

Evaluation of female fertility in dairy cattle enterprises – A review

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Abstract

The aim of this article was to review the state of fertility of female dairy cattle in South Africa and to compare it with international efforts at improving fertility. Fertility in dairy cows is defined as the ability to conceive from first insemination soon after calving and to carry the calf full term to calving. It is one of the main profit drivers in the dairy industry and is a complex trait that is influenced by the environment, genetics, and their interaction. Generally, there has been a decline in dairy cow fertility across breeds worldwide because of intense selection for milk yield, milk components, and body conformation traits. In addition, most fertility traits are negatively correlated to milk production traits. Milk production has been the focal point of selection programmes as it is linked directly to the profitability of the dairy enterprise. The low heritability of fertility traits is one of the factors that discouraged efforts to include fertility in genetic evaluations. However, owing to its economic importance, female fertility was later included in the breeding objectives for dairy cattle in several countries. Although most fertility traits are heritable to a low degree, some additive genetic variability can be exploited.

Keywords: breeding values, cow fitness, genetic improvement, heritability

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Introduction

Female fertility is a complex multi-factorial trait that includes the animal's genetic composition (Miglior, 1999) and environmental conditions such as nutrition and climate (Muller *et al.*, 2014), the endocrine system (Potgieter, 2012), the age of the animal and on-farm management practices. In enhancing fertility through advanced reproductive biotechnologies, a clear understanding of the hormonal mechanisms that control the oestrus cycle is required for inseminators to detect oestrus signs accurately to increase pregnancy rates.

The breeding goal of most dairy farmers is to increase the profitability of their enterprise. This should be achieved without any detriment to animal health and welfare and the environment. The milk yield of cows determines the profitability of a dairy enterprise. However, there are several other profit drivers, for example longevity, disease resistance, feed efficiency and fertility. These traits should be incorporated into the dairy breeding plan and each should play a role in determining the profitability of dairy herds by decreasing input costs of production. These expenses include repeated artificial insemination (AI) services, extra hormonal treatments, veterinary examinations and treatments of cows that are susceptible to disease, and outsourcing of replacement heifers. Major economic losses are also incurred through culling as a result of reproductive problems and reduced incomes because of long calving intervals (Seegers, 2006). In a poor reproductive performance scenario, an average net economic loss of €231 per cow per year was observed in The Netherlands (Inchaisri *et al.*, 2010).

Breeding programmes have focused on selecting for increased milk production (Evans *et al.*, 1999; Pryce & Veerkamp, 2001). However, fertility in dairy cows has decreased strongly over the last decades as milk production per cow increased significantly (Dillon *et al.*, 2006; Makgahlela *et al.*, 2007; Cassandro, 2014), because of the antagonistic relationship between fertility and milk production that is associated with pleiotropic effects of alleles for production and fertility (Glaze, 2011). Conventional breeding programmes have neglected fertility for several reasons including that it does not produce a saleable commodity.

Generally, fertility traits have low heritabilities (Table 1), indicating that they are heavily influenced by the environment. However, there is sufficient additive genetic variation to warrant their genetic improvement through selection (Miglior *et al.*, 2005; Makgahlela *et al.*, 2007; Banga *et al.*, 2009; Muller *et al.*, 2014).

Table 1 Heritability (h^2) estimates and standard errors (SE) of fertility traits observed in various breeds worldwide

Fertility trait	Breed	$h^2 \pm SE$	Country	Reference
Calving Interval	Holstein-Friesian	0.07 \pm 0.00	Italy	Biffani <i>et al.</i> , 2003
	Holstein	0.03 \pm 0.01	South Africa	Makgahlela <i>et al.</i> , 2007
	Simmental	0.02 \pm 0.07	Turkey	Ulutas & Sezer, 2009
	Fogera Holstein-Friesian	0.05 \pm 0.09	Ethiopia	Zelege <i>et al.</i> , 2016
Age at first Calving	Multiple breeds	0.13 \pm 0.01	New Zealand	Grosshans <i>et al.</i> , 1997
	Ayrshire	0.09 \pm 0.05	Kenya	Amimo <i>et al.</i> , 2006
	Holstein	0.24 \pm 0.02	South Africa	Makgahlela <i>et al.</i> , 2007
	Fogera Holstein-Friesian	0.15 \pm 0.23	Ethiopia	Zelege <i>et al.</i> , 2016
	Girolando	0.27 \pm 0.03	Brazil	Canaza-Cayo <i>et al.</i> , 2017
Days Open	Multiple breeds	0.02 \pm 0.00	Brazil	Grosshans <i>et al.</i> , 1997
	Holstein	0.05 \pm 0.02	China	Guo <i>et al.</i> , 2014
	Holstein	0.03 \pm 0.00	Tunisia	Zaabza <i>et al.</i> , 2016
	Holstein	0.02 \pm 0.01	Iran	Rahbar <i>et al.</i> , 2016
	Fogera Holstein-Friesian	0.01 \pm 0.05	Ethiopia	Zelege <i>et al.</i> , 2016
Services per conception	Multiple breeds	0.01 \pm 0.01	New Zealand	Grosshans <i>et al.</i> , 1997
	Swedish Red and White	0.02 \pm 0.16	Sweden	Roxstroem <i>et al.</i> , 2001
	Holstein	0.10 \pm 0.02	South Africa	Potgieter, 2012
	Holstein	0.01 \pm 0.01	Iran	Eghbalsaied, 2011
	Holstein	0.04 \pm 0.03	Iran	Rahbar <i>et al.</i> , 2016
Calving to first service	Multiple breeds	0.03 \pm 0.00	Brazil	Grosshans <i>et al.</i> , 1997
	Holstein	0.14 \pm 0.02	Iran	Eghbalsaied, 2011
	Holstein	0.04 \pm 0.01	Czech Rep	Zink <i>et al.</i> , 2012
	Holstein	0.04 \pm 0.01	Iran	Toghiani, 2012
	Holstein-Friesian	0.07 \pm 0.00	Ireland	Berry <i>et al.</i> , 2013
Non return rate 56 d	Holstein-Friesian	0.02 \pm 0.00	Italy	Biffani <i>et al.</i> , 2003
	Holstein-Friesian	0.01 \pm 0.00	Netherlands	De Haer <i>et al.</i> , 2013
	Holstein	0.01 \pm 0.00	China	Liu <i>et al.</i> , 2017
	Holstein-Friesian	0.03 \pm 0.01	Germany	Yin & König, 2018

Denmark, Sweden, and Finland were the first to include health and fertility traits in selection programmes in the mid 1990s, whereas countries such as New Zealand followed in 1998 and the USA in 2001 (Wesseldijk, 2004). The inclusion of fertility traits in South African selection programmes was recommended only in 2007 (Makgahlela *et al.*, 2007). To date, the genetic evaluation for fertility in South Africa is based on traits derived from calving dates (that is, age at first calving (AFC) and calving interval (CI)). But these traits become available late in an animal's life and can easily be influenced by management or breeder.

Calving interval and AFC are the result of actions that could be used as fertility indicators. The inclusion of fertility in dairy cattle selection programmes is based on its economic value to the herd. Advances in genomic technologies promise a leap forward in the genetic improvement of difficult to measure traits such as fertility. For example, genomic selection exploits genome-wide dense single nucleotide

polymorphism (SNP) markers to predict breeding values for breeding stock (Meuwissen *et al.*, 2001). The accuracy of genomic predictions in low heritable traits exceeds that of parental averages for young animals without phenotypes of their own, which would accelerate the rate of genetic improvement for low heritable traits (Viana *et al.*, 2016).

South Africa was among developing countries that lagged behind developed countries in the inclusion of fertility traits in selection programmes (Wesseldijk, 2004). This article reviews the state of female dairy cattle fertility in South Africa, and comparisons are made with international efforts at genetic improvement of this complex trait. This study indicates progress after the inclusion of fertility in South African selection indexes.

The profitability of dairy cattle depends not only on milk production, but also on non-production characteristics such as fertility and health traits (Toghiani, 2012). These are important in minimising cost and maximizing the net return of the dairy enterprise (that is, they increase biological and economic efficiency). Sound reproductive management can have tremendous positive effects on profitability, and one of the key components of modern dairy production is the analysis of reproductive records. Accurate and reliable on-farm records can help guide producers, veterinarians and consultants to make better decisions about reproductive management (Overton, 2009).

Poor reproductive performance affects profitability greatly in a dairy herd as it is one of the reasons for involuntary culling, for example 25% in France (Colleau & Moureaux, 1999), 21% in Iran (Ghaderi-Zefrehei *et al.*, 2017) and 18.5% in South Africa (Anonymous, 2017). Involuntary culling also has a negative impact on dairy economics because rearing or purchasing a replacement heifer is far more expensive than the salvage value of culled cows (Lavern, 2017). Economic losses can also be owing to a loss of production because of prolonged CIs (Van Arendonk *et al.*, 1989; Olori *et al.*, 2002). Banga *et al.* (2009) showed that an increase in CI caused a decrease in profit, which agrees with several other studies (Visscher *et al.*, 1994; Du Plessis & Roux, 1998; Holmes *et al.*, 2000; Olori *et al.*, 2002; Veerkamp *et al.*, 2002). This highlights the need to include most traits of economic importance in breeding objectives and selection indices with accurately weighted economic values. Little research has been done in South Africa on the economics of dairy cow fertility. A study by Cervo *et al.* (2017) reported a decrease in profit margins for age at first calving (-1 to -25) and CI (-0.4 to -24), indicating that producers need to select for early calving animals and shorter CIs to increase profit margins. Inclusion of these non-yield traits in selection indices is important for the dairy producer's profits, even though there is wide variation among countries in traits that are included in selection indexes and in relative economic weights (Shook, 2006).

Female fertility is influenced largely by the environment, but genetics also plays a significant role in the reproductive performance of dairy herds. Cows selected for high milk yields have shown declines in fertility (Walsh *et al.*, 2011) because of the pleiotropic effect of genes for production and fertility in which similar genes underlie expression of these traits, but in reverse modes (Glaze, 2011). Efforts to select for improved fertility were in part discouraged by the low heritabilities exhibited by fertility traits. Thus, breeders thought that fertility could then be improved through better management systems. However, studies showed that there is sufficient additive genetic variation among fertility traits to warrant their improvement through selection (De Jong, 1998; Weigel & Rekaya, 2000; Norman *et al.*, 2009; De Haer *et al.*, 2013).

In the 1990s, some Scandinavian countries included fertility in their selection indices by using multi-trait selection (Leitch, 1994). Functional traits are currently included in selection indices of various countries (Table 2). Although the South African index previously included only production (63%) and type (37%) traits (Wesseldijk, 2004), the breeding objectives for dairy cattle were revised to include a small proportion of selection for milk production traits because a turnaround has been made in selection goals for dairy cattle bulls by emphasising body conformation traits (e.g. udder, feet and legs, and size), health traits (somatic cell counts indicating mastitis), fertility and longevity (Theron & Mostert, 2019). The percentages or weights of the traits in the indices change as production and market prices change and new estimated breeding values (EBV) for the traits become available.

Interval traits are most commonly used for fertility evaluation, in part because they are simple to measure and record, and are available on a large scale (Table 3). Often the only count trait that is used is services per conception (Potgieter, 2012), which is seldom explored because it requires insemination and pregnancy records, which are not routinely recorded in South Africa (Mostert *et al.*, 2010). Lack of sufficient data therefore makes it difficult to evaluate fertility broadly. Hence genetic evaluations for fertility are based only on CI and AFC (Makgahlela *et al.*, 2007; Banga *et al.*, 2009; Potgieter *et al.*, 2011). Although the genetic evaluation of CI ensures that fertility is included in breeding objectives, which is a good step towards the improvement of fertility in dairy cows, it has its limitations because of the lack of animal information until the second parturition. It results in biased management decisions and inaccurate prediction of breeding values because the evaluations are based only on cows that calved at least twice, excluding heifers and cows that are perceived to be least fertile and those culled for not becoming pregnant (Esslemont, 1992; Haile-Mariam

et al., 2003; Muller *et al.*, 2012). The use of CI and AFC as the main fertility traits represents a setback because the estimated breeding value (EBV) for CI become available to the industry at least a year later than those of production traits, whereas AFC is open to management bias.

Table 2 Various selection indices and their corresponding relative economic weight for each trait

Index	Country	Trait	%	Reference
Nordic total merit index (NTM)	Denmark Finland Sweden	Health and fertility	53	NTM unlocked, 2017
		Production	30	
		Functional conformation	17	
Total merit index (TMI)	Germany	Production	50	Rensing <i>et al.</i> , 2002
		Longevity	25	
		Conformation	15	
		Udder health	5	
		Reproduction	5	
Total performance index (TPI)	USA	Production	43	Meyer & Zwald, 2014
		Health	28	
		Conformation	29	

Table 3 Measures of reproductive performance that can be derived from artificial insemination events recorded from on-farm automated systems.

Trait	Trait category	Description of the trait
Age at first service	Interval	Age at which a heifer was first inseminated (months)
Age at first calving	Interval	Age at which a heifer gives birth to its first calve (months)
Days Open	Interval	Number of days from calving to conception
Calving to first service	Interval	Number of days from calving date to the date of the next first service
First service <80 days	Success	If a cow was inseminated within 80 days post partum
Services per conception	Count	Number of services required for a cow to conceive
Pregnant <100 days	Success	If a cow was confirmed pregnant within 100 days post partum
Pregnant <200 days	Success	If a cow was confirmed pregnant within 200 days post partum

Potgieter *et al.* (2011) and Muller *et al.* (2012) explored the possibility of using farmers' service records to derive additional measures of fertility using small datasets. They concluded that there is sufficient scