiency as it reduces beef farm income and affects the number of animals available for selection, thus influencing both selection intensity and genetic progress (Gianola, 1982; Gianola and Foulley, 1983; Magalhaes Silva et al., 2017). Guerra et al. (2006) and Cecchinato et al. (2010) stated that survival trait has a binomial phenotypic expression, but with underlying continuous genetic and environmental influences. Casellas et al. (2006) reported that calf survival and longevity are traits of interests to animal breeders due to their effects on economic performance and animal welfare. However, there is no previous study reported on the reproductive as well as calf survival traits for Tswana cattle in Botswana. The objective of this study was therefore to determine the environmental and genetic factors influencing age at first calving, calving interval and calf survival to weaning in Tswana cattle selected for weaning and eighteen-month weights.

### MATERIALS AND METHODS

Data obtained from Department of Agricultural Research (DAR), consisting of 2940 records for 7 months selection line (S1), 3034 for 18 months selection line (S2) and 1252 records for the unselected control line (S3). In both S1 and S2. The data comprised of the following: pedigree information i.e. calf identity number (CALFID), sire identity number (SIREID), dam identity number (DAMID) and associated important information such as birth date, sex of the calf, cow parturition number and date, calf survival code and selection line. Data was edited and extracted for records as shown in Table 1 which were then used for analysis of age at first calving, calving interval and calf survival to weaning. Calving interval (CI) was derived as the difference between the two subsequent calving dates.

Fixed effects fitted for the analysis of the reproductive traits were selection line, calving season and calving year. Since seasonal mating was practiced which started in January and ended in March, calving seasons started in September and ended in January. Few animals calved in the months of September and January therefore calving or birth seasons were categorized into 3 groups as follows: season 1 comprised cows that calved in September and October while season 2 comprised those that calved in November and season 3 comprised cows that calved in December and January (Table 1).

Variance components for age at first calving and calving interval were estimated by fitting univariate individual animal models in ASREML program (Gilmour et al., 2015). Calving interval was estimated using repeatability model. These variance components were later used to compute, phenotypic variance ($\sigma^2_p$), direct heritability ($h^2_d$), the ratios for permanent maternal environmental effects ($h^2_m$) and random residual effects ($h^2_e$). Fixed effects fitted for both calving interval and age at first calving were selection line, calving year and season. The mixed statistical model used for analyzing data of calving interval and age at first calving was as follows:

$$Y = X\beta + Z_d u_d + Z_e u_e + \varepsilon$$

Where,

- $Y$ = the observed reproductive trait of the cow (age at first calving and calving interval)
- $X$ = the incidence matrix relating fixed effects to the observations of a trait
- $\beta$ = vector of fixed effects,
- $Z_d$ = incidence matrix relating direct additive genetic effects the observations of a trait,
- $Z_e$ = incidence matrix relating permanent environmental effects to the observations of a trait,
- $u_d$ = a vector of direct additive genetic effects,
- $u_e$ = a vector of permanent cow environmental effects and $\varepsilon$ = a vector of random residual effects.

The random effects in the mixed models are assumed to have the following distributions: $[\mu_d', \mu_e', \varepsilon'] \sim N ([0', 0', 0'], \Sigma)$. The age
at first calving was analyzed using a univariate mixed model with animal direct genetic as the only random effect other than the residual term. Expected variance-covariance structure fitted in the genetic analysis model was as follows:

\[
\sum = \begin{bmatrix}
A \sigma_\lambda^2 & 0 & 0 \\
0 & I_s \sigma_e^2 & 0 \\
0 & 0 & I_n \sigma_e^2
\end{bmatrix}
\]

Where \( I_s \) is an identity matrix equal to number of cows (\( q \times n \)); \( I_n \) is an identity matrix with the size equal to \( n \times n \); \( A \) is a numerator relationship among the animals; \( \sigma_\lambda^2, \sigma_e^2, \sigma_a^2 \) are additive genetic, permanent environmental and residual variances, respectively.

Calf survival was measured as 1 if the calf was born alive and survived to weaning age and 0 if the calf was born as still birth or born alive but died before reaching weaning age. Since calf survival was examined as a binomial trait, log-linear logistic model fitted to analyse the data. The fixed effects fitted for calf survival trait were selection line, dam age at calf’s birth, sex of the calf, linear and quadratic birth weight effects and contemporaneous group formed from concatenating year and month of birth as described in the previous study that focused on the estimates of covariance component and genetic parameters for growth traits. All fixed factors were fitted as class variables except birth weight which was fitted as a covariate.

The model was used to analyse pre-weaning mortality as a binary outcome such that it postulated a random variable called liability: \( \lambda_i \) where \( i = 1, \ldots, n \) and the observed binary response: \( y_i \) was the result of the following relationship:

\[
y_i = \begin{cases} 
0 & \text{if } \lambda_i < \tau \\
1 & \text{if } \lambda_i \geq \tau 
\end{cases}
\]

Where: \( \tau = \) fixed threshold, \( \lambda \) = liability assumed to be normally distributed with a mean, \( \mu \) and a covariance matrix, \( R = \sigma_a^2 I \), where \( \sigma_a^2 \) is the residual variance, \( y \) = observation of binary response corresponding to the calf survived to weaning or not.

The results for the analysis of environmental factors affecting both age at first calving and calving interval are shown in Table 2. The two traits were significantly influenced (\( P<0.001 \)) by selection line, calving year and season.

### RESULTS AND DISCUSSION

The results indicated that age at first calving was not significantly influenced by any of the environmental factors considered. However, calving interval was significantly influenced by selection line, calving year, and contemporary group. Further investigation into the genetic and environmental factors affecting these traits is necessary to develop strategies for improving calf survival and calving interval in this native population.
significant between the control population (S3) and animals selected for weaning weight (S1). However, animals selected for eighteen months weight (S2) calved at older age than the other two lines (Table 2). The result revealed that selection for eighteen months weight increased age at first calving by 1.78 and 1.10 months when compared to the control population and animals selected for weaning weight, respectively. The results are consistent with the findings by Luna-Nevarez et al. (2010) who reported a negative relationship between improved growth traits (birth weight, yearling weight and post weaning ADG) and age at first calving in Brangus cattle managed under desert production system. Cooke et al. (2013) also established that both increased birth weight and growth rate led to increased age at first calving in Holstein heifers. Likewise, Meyer et al. (1991) reported low and negative association between age at calving and growth traits in Australian beef cattle. However, contrary to the current results Mercadante et al. (2003) reported that selection for post-weaning growth traits did not compromise reproductive performance of the cows.

The current results showed that calving interval significantly varied with selection line. The shortest (536.97±13.87) calving interval was observed in the unselected control population while longest (569.21±9.85) was witnessed in the population selected for weaning weight. The current results are consistent with some literature reports (Albera et al., 2004; Luna-Nevarez et al., 2010; Berry and Evans, 2014) that described negatively correlated responses on reproduction of cows selected for growth rate. However, since the animals were grazing on a natural pasture, the variation may be attributed to lack of improved pasture quality to match the nutritional requirements for relatively larger cows from the selected lines and failure of management to cull cows that failed to conceive in mating season.

The mean difference in age at first calving remained non-significant between animals that calved in November and December. However, the trait differed significantly between October and the other two calving seasons. Age at first calving for those that calved in October was 1.38 and 2.45 months greater than for those calved in November and December, respectively. The estimates obtained currently for age at first calving were consistent with the range reported by Berry and Evans (2014) of 936±51.4 days in Irish beef cattle, McHugh et al. (2014) of 660 to 1275 days in Irish beef cattle and Luna-Nevarez et al. (2010) of 722.4±19 days in Brangus cattle. However, since seasonal mating was practiced in the current study the increased age at first calving in October may be due to the circumstance that animals born in this season were exposed to breeding at the same time as those born in the later seasons hence their chances of being younger at first mating season and ultimately at calving were eliminated.

Calving interval varied significantly between the three calving seasons. The longest calving interval was exhibited in cows that calved in October followed by those that calved in November and December. Cows that calved in December exhibited the shortest calving interval. Calving interval for cows that calved in October were 152.17 and 211.30 days longer than those that calved in November and December, respectively. The difference between calving intervals of cows that calved in seasons November and December was 59.13 days. The values for calving interval obtained in the present study are within the range of 300 to 799 days reported by McHugh et al. (2014) for Irish beef cattle and by Luna-Nevarez et al. (2010) of 414.9±5.4 for Brangus cattle. The current results also agreed with the findings by Short et al. (1990) who reported that calving season is one of the factors mostly associated with postpartum anoestrus hence influencing calving interval. Hansen (1985) also acknowledged the seasonal effect on postpartum interval and stated that it was due to nutrition and other factors such as genotype and suckling. However, Sharpe et al. (1986) concluded that not much can be done through management to correct seasonal effects rather than adjusting for them. Since mating

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**Table 2. Least square means (± S.E.) for selection lines and calving seasons.**

| Effect                        | Trait                          |  
|-------------------------------|-------------------------------|
| Selection line                | Age at first calving (months)  | Calving interval (days) |
| S1                            | 40.34±0.46^a                   | 569.21±9.85^a               |
| S2                            | 41.44±0.46^b                   | 554.49±10.17^b              |
| S3                            | 39.66±0.60^a                   | 536.97±13.87^c              |

Birth/calving season

| Trait                          |  
|-------------------------------|  
| October                       | 41.75±0.51^a                   | 625.95±7.93^a               |
| November                      | 40.37±0.48^b                   | 473.78±6.40^b               |
| December                      | 39.30±0.53^b                   | 414.65±6.77^c               |

S.E. = standard error; ***regression coefficients differ significantly from zero (P<0.0001), S1 = selected for weaning weight, 2 = selected for 18 month weight and S3 = unselected control population.
Table 3. Least square means (± S.E.) for calf survival to weaning by selection line, dam age, calf sex and regression coefficient (± S.E.) for calf birth weight.

| Effect                | Means ± S.E. |
|-----------------------|--------------|
| **Selection line**    |              |
| S1                    | 0.91±0.007   |
| S2                    | 0.91±0.006   |
| S3                    | 0.92±0.009   |
| **Sex of the calf**   |              |
| Male                  | 0.904±0.005a |
| Female                | 0.910±0.007b |
| **Dam age (years)**   |              |
| ≤5                    | 0.904±0.008a |
| >5 to ≤9              | 0.932±0.006b |
| >9                    | 0.937±0.007b |
| **Birth Weight**      |              |
| Linear                | 0.0550±0.0061*** |
| Quadratic             | -0.0008±0.0001*** |

S.E. = standard error; *** = P<0.001, S1 = selected for weaning weight, 2 = selected for 18 month weight and S3 = unselected control population.

season which started in January and ended in March was practiced in the current study, prolonged calving interval may be attributed to the situation that cows calving in October had to wait until January to be served with a bull compared to those calving in November and December which waited for a short period to be served with a bull or calved with the bull around. The other reason may be that grazing on natural pasture was practiced and the rainy season starts in September and end in April hence cows calving in October possibly had poor body condition score at calving and also may not have had adequate postpartum nutrition compared to those that calved in November and December when adequate nutritious pasture is well established. Therefore good body condition score at calving and adequate postpartum nutrition improved the chances for both postpartum cycling and re-conception rate of cows that calved in November and December hence shortening their calving intervals (Short et al., 1990 and Berry and Evans, 2014).

The least square mean estimates of calving interval and age at first calving ranged from 447±22 days in 1999 to 577±22 days in 2010 and 35.6±3.63 months in 1999 to 48.4±0.83 months in 2011 for calving and birth year, respectively (the detailed data is not shown). The results showed a clear regression on the performance of the cows for the two traits. The declining trend observed on both traits over the years in the current study seems to be in agreement with the previous literature reports by Do et al. (2013) and Oltenacu and Broom (2010) that selection for high growth and milk performance in cattle generally is accompanied by a decline in reproductive performance unless the increased nutritional requirements of the cows is maintained through supplementary feeding. Since the animals in the current study were dependent on natural pasture for the better part of their nutritional needs the results may indicate a continuous deterioration in pasture quality over the years. Hence, this call for improving the quantity and quality of grazing pasture as well as implementation of supplementary feeding strategy in order to keep up with the continuous improvement on livestock performance through selection.

There was no significant difference in pre-weaning survival of calves among the selection lines, while calf survival was significantly affected by calf sex and dam age (Table 3). The female calves survival was 1% higher (P<0.05) than male calves. This may be attributed to male calves being born heavier than their female counterparts hence more calving difficulties and dystocia cases that lead to high mortality in male calves than in females especially those calves born from primiparous cows.

Calf survival rate increased from 90% for young dams aged less than 5 years to 93% for mature dams aged 5 to 9 years. However, calf survival rate was not significantly different between mature dams, aged between 5 to 9 years and older dams aged above 9 years (Table 3). Variation in calf survival with dam age may be attributed to young dams being either prone to calving difficulty or failing to meet the calf’s environmental and nutritional requirements during prenatal and postnatal period hence leading to weak calves with low birth weight being born and failing to survive to weaning age.
The results of the current study are consistent with the findings by Goyache et al. (2003) who reported that an average survival rate difference of 0.15 to 2.44% in favour of female calves at different pre-weaning ages in beef cattle. Likewise, Tarres et al. (2010) observed that calving difficulty varies with calf sex and is more extreme in male calves than in their female counterparts. The lower calf survival observed in the current study for younger dams might be attributed to calving difficulties and inability of providing sufficient nutrients for weaker calves during the nursing stage. Cole et al. (2007) reported that calving difficulty negatively affect calf survival via prolonged hypoxia and associated potential traumas. Tarres et al. (2010) reported that calving difficulty is one of the factors leading to reduced pre-weaning calf survival and it extremely affects young primiparous dams aged less than 5 years than mature dams aged 5 years and older. On the other hand, Correa et al. (2000) reported that dystocia and calving difficulty are not the main cause of death in tropical beef breeds.

In general, the range of values (90 to 94%) obtained for calf survival rate in Tswana cattle in the current study is within the range of values reported for other beef breeds by Cervantes et al. (2010) for Asturiana de los Valles beef cattle (80 to 94%), by Magalhaes Silva et al. (2017) for Nellore cattle (93%) and by Guerra et al. (2006) for multibreed beef cattle (91%). Both linear and quadratic birth weight effects had significant (P<0.001) influence on calf survival (Table 3). The implication of the result is that the calf survival rate increased with increasing weight of calves towards average weight and then declined with increasing calf birth weight. This may happen as a result of some calves being born with extremely lighter and heavier weight than average birth weight leading to death from various stressful environmental factors including inability of the dams to care and provide sufficient nourishment required for early growth.

The results are consistent with a report by Bunter et al. (2014) who observed higher mortality rate in Brahman and tropical composite calves with low birth weight. The same authors further found that generally pre-weaning mortality in beef cattle is associated with calving difficulty and extreme birth weights. Riley et al. (2004) and Vostry et al. (2014) reported that new born calves with low vigour were frequently observed in Bos indicus. The authors further established that most pre-weaning deaths occurred within thirty days after birth and cited calf weakness as the major cause of death, followed by diarrhea and navel inflammation. Magalhaes Silva et al. (2017) also found that factors most significantly associated with mortality for large number of calves were production environment presented by site-year and low birth weight more so than high birth weight. Direct genetic and environmental variances contributed 10 and 90% to the phenotypic variance of age at first calving, while the direct genetic and environmental variance contributions to the phenotypic variance of calving interval were 7 and 93%, respectively. The permanent environmental variance estimate for the calving interval was zero (Table 4). This might indicate lack of predicting ability of current calving interval for the future calving interval within a cow.

Direct heritability estimate currently obtained for age at first calving was 0.10±0.07 and it did not differ significantly from zero. The estimate was low and within the lower range of reported values. For example, the reported heritability values range from 0.11 to 0.31 (Makgaaliela et al., 2008; McHugh et al., 2014; Berry and Evans, 2014; Park and Lee, 2013; Solemani-Baghshah et al., 2014; Gutierrez et al., 2002) in beef and dairy cattle. Direct heritability estimate obtained in the current study for the calving interval was 0.07±0.02. This estimate was also low but significantly different from zero. Direct heritability value obtained in the current study was comparable with the range of 0.01 to 0.06 as reported (Gutiérrez et al., 2002; Berry and Evans, 2014; McHugh et al., 2014) for beef cattle. The results show that in general heritability for reproductive traits is very low and also they are having lower repeatability. As it has been established in several previous studies, the high estimates of environmental variance obtained for the two traits indicate that significant performance improvement on the two traits can be attained through modifying environmental factors associated with cow management.

The results presented in Table 5 show that the sire

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**Table 4. Variance components and heritability estimates (± S.E.) for age at first calving and calving interval.**

| Parameter | Age at first calving | Calving interval |
|-----------|----------------------|-----------------|
| σ²_a      | 2.47±1.85            | 2150.3±792.50   |
| σ²_e      | 22.83±2.1            | 29979±1184.5    |
| σ²_pe     | -                    | 0.0             |
| σ²_pe     | 25.306±1.27          | 32129±1088      |
| h²_a      | 0.10±0.07            | 0.07±0.02       |
| h²_e      | 0.90±0.07            | 0.93±0.02       |

S.E. = standard error, σ²_a = direct genetic variance; σ²_e = residual variance; σ²_pe = permanent environmental variance; σ²_pe = phenotypic variance; h²_a = direct heritability and h²_e = environmental proportion.
variance for the survival accounts only for 10% of the phenotypic variance. This result indicates that much of the phenotypic variance for calf survival may be defined by other components other than direct genetic effects possibly by environmental components. The lower estimate for direct genetic effect obtained in the current study is in line with the findings by Gregory and Maurer (1991) and Von-Keyserlingk and Weary (2007). These authors reported that pre-weaning mortality has an important maternal component which decreased from birth to weaning period. The authors further described maternal effects to be in the form of intrauterine effects, milk production and protection provided through behaviour and passive immunity (colostrum). The lower estimate currently obtained for direct genetic variance was not significantly different from zero. However, it is well documented that the survival is one of the traits with low heritability and most of the variation comes from other environmental aspects (Cox, 1972; Prentice and Gloekler, 1978; Casellas et al., 2006; Cecchinato et al., 2010; Cervantes et al., 2010; Bunter et al., 2014; Magalhaes Silva et al., 2017). Therefore a significant improvement on calf survival rate may be attained through improvement on the environmental part such a management system.

The current direct heritability estimate of 0.074±0.045 is consistent with other reported heritability estimates (Guerra et al., 2006; Schmidek et al., 2013 and Magalhaes Silva et al., 2017) for pre-weaning calf survival ranging from 0.02±0.002 to 0.190±0.078 for the Nellore and multibreed beef cattle. Schmidek et al. (2013) observed higher genetic variability for calf survival during the perinatal period up to 2 to 3 days after birth compared to the rest of the pre-weaning period. In general, the low and non-significant genetic component found in the current results as shown in Table 5 reveals that there is insufficient genetic variability to improve calf survival to weaning through genetic selection.

### Table 5. Variance components and heritability estimates (± S.E.) for calf survival to weaning.

| Parameter | Estimate ± S.E. |
|-----------|----------------|
| $\sigma_s^2$ | 0.062±0.040 |
| $\sigma_a^2$ | 0.249±0.159 |
| $\sigma_e^2$ | 3.290±0.040 |
| $\sigma_p^2$ | 3.352±0.040 |
| $h^2$ | 0.074±0.045 |

S.E. = standard error, $\sigma_s^2$ = sire variance, $\sigma_a^2$ = genetic variance, $\sigma_e^2$ = phenotypic variance = $\sigma_s^2 + \sigma_a^2$, and $h^2$ = heritability = $4(\sigma_a^2)/ (\sigma_s^2 + \sigma_a^2)$.

Conclusion

The current study revealed that both age at first calving and calving interval have low direct heritability and are more influenced by environmental factors than genetic effects. The low repeatability estimate for calving interval proved that the trait is poorly repeatable. Improvement of these traits can therefore rapidly be achieved through modification of the management aspects than selection for these traits.

Sex of the calf, dam age and birth weight significantly influenced calf survival to weaning. The significant influence of birth weight on calf survival to weaning trait suggests that management intervention should be in place to avoid pre-weaning death of calves born with very low and high birth weights. Calf survival to weaning had low and non-significant genetic variability indicating that this trait is largely affected by environmental effects hence may not improve rapidly through genetic selection.

### CONFLICT OF INTERESTS

The authors have not declared any conflict of interests.

### REFERENCES

Albera A, Groen AF, Carrier P (2004). Genetic relationships between calving performance and beef production traits in Piemontese cattle. Journal of Animal Science 82:3440-3446.

Arang JA, Van Vleck LD (2002). Size of beef cows: early ideas, new developments. Genetics and Molecular Research 1:51-63.

Azzam SM, Azzam AM (1991). A Markovian decision model for bee cattle replacement that considers spring and fall calving. Journal of Animal Science 69:2329-2341.

Berry DP, Evans RD (2014). Genetics of reproductive performance in seasonal calving beef cows and its association with performance traits. Journal of Animal Science 92:1412-1422.

Bunter KL, Johnston DJ, Wolcot ML, Fordyce G (2014). Factors associated with calf mortality in tropicallyadapted beef breeds managed in extensive Australian production systems. Animal Production Science 54:25-36.

Casellas J, Tarres J, Piedrafita J, Varona L (2006). Parametric bootstrap for testing model fitting in the proportional hazards framework: An application to the survival analysis of Bruna dels Pirineus beef calves. Journal of Animal Science 84:2609-2616.

Cecchinato A, González-Recio O, López de Maturana E, Gallo L, Carrier P (2010). A comparison between different survival and threshold models with an application to piglet preweaning survival in a dry-cured ham-producing crossbred line. Journal of Animal Science 88:1990-1998.

Cervantes I, Gutiérrez JP, Fernández I, Goyache F (2010). Genetic
relationships among calving ease, gestation length, and calve survival in the Asturiana de los Valles beef cattle breed. Journal of animal science 88(1):96-101.

Cole JB, Wiggans GR, Vanraden PM, Miller RH (2007). Stillbirth (co)variance components for sire-maternal grandsire threshold model and development of a calving ability index for sire selection. Journal of Dairy Science 90:2489-2496.

Cooke JS, Cheng Z, Bourne NE, Wathes DC (2013). Association between growth rates, age at first calving and subsequent fertility, milk production and survival in Holstein-Friesian heifers. Open Journal of Animal Science 3:1-12.

Correa ES, De Andrade P, Euclides Filho K, De Alves RG (2000). Avaliacao de um sistema de producao de gado de corte. I Desempenho reprodutivo. Brazilian Journal of Animal Science 29(supl. 2):2209-2215.

Cox DR (1972). Regression models and life tables. Journal of Research Statistical Society Series B 34:187-220.

De Rensis F, Lopez-Galtius F, Capelli T, Molina E, Techakumphu M, Scogna ES, De Andrade P, Euclides Filho K, De Alves RG (2000).

Dickerson GE (1970). Techniques for research in quantitative animal genetics. In: techniques and procedures in animal science research. American Society of Animal Science Champaign, IL.

Do C, Wasana N, Choi K, Choi Y, Choi T, Park B, Lee J, Shin J, Lee K, Lee J, Kim J, Park D (2001). Overian hormone patterns and ovariole development in prenatal and postnatal beef cattle. Journal of Animal and Veterinary Advances 3(3):197-205.

Guerra JLL, Franke DE, Blouin DC (2006). Genetic parameters for prenatal and postnatal mortality in Nellore cattle. Journal of Animal Science 84:107-111.

Goyache F, Gutierrez JP, Alvarez I, Fernandez I, Royo LJ, Gomez E (2003). Genetic analysis of calving survival at different preweaning ages in beef cattle. Livestock Production Science 83:13-20.

Gregory KE, Maurer RR (1991). Prenatal and Postnatal maternal contributions to reproductive, maternal, and size related traits of beef cattle. Journal of Animal Science 69:961-976.

Guerra JLL, Franke DE, Blouin DC (2006). Genetic parameters for calving rate and calve survival from linear, threshold, and logistic models in a multibreed beef cattle population. Journal of Animal Science 84:197-333.

Gutiérrez JP, Goyache F, Fernández I, Alvarez I, Royo LJ (2007). Genetic relationships among calving ease, calving interval, birth weight, and weaning weight in the Asturiana de los Valles beef cattle breed. Journal of Animal Science 85:69-75.

Gutiérrez JP, Alvarez I, Royo I, Fernández L J, Díez J, Goyache F, (2002). Genetic relationships between calving date, calving interval, age at first calving and type traits in beef cattle. Livestock Production Science 78:215-222.

Hansen PJ (1985). Seasonal modulation of puberty and the postpartum anestrus in cattle: A review. Livestock Production Science 12:309.

Janson L (1980). Studies on fertility traits in Swedish dairy cattle. II. Genetic parameters. Acta Agriculturae Scandinavica 30:427.

Lamming GE, Royal MD (2001). Overian hormone patterns and subfertility in dairy cows. In: fertility in high-producing dairy cows. British society of animal science, Edinburg, UK. Occasional Publication 26:105-118.

Lopez-Galtius F, Santolaria P, Yaniz J, Rutllant J, Lopez-Bejar M (2001). Persistent ovarian follicles in dairy cows: a therapeutic approach. Theriogenology 56:649-659.

Luna-Navarez P, Bailey DW, Bailey CC, VanLeeuwen DM, Enns RM, Silver GA, DeAlley KL, Thomas MG (2010). Growth characteristics, reproductive performance, and evaluation of passive immunity of Holstein and Jersey relationships in Brangus cattle managed in a Chihuahuan Desert production system1. Journal of Animal Science 88:1891-1904.

MacNeil MD (2005). Genetic evaluation of the ratio of calving weight to cow weight. Journal of Animal Science 83:794-802.

Magalhaes Silva LC, Baldi F, Aboujaoude C, Venturini GC, Albuquerque LG, Paranhas da Costa MJ, R (2017). Genetic parameter estimates for prenatal and postnatal mortality in Nellore cattle. Journal of Animal Breeding and Genetics 134:27-33.

Makgahlela ML, Banga CB, Norris D, Dzama K, Ngambi JW (2008). Genetic analysis of age at first calving and calving interval in South African Holstein cattle. Asian Journal of Animal and Veterinary Advances 3(3):197-205.

Marshall DM, Minqiang W, Freking BA (1990). Relative calving date of first-calf heifers as related to production efficiency and subsequent reproductive performance. Journal of Animal Science 68:1812.

McHugh N, Cromie AR, Evans RD, Berry DP (2014). Validation of national genetic evaluations for maternal beef cattle traits using Irish field data. Journal of Animal Science 92:1423-1432.

Meacham NS, Norter DR (1987). Heritability estimates for calving date in Simmental cattle. Journal of Animal Science 64:701-705.

Mercadante MEZ, Packer IU, Razoook AG, Cyrillo JNSG, Figueiredo LA (2003). Direct and concomitant responses to selection for yearling weight on reproductive performance of Nelore cows. Journal of Animal Science 81:376-384.

Meyer K, Hammond K, Mackinnon MJ, Parnell PF (1991). Estimates of covariation between reproduction and growth in Australian beef cattle. Journal of Animal Science 69:3533-3543.

Milagres JE, Dillard EU, Robinson OW (1979). Heritability estimates for some measures of puberty in Hereford heifers. Journal of Animal Science 49:668.

Mwaanga ES, Janowski T (2000). Anoestrus in dairy cows, prevalence and clinical forms. Reproduction in Domestic Animals 35:193-200.

Oltenacu PA, Broom DM (2010). The impact of genetic selection for increased milk yield on the welfare of dairy cows. Animal Welfare 19:39-49.

Opdammer G, Grohn YT, Hertl J, Coryn M, Deluyker H, De Kruijf A (2000). Risk factor for post-partum ovarian dysfunction in high-producing dairy cows in Belgium: a field study. Theriogenology 53:841-857.

Phocas F, Bloch C, Chapelle P, Becherel F, Renand G, Menissier F (1998). Developing a breeding objective for a French purebred beef cattle selection program. Livestock Production Science 57:49-65.

Prentice R, Gloecker L (1978). Regression analysis of grouped survival data with application to breast cancer data. Biometrics 34:57-67.

Riley DG, Jr., Chase CC, Olson TA, Coleman SW Hammond AC (2004). Genetic and nongenetic influence on vigor at birth and preweaning mortality in Brahman calves. Journal of Animal Science 82:1581-1588.

Robinson KP, Sim TMC, Culloch RM, Bean TS, Jordoba AI, Eistfeld SM (2017). Female reproductive success and calf survival in a North Sea coastal bottlenose dolphin (Tursiops truncatus) population. R. Soc. Proc. ONE 12(9): e0185000. https://doi.org/10.1371/journal.pone.0185000.

SAS (2012). Statistical Analysis Systems version 9.4, Institute Inc., Cary, NC, US.

Schmidek A, Paranhas MJR, Da Costa Mercadante MEZ, Toledo LM, Cyrillo S, Branco RH (2013). Genetic and non-genetic effects on calf vigor at birth and preweaning mortality in Nelore calves. Revista Brasileira de Zootecnia 42(6):421-427.

Shanks BC, Tess MW, Kress DD, Cunningham BE (2001). Genetic evaluation of carcass traits in simmental-sired cattle at different slaughter end points. American Journal Of Animal Science. 79:595-604.

Sharpe PH, Gifford DR, Flavel PF, Nottle MG, Armstrong DT (1986). Effect of melatonin on postpartum anestrus in beef cows. Theriogenology 26:621.

Short RE, Bellsows RA, Stagmillwer RR, Berardineili JG, Custer EE (1990). Physiological mechanisms controlling anestrus and infertility in postpartum beef cattle. Journal of Animal Science 68:799-816.

Solemani-Baghshah S, Ansari-Mahyari S, Edris MA, Asadollahpour-Nanaei H (2014). Estimation of Genetic and Phenotypic Trends for Age at First Calving, Calving Interval, Days Open and Number of Insemination to conception for Isfahan Holstein Cows. International Journal of Advanced Biology and Biometric Research 2(5):1307-1314.

Stevenson JS (2001). A review of oestrus behaviour and detection in dairy cows. In: fertility in high-producing dairy cows, British society of animal science Champaign, IL.
animal science, Edinburg, Uk. Occasional Publication 26:43-62.
Tarres J, Fina M, Piedrafita J (2010). Parametric bootstrap for testing model fitting of threshold and grouped data models: An application to the analysis of calving ease of Bruna dels Pirineus beef cattle. Journal of Animal Science 88:2920-2931.
Van Doormaal B (2007). Calf survival: A new trait of interest. Canadian Dairy Network. February 2007 pp 1-2.
Von-keyserlingk MAG, Weary DM (2007). Maternal behavior in cattle. Horm. Behaviour 52:106-113.
Vostry L, Vesela Z, Svitakova A, Vostra HV (2014). Comparison of models for estimating genetic parameters and predicting breeding values for birth weight and calving ease in Czech Charolais cattle. Czech Journal of Animal Science 59:302-309.
Yilmaz A, Davis ME, Simmen RCM (2004). Estimation of (co)variance components for reproductive traits in Angus beef cattle divergently selected for blood serum IGF-I concentration. Journal of Animal Science 82:2285-2292.