Review Article

Variance component estimation on female fertility traits in beef cattle

T. Rust[1#] and E. Groeneveld[2]

[1] ARC Animal Improvement Institute, Irene 0062, South Africa; [2] Institute of Animal Husbandry and Animal Behaviour, Federal Agricultural Research Centre, 31535, Mariensee, Germany

Abstract

The purpose of this review is to define possible breeding objectives for Southern African beef cattle farmers and to review different means of expressing genetic reproductive merit. The breeding objective considered was to maximize the number of calves born or weaned for a given number of cows in a herd under prevailing environmental and management conditions. This is a complex trait that has many components. While this trait is clearly a function of the reproductive ability of each cow, it is also affected by the age structure of the herd. A number of auxiliary or index traits are used to assess this objective and their merits, shortfalls and requirements in terms of data collection are discussed. It was evident that the trait of choice was influenced by the management system. Fewer component traits can be measured and incorporated as variables in a genetic model in more extensive systems. Since South African beef cattle production systems tend to be semi-extensive or extensive, traits to consider include calving rate, calving success, calf survival, days to calving, age at first calving, calving date, calving ease and calving interval.

Keywords: beef cattle, reproduction, genetics, variance components
[#]Author to whom correspondence should be addressed; e-mail: tina@idpi1.agric.za

Introduction

Estimated breeding values for growth traits are reported without any indication of reproductive ability in the South African national genetic evaluation scheme. This can lead to the assumption that differences between animals in respect of genetic merit for reproduction and fitness traits are trivial, a view often shared by beef cattle breeders. The current recording scheme of the National Beef Cattle Performance Testing Scheme of South Africa was implemented in 1959. In Phases A and B of this scheme, farmers keep pedigree records and weigh animals at birth, weaning, yearling age and 18 months of age. A few farmers weigh cows at birth and at weaning of the calves. Thus, reproduction information for cows can only be derived from birth notifications and weights of their offspring, since no data on the reproductive performance of the female animals themselves are recorded.

Estimated breeding values for fertility traits in females are difficult to estimate because the expression of reproductive potential is often constrained by the management system employed (Notter, 1988; Notter & Johnson, 1988; Meyer *et al.*, 1990; Notter, 1995a), and depends on the existing recording scheme used for the breed. Most animals will reproduce when managerial and nutritional conditions are optimal, but in less favourable conditions only those with the highest genetic merit for reproductive fitness will reproduce (Morris, 1980; Notter, 1995a). Relatively few heritability estimates have been reported for female reproductive traits in beef cattle. These reports do, however, indicate that reproductive traits in beef cattle are heritable. Although heritabilities for cow reproductive traits are reported to be low (Davenport *et al.*, 1965; Dearborn *et al.*, 1973), some studies from subtropical environments have reported moderate heritabilities (Deese & Koger, 1967; Cruz *et al.*, 1978; Thorpe *et al.*, 1981; Turner, 1982; Rust & Kanfer, 1998).

The purpose of this review is to define possible reproductive breeding objectives for Southern African beef cattle farmers and to assess the suitability of different measures of reproductive merit for use in the South African National Genetic Evaluation scheme.

The breeding objective and selection criteria

An objective must be defined for the breeding program under consideration prior to performing a genetic evaluation of female reproduction traits. We consider the overriding objective to be the maximisation of the number of calves born or weaned for a given number of cows in a herd under prevailing environmental and management conditions. It should be noted that this is a complex trait that has many components. While this is clearly a function of the reproductive ability of each cow, it is also affected by the age structure of the herd. In the following discussion we concentrate on the performance of individual animals only, and disregard herd structure as well as between-breed variation in the onset of puberty. A number of auxiliary or index traits have been used to assess this objective.

Figure 1 gives examples of the reproductive events in the lifespan of two cows within a herd. The first cow produced three calves over the time t_{1E} to t_{1X} (the time the cow was in the herd). Likewise, cow 2 produced three calves while in the herd, but over a shorter time span - t_{2E} to t_{2X}. Unfortunately, very few of the events listed in Figure 1 are measured in South Africa, as is the case in most beef-rearing countries. In most instances only calving dates and weights at specified times of the calf's life are recorded.

Cow 1	B---EH_1O_1---$J_1M_1P_1$------$*_1H_2O_2$-$J_2M_2P_2$------$*_2$---H_3O_3—J_3M_3------_H_4O_4-$J_4M_4P_4$------$*_3$-----H_5O_5—$J_5M_5P_5$----X
Time	t_{1E} ←--→t_{1X}
Recordings	$BW_o + BD_o$ $BW_{c1}+BD_{c1}$ $BW_{c2}+BD_{c2}$ $BW_{c3}+BD_{c3}$
Cow 2	B--E-H_1O_1-$J_1M_1P_1$-----$*_1$-H_2O_2-J_2M_2----_H_3O_3-$J_3M_3P_3$-----$*_2$-H_4O_4-$J_4M_4P_4$-----$*_3$-H_5O_5-J_5M_5-X
Time	t_{2E} ←---→ t_{2X}
Recordings	$BW_o + BD_o$ $BW_{c1}+BD_{c1}$ $BW_{c2}+BD_{c2}$ $BW_{c3}+BD_{c3}$

B = birth date of the cow; E = date of entering the herd; H_{1-n} = oestrus; O_{1-n} = ovulation; J_{1-n} = joining; M_{1-n} = mating; P_{1-n} = pregnancy; $*_{1-n}$ = calving; _ = no calving; X = exit date; BW_o = cow's own birth weight; BD_o = cow's own birth date; $BW_{c1\ldots n}$ = birth weights of calves; $BD_{c1\ldots n}$ = birth dates of calves; t_{nE} = time of entry into herd; t_{nX} = time of exit from herd

Figure 1 Schematic representation of the reproductive cycle of two cows and times at which measurements are made in the current South African Beef recording scheme

Attempts to understand the genetics of a composite trait such as overall reproductive performance can involve two approaches. The trait to be investigated can consist of the overall reproductive performance itself or, alternatively, its constituent components. It is to be expected that these "component" traits will have different heritabilities. This invokes the possibility of concentrating on the most important components during selection and thereby possibly achieving a higher overall selection response. The first group of traits shown in Figure 1 refer to events in the reproductive cycle of the cow, and represent component traits. Calving ease is only indirectly related to reproductive performance in that a difficult calving may impact on the following conception. The second groups of traits, the aggregate traits, are compositions of more than one event in the reproductive cycle of the cow. Traits that do not rely on an event happening are grouped under other traits.

Component traits

For a fixed breeding season, time to first oestrus is defined as the number of days elapsed until a cow shows first oestrus. As such it can be measured on each animal at each parity. Evidence of a link between time to first oestrus and overall reproductive performance is not strong. Clearly, an animal with a longer time to oestrus will produce fewer calves over a given period. Because the conditions under which South African farms are managed are mainly extensive, time to first oestrus cannot be measured easily as it involves close observation of the herd on a regular basis. Heritabilities for time to first oestrus for first, second and last parity are 0.05, 0.10 and -0.03 respectively (Azzam & Nielsen, 1987).

Number of services per conception is an indirect measure of one of the major time components in the reproductive cycle that shows large variation between animals; i.e. the time lapse between two calves. It requires the recording of each service, which is rarely available under natural service conditions. Heritability estimated from paternal half sister correlations was 0.64, indicating considerable genetic variation among heifers for the number of services needed for conception in the first calving (Milagres *et al*., 1979).

Pregnancy rate is defined for each cow in each year. A score of '1' is allocated for a successful pregnancy and a score of '0' is assigned to other cases. It is a binary trait and requires pregnancy detection to be done on the herd. Dearborn *et al.* (1973) estimated a heritability of 0.09, which corresponds well with the simulated heritability of 0.096 used by Johnson & Notter (1987). Results of Morris & Cullen (1994) generally showed a negative genetic correlation with yearling (-0.30) or lifetime pregnancy rate (-0.29). Recording of this trait is time consuming and expensive (Morris & Cullen, 1994).

Gestation length varies between animals. Being a time component in the reproductive cycle, this will also impact on the overall reproductive performance of the animal. However, this relationship will not be strong, as the variance in gestation length is small relative to the variation in calving interval. It also requires that two dates, i.e. service and calving, be observed and recorded. The date service date, in particular, is rarely recorded under natural service conditions. Bourdon & Brinks (1982) used a paternal half-sib analysis and least-squares procedure to compute a heritability of 0.36 for bulls and 0.37 for heifers for gestation length. These estimates were similar to those compiled by Andersen & Plum (1965), but were smaller than the heritability of 0.48 estimated by Burfening *et al.* (1978) for Simmentaler cattle. Heritabilities for gestation length for first, second and last parities were 0.14, 0.45 and 0.36 respectively (Azzam & Nielsen, 1987). Using Herderson's Method III, Wray *et al.* (1987) estimated the heritability for gestation length for Simmentaler cattle to be 0.374 from the sire variance and 0.09 from the maternal grandsire variance.

Days-to-calving was computed by Meyer *et al.* (1990) and Johnston & Bunter (1996) as the interval in days between the first joining date for cows and subsequent calving. This is a continuous variable. Johnston & Bunter (1996) suggested that a penalty of 21 days should be applied to non-calvers in joining management groups. Days-to-calving and calving date give the same information when the cows to be compared went into breeding on the same day. This is almost never the case with field-data, especially with between-herd analysis. Meyer *et al.* (1990) fitted an animal repeatability model that included an effect due to animal other than additive genetic as an additional random effect for each animal. This effect was assumed to be identically, independently distributed and not correlated with the animals' additive genetic effects. Meyer *et al.* (1990) estimated pooled heritabilities for days to calving of 0.05 for Hereford, 0.08 for Angus and 0.09 for Zebu crosses, with repeatabilities of 0.22, 0.10 and 0.18 respectively. Pooled heritability estimated by Johnston & Bunter (1996) was 0.11 for subsequent days to calving. Johnston & Bunter (1996) estimated a heritability of 0.11 (Table 1) for calving success, and a very high genetic correlation (r_g = -0.97) between days to calving and calving success.

A reduced age at first calving will increase the number of calves born for a given number of animals (i.e. the herd). An advantage of this index is that age at first calving can be computed without the need for additional data recording as the birth date of the cow and its first calving date are generally known. The biggest disadvantages are that it only represents one component in the reproductive life of a cow, and that it is only recorded for heifers. Furthermore, in a variable seasonal environment, age at first calving reflects management decisions to a greater extent than genetic merit. Because of seasonal nature of production differences due to management strategies, the resulting variance in reproductive performance will not reflect true genetic differences. Thus, under South African conditions, age at first calving would not seem to be a useful trait for predicting female reproductive performance. Repeatability for early calving was found to be low (0.14) in the study of Harwin *et al.* (1969). In a study reported by Lesmeister *et al.* (1973), heifers that initially calved earlier tended to calve earlier throughout the remainder of their productive lives; however, repeatability estimates from this study were low (0.092 and 0.105). A low heritability estimate (0.07) was calculated by Bourdon, & Brinks (1982) who found the correlations between age at first calving and growth traits consistently negative, indicating a favourable relationship between breeding values for growth and early reproduction. Rust and Kanfer (1998) reported heritabilities for two indigenous South African beef cattle breeds of 0.27 and 0.30 respectively.

Calving date is defined as the day of the year on which the cow calves (Notter, 1995b). It allows comparison between cows when joining is of the same duration and starts on the same date, but does not distinguish between cows calving in the same 21-day period (one oestrus cycle) (Notter, 1988). To overcome this, cows can be classified into 21-day calving groups (Lesmeister *et al.*, 1973; Bailey *et al.*, 1985; Marshall *et al.*, 1990).

The classification of cows that do not calve in a specific year is problematic. A procedure using threshold theory to calculate penalties for open cows was proposed by Notter & Johnson (1988). This method assumes a normal distribution of the trait and a predicted value for all non-calvers (x) of

$$x_2 = \bar{x}_1 + (z / p[1-p])\, s$$

where p = the proportion of cows calving; z = the height of the ordinate at the truncation point (t) of the normal distribution; $s = \{s^2_1\, p / [\, p\text{-}z\,(\, z / p - t]\}^{½}$ the standard deviation of the trait; s^2_1 = the observed variance amongst calves. This method was used by several researchers (Buddenberg *et al*, 1990; Meyer *et al.*, 1990) to calculate the value for non-calvers. In the study of Meacham & Notter (1987), first and second calving date records of animals that calved at the age of two years for the first time were used in variance component estimation. Calculations were performed using the nested analysis of variance procedure of SAS (1985). Heritabilities (h^2) were estimated as $h^2 = 4\sigma^2_s / (\sigma^2_s + \sigma^2_e)$. Genetic correlations ($r_G$) were estimated from sire components of variance and covariance. The pooled heritability estimates were 0.17 for first calving and 0.07 for second calving. The genetic correlation between first and second calving dates was 0.66, and it seemed to be a useful selection criterion for improving reproductive fitness. Heritability estimates for calving date are presented in Table 1. In contrast to the study of Azzam & Nielsen (1987), Buddenberg *et al.* (1990) reported that heritability estimates declined from first to last parity. Repeatabilities for calving date of 0.14, 0.10, 0.12, 0.26 and 0.23 were estimated by Harwin *et al.* (1969), Lesmeister *et al.*, (1985), López de Torre & Brinks (1990) and Rege & Famula (1993) respectively. This trait is not appropriate for use in the South African National Analysis scheme because the starting date and duration of joining within the same breed differs between breeders in different climatic regions.

Calving ease has an indirect effect on overall reproductive performance in that the calving interval tends to be extended following a difficult calving. The trait requires observation of calving in order to distinguish between more than two categories of ease of calving, and can therefore only be obtained in well-controlled production environments. Sire is a significant source of variation for calving ease score in 2-year old and mature dams (Burfening *et al.*, 1979). The correlations of sire estimated progeny differences for calving ease between 2-year old dams and 3-year old dams with mature dams, were estimated to be 0.46 and 0.21 respectively. Notter (1988) summarized direct heritabilities for calving ease ranging from 0.07 to 0.38 and for maternal effects ranging from 0.07 to 0.18.

Calving interval is a trait that combines many of the component traits discussed above, and is similar to aggregate traits. CI is the time between two successive calvings. Thus, it is only available for cows from the second parity onwards. Because it is based only on the period between two calvings, it can be computed from minimal data, but does not take information from the first parity or the end of a cow's life span into account. Bourdon & Brinks (1983) and Meacham & Notter (1987) concluded that calving interval did not appear to be a useful criterion for improving female reproduction because of the relatively low estimated heritability for calving interval. However, calving interval is useful as a measure of reproductive ability when there is no fixed breeding season and cows calve throughout the year. Heritability estimates for calving interval are low. Estimates reported by Brown *et al.* (1954), Lindley *et al.* (1958), Fagerlin (1968), Schalles & Marlowe (1969) and López de Torre & Brinks (1990) were 0.01, 0.07, 0.03, 0.03 and -0.03 respectively. Repeatability of calving interval was estimated to be 0.03 (Plasse *et al.*, 1966), 0.02 (Schalles & Marlowe, 1969), -0.05 (Bailey *et al.*, 1985) and 0.14 (López de Torre & Brinks, 1990). Repeatability estimates of calving interval between the second and third years of age and between the third and fourth years of age were found to be negative (Werth *et al.,* 1996).

Aggregate traits

While component traits refer to one event in the lifetime of a cow, aggregate traits are composites of more than one event. For the aggregate traits to be measured more than one event must occur and be measured.

Calving rate is a lifetime measure of the reproductive performance of a cow. It is defined as the number of calves born divided by the number of opportunities a cow has had to calve. Calving rate is a binary trait for cows with one parity, but becomes more continuous as the number of parities increases. Because it is an average of the (different) number of parities of each cow, calving rate has variable accuracy depending on the number of parities involved. This must be taken into account by using a different residual variance for each record. Furthermore, herd entry and exit dates as well as the pregnancy status of cows exiting the herd must be recorded to enable this trait to be computed correctly. This information is rarely available in the South African recording system.

Lifetime pregnancy rate, defined as the number of pregnancies divided by the number of mating years for an animal (Morris & Cullen, 1994) can be calculated from pregnancy rate. As discussed previously, this trait is time consuming and expensive to record.

Calving success can be defined for each cow in the herd for each year. Calving success is, thus, a binary trait with scores of '1' for successful calvings and '0' when no calves was born. In addition to calving date, entry and exit dates of each cow must be available. As in the case of calving rate, information on the pregnancy status of cows exiting the herd is crucial. Although it is similar to calving rate, this trait has multiple measurements for each cow and is evaluated as a repeatability trait in genetic analysis. Johnston & Bunter (1996) estimated a heritability of 0.11 (Table 1) for calving success. Deese & Koger (1967) estimated moderate to high heritabilities for calving success (they termed it calving rate and defined it as a binary trait: pregnant = 1; other = 0). Heritabilities of binary data were adjusted to a normal basis with the equation suggested by Van Vleck (1972):

$$h^2 = h^2_b \ P[p\text{-}1] / z^2$$

where h^2_b = heritability estimated in binomial scale; h^2 = heritability in normal scale; p = frequency of non-calvers; z = height of the distribution at the threshold point.

Milagres *et al.* (1979) estimated heritabilities for early calving rate at two years of age, defined as calf born = 1 and no calf = 0, from paternal half sister correlations using Harvey (1976).

The survival of a calf after birth is clearly a component of overall reproductive performance. It is a binary trait and is available for each parity for each cow that has calved. Calf survival was defined by Milagres *et al.* (1979) as the dependent variables calf born alive (1) or dead (0). This is similar to the calving rate defined by Deese & Koger (1976), Milagers *et al.* (1979) and Mackinnon *et al.* (1990), and calving success defined by Meyer *et al.* (1990). The heritability estimated from paternal half sister correlations was 0.64 on the binary scale, with the adjusted heritability (calculated using the equation proposed by van Vleck, 1972) greater than one (1.25 ± 0.35).

Other traits

Traits in this category were defined as those whose measurement does not require an event or number of events to occur.

Twinning rate appears to be promising method of increasing the number of calves produced by a cow in her lifetime. This will increase the overall productive performance in a herd. Heritability estimates for ovulation rate are summarized in Table 1. Large differences between breeds are evident. Van Vleck *et al.* (1991) reported genetic correlations between twinning rate and ovulation rate of between 0.38 and 1.00. This suggested that selection for twins can be done indirectly by measuring ovulation rate in estrus cycles of pubertal heifers (Echternkamp *et al.*, 1990; Van Vleck *et al.*, 1991). While there may be circumstances where twinning is desirable, the study by Gregory *et al.* (1990b) documented various negative consequences of increased twinning rate that must be addressed before the potential of twinning can be exploited. These include increased dystocia, reduced calf survival at birth and reduced re-breeding performance of cows that gave birth to twins. Twins are usually considered a disadvantage due to the extra management input they require under extensive South African farming conditions.

Table 1 Summary of literature estimates of heritabilities (h^2) and repeatabilities (r) for various female reproductive traits.

Trait	Author	Breed	Parity	Comment	h²	r²
Time to 1st oestrus	Azzam & Nielsen (1987)		1st		0.05	
			2nd		0.10	
			3rd		-0.03	
No. of services/conception	Milagres *et al.* (1979)			Puberty heifers	0.64	
Pregnancy rate	Dearborn *et al.* (1973)				0.09	
Gestation length	Bourdon & Brinks (1982)			Male	0.36	
				Female	0.37	
	Burfening *et al.* (1978)	Simmentaler			0.48	
	Azzam & Nielsen (1987)		1st		0.41	
			2nd		0.45	
			3rd		0.36	
	Wray *et al.* (1987)	Simmentaler		sire model	0.37	
				maternal grandsire	0.09	
Days to calving	Meyer *et al.* (1990)	Hereford			0.05	0.22
		SA Angus			0.08	0.10
		Zebu crosses			0.09	0.18
	Johnston & Bunter (1996)				0.11	
Age at first calving	Harwin *et al.* (1969)				0.14	
	Lesmeister *et al.* (1973)				0.09	
					0.11	
	Bourdon & Brinks (1982)				0.07	
	Rust & Kanfer (1998)	Afrikaner			0.27	
		Dr'berger			0.30	
	Van der Westhuizen *et. al.* (in press)	Multibreed composites			0.40	
Calving date	Harwin *et al.* (1969)					0.14
	Lesmeister *et al.* (1973)					0.10
	Itulya (1980)	Hereford			0.09	
	Bourdon & Brinks (1982)				0.07	
	Bailey *et al.* (1985)					0.12
	Johnson & Notter (1987)			Simulation	0.04	
	Meacham & Notter (1987)		1st	calving	0.17	
			2nd	calving	0.07	
	Azzam & Nielsen (1987)		1st	parity	0.09	
			2nd	parity	0.03	
			Last	parity	0.17	
	Smith *et al.* (1989)				0.09	
	López de Torre & Brinks (1990)				0.16	0.26
			1st	parity	0.20	
	Buddenberg *et al.* (1990)		2nd	Excluding	0.04	
			Last	open cows	0.03	
			1st	parity	0.39	
			2nd	Including open	0.13	
			Last	cows	0.00	
	Rege & Famula (1993)	Hereford			0.16	0.23
	Notter *et al.* (1993)	Angus			0.18	
	Van der Westhuizen *et al.* (submitted)	Multibreed composites			0.04/ 0.06	
Calving ease	Notter (1998)				0.07	
					0.38	

Table 1 (*continued)* Summary of literature estimates of heritabilities (h^2) and repeatabilities (r) for various female reproductive traits.

Trait	Author	Breed	Parity	Comment	h²	r²
Calving interval	Brown *et al.* (1954)				0.01	
	Lindley *et al* (1958)				0.07	
	Plasse *et al.* (1966)					0.03
	Fagerlin (1968)				0.03	
	Schalles & Marlowe (1969)				0.03	0.02
	Bailey *et al.* (1985)					-0.05
	Meacham & Notter (1987)				0.04	
	López de Torre & Brinks (1990)				-0.03	0.14
	Van der Westhuizen *et al.* (in press)	Multibreed composites			0.01	
Calving rate	Milagres *et al.* (1979)			Including open cows	0.02	
				Excluding open cows	0.45	
	Mackinnon *et al.* (1990)			Female	0.11	
				Male	0.08	
	Meyer *et al.* (1990)	Hereford			0.07	
		SA Angus			0.02	
		Zebu crosses			0.17	
Calving success	Meyer *et al.* (1990)	Hereford			0.08	
		SA Angus			0.02	
		Zebu crosses			0.08	
	Johnston & Bunter (1996)				0.11	
	Van der Westhuizen *et al.* (2001)	Multibreed composites			0.03	
Calf survival	Milagres *et al* (1979)			Binary scale	0.64	
				Adjusted h² (van Vleck, 1972)	1.25	
Ovulation rate	Echternkamp *et al* (1990)			Pubertal heifers	0.07	
	Gregory *et al* (1990a)			DFREML	0.03	
	Gregory *et al* (1990b)				0.07	
	Van Vleck *et al* (1991)			Pubertal heifers	0.16	

Conclusions

The times at which measurements for various traits have to be taken are shown in Table 2. It is evident that only two traits consider the lifetime production of the animal as one measurement, *viz.* age at first calving and calving rate. All other traits must be measured repeatedly over the lifetime of the cow. The intensity of the farming management system will limit the number of traits that can be measured as well as the frequency with which they can be measured. For example, measurement of a trait such as number of services per conception is feasible in an intensive farming system but almost impossible in semi-intensive or extensive management systems. Measurement of pregnancy rate and ovulation rate requires specialised skills and apparatus, and is expensive. Indices of genetic reproductive merit that are easily measured in most management systems at low cost would be appropriate for use in the South African National Genetic Evaluation scheme. Such traits include age at first calving, calving success, calving interval, calving rate, calf survival, days to calving and caving date. It should be noted that inclusion of these traits may jeopardize the reliability of breeding values, and that model specification for these traits is usually difficult. It is recommended that joining dates, herd entry and exit dates and the pregnancy status of animals exiting the herd should be recorded.

Table 2 Times at which measurements for various female reproductive traits should be taken

Trait	Life time	Each Parity	Birth	Herd entry	Joining$_1$	Oestrus$_1$	Heat$_1$	Heat$_{1n}$	Pregnancy$_1$	Calving$_1$	Calving Ease$_1$	Calf Survival$_1$	Joining$_n$	Oestrus$_n$	Heat$_n$	Heat$_{nn}$	Pregnancy$_n$	Calving$_n$	Calving Ease$_n$	Calf Survival$_n$	Exit from herd
Age First Calving	x	-	x							x											
Time to 1st Oestrus	-	x			x		x						x		x						
Gestation Length	-	x					x			x					x			x			
No. Services /Conception	-	x					x	x		x					x	x		x			
Pregnancy Rate	-	x							x								x				
Calving Success	-	x										x								x	
Calving Ease	-	x									x								x		
Calving Interval		x								x								x			
Calving Rate	x	-		x						x								x			x
Calf Survival	-	x		x						x								x			x
Days to Calving	-	x			x					x			x					x			
Ovulation Rate	-	x				x								x							
Calving Date	-	x								x											

References

Andersen, H. & Plum, M., 1965. Gestation length and birth weight in cattle and buffaloes: A review. J. Anim. Sci. 48, 1224.

Azzam, S.M. & Nielsen, M.K., 1987. Genetic parameters for gestation length, birth date and first breeding date in beef cattle. J. Anim. Sci. 64, 348-356.

Bailey, D.W., Brinks, J.S. and Bourdon, R.M., 1985. Repeatability estimates of beef cow reproductive traits by degree of adjacency. Proc. West. Sec. Am. Soc. Ani. Sci. 36,26.

Bourdon, R.M. & Brinks, J.S., 1982. Genetic, environmental and phenotypic relationships among gestation length, birth weight, growth traits and age at first calving in beef cattle. J. Anim. Sci. 55, 543–553.

Bourdon, R.M. & Brinks J.S., 1983. Calving date versus calving interval as a reproductive measure in beef cattle. J. Anim. Sci. 57, 1412-1417.

Brown, L.O., Bourdon, R.M., Cobb, E. and Knox, J.H., 1954. An analysis of the components of variance of calving interval in a range herd of beef cattle. J. Anim. Sci. 13, 511.

Buddenberg, B.J., Brown, C.J. and Brown, A.H., 1990. Heritability estimates of calving date in Hereford cattle maintained on range under natural mating. J. Anim. Sci. 68, 70-74.

Burfening, P.J., Kress, D.D., Friedrich, R.L. and Vaniman, D., 1978. Phenotypic and genetic relationships between calving ease, gestation length, birth weight and pre-weaning growth. J. Anim. Sci. 47, 595.

Burfening, P.J., Kress, D.D., Friedrich, R.L. and Vaniman, D., 1979. Ranking of sires for calving ease. J. Anim. Sci. 48, 293-297.

Cruz, V., Koger, M. and Warnick, C., 1978. Heritability estimates of reproductive efficiency in Brahman beef cattle. 4th World Conf. Anim. Prod., Buenos Aires, pp. 605.

Davenport, R.L., Stonaker, H.L., Riddle, K. and Sutherland, T.M., 1965. Heritability of reproductive performance in inbred and linecross beef cows. J. Anim. Sci. 24, 434.

Dearborn, D.D., Koch, R.M., Cundiff, L.V., Gregory, K.E. and Dickerson, G.E., 1973. An analysis of reproductive traits in beef cattle. J. Anim. Sci. 36, 1032.

Deese, R.E. & Koger, M., 1967. Heritabilty estimates of fertility in Brahman and crossbred cattle. J. Anim. Sci. 26, 984.

Echternkamp S.E., Gregory, K.E., Dickerson, G.E., Cundiff, L.V., Koch, R.M. and Van Vleck, L.D., 1990. Twinning in cattle: II. Genetic and environmental effects on ovulation rate in pubertal heifers and postpartum cows and the effects of ovulation rate on embryonic survival. J. Anim. Sci. 68, 1877-1888.

Fagerlin, P.T., 1968. Aspects of calving interval in Herefords. M.S. Thesis. Colorado State University, Fort Collins.

Gregory, K.E., Echternkamp, S.E., Dickerson, G.E., Cundiff, L.V., Koch, R.M. and Van Vleck, L.D., 1990a. Twinning in cattle: I. Foundation animals and genetic and environmental effects on twinning rate. J. Anim. Sci. 68, 1867-1876.

Gregory, K.E., Echternkamp, S.E., Dickerson, G.E., Cundiff, L.V., Koch, R.M. and Van Vleck, L.D., 1990b. Twinning in cattle II. Effects of twinning on dystocia, reproductive traits, calf survival, calf growth and cow productivity. J. Anim. Sci. 68, 3133-3144.

Harvey, W.R., 1976. General outline of computing procedures for six types of mixed models. Ohio State Univ., Columbus (Mimeo).

Harwin, G.O., Lamb, R.D. and Bisschop, J.H.R., 1969. Some factors affecting reproductive performance in beef females. Anim. Breed. Abstr. 37, 606.

Itulya, S.B., 1980. Most probable producing ability, fertility and related selection criteria for Hereford cows. Anim. Breed. Abstr. 49, 817.

Johnson, M.H. & Notter, D.R., 1987. Simulation of genetic control of reproduction in beef cows. II. Derived genetic parameters. J. Anim. Sci. 65, 76-87.

Johnston, D.J. & Bunter, K.L., 1996. Days to calving in Angus cattle: Genetic and environmental effects, and covariances with other traits. Livest. Prod. Sci. 45, 13-22.

Lesmeister, J.L., Burfening, P.J. and Blackwell, R.L., 1973. Date of first calving in beef cows and subsequent calf production. J. Anim. Sci. 36, 1-6.

Lindley, C.E., Earley, G.T., Whatley, J.A. Jr. and Chambers, D., 1958. A study of the reproductive performance of a purebred Hereford herd. J. Anim. Sci. 17, 336.

López de Torre, G. & Brinks, J.S., 1990. Some alternatives to calving date and interval as measures of fertility in beef cattle. J. Anim. Sci. 68, 2650-2657.

Mackinnon, M.J., Taylor, J.F. and Hetzel, D.J.S., 1990. Genetic variation and co-variation in beef cow and bull fertility. J. Anim. Sci. 68, 1208-1214.

Marshall, D.M., Mingiana, W. and Freking, B.A., 1990. Relative calving date of first-calf heifers as related to production efficiency and subsequent reproductive performance. J. Anim. Sci. 86, 1812-1817.

Meacham, N.S. & Notter, D.R., 1987. Heritabilty estimates for calving date in Simmental cattle. J. Anim. Sci. 64, 701-705.

Meyer, K., Hammond, K., Parnell, P.F., Mackinnon, M.J. and Sivarajasingam, S., 1990. Estimates of heritability and Repeatability for reproductive traits in Australian Beef Cattle. Livestock Prod. Sci. 25, 15-30.

Milagres, J.C., Dillard, E.U. and Robison, O.W., 1979. Heritability estimates for some measures of reproduction in Hereford heifers. J. Anim. Sci. 49, 668-674.

Morris, C.A., 1980. A review of relationships between aspects of reproduction in beef heifers and their lifetime production. 2. Associations with relative calving date and with dystocia. Anim. Breed. Abstr. 48, 753-767.

Morris, C.A. & Cullen, N.G., 1994. A note on genetic correlations between pubertal traits of males or females and lifetime pregnancy rate in beef cattle. Livest. Prod. Sci. 39, 291-297.

Notter, D.R., 1988. Evaluating and reporting reproductive traits. Proc. Beef Improvement Fed. Res. Symp. Albuquerque, NM, pp.21-42.

Notter, D.R. & Johnson, 1988. Simulation of genetic control of reproduction in beef cows. IV. Within-herd breeding value estimation with pasture mating. J. Anim. Sci. 66, 280-286.

Notter, D.R., McFadden, L.G. and Bergmann, J.A.G., 1993. Relationships between yearling scrotal circumference and measures of female reproduction in Angus cattle. Proc. Beef Improve. Fed. Res. Symp. Areville, NC, pp.180-184.

Notter, D.R., 1995a. Genetic improvement of fertility using correlated traits and molecular markers. Proc. 11th Cong. Brussileiro de Reprodução Animal, Belo horizonte, MG, Brazil, pp. 121-130.

Notter, D.R., 1995b. Workshop on maximizing fertility in animal breeding programs. Department of Animal and Poultry Sciences, Virginia Polytechnic Institute and State University, Blacksburg, Virginia, USA.

Plasse, D., Koger, M. and Warnick, A.C., 1966. Length of calving interval and time of conception in relation to calving and the beginning of the mating season in four herds of purebred Brahman cows in Florida. Anim Breed Abstr, 34, 50.

Rege, J.E.O. & Famula, T.R., 1993. Factors affecting calving date and its relationship with production traits of Hereford dams. Anim. Prod. 57, 385-395.

Rust, T. & Kanfer, F.H.J., 1998. Variance component and breeding value estimation for age at first calving of Afrikaner and Drakensberger beef cattle. Proc. 36th Nat. Congr. S.A. Soc. Anim. Sci., Stellenbosch, S.A., 85.

SAS, 1985. SAS/IML Guide. SAS Inst., Inc., Cary, NC.

Schalles, R.R. & Marlowe, T.J., 1969. Reproductive patterns in a herd of Angus cows. Anim. Breed. Abstr. 37, 53.

Smith, B.A., Brinks, J.S. and Richardson, G.V., 1989. Estimation of genetic parameters among reproductive and growth traits in yearling heifers. J. Anim. Sci. 67, 2886-2891.

Thorpe, W., Cruickshank, D.K.R. and Thompson, R., 1981. Genetic and environmental influences on beef cattle production in Zambia. 4. Weaner production from purebred and reciprocal crossbred dams. Anim. Prod, 33, 165.

Turner, H.G., 1982. Genetic variation of rectal temperature in cows and its relationship to fertility. Anim. Prod. 35, 401.

Van der Westhuizen, R.R., Schoeman, S.J., Van Wyk, J.B. & Jordaan, G.F., 2001a. Heritability estimates derived from threshold analyses for reproduction and stayability traits in a beef cattle herd. S. Afr. J. Anim. Sci. 31, 25-32.

Van Vleck, L.D., 1972. Estimation of heritability of threshold characters. J. Dairy Sci. 55, 218.

Van Vleck, L.D., Gregory, K.E. and Echtemkamp. S.E., 1991. Ovulation rate and twinning rate in cattle: Heritabilities and genetic correlation. J. Anim. Sci. 69, 3213-3219.

Werth, L.A., Azzam, S.M. and Kinder, J.E., 1996. Calving intervals in beef cows at 2, 3 and 4 years of age when breeding is not restricted after calving. J. Anim. Sci. 74, 593-596.

Wray, N.R., Quaas, R.L. and Pollak, E.J., 1987. Analysis of gestation length in American Simmental cattle. J. Anim. Sci. 65, 970-974.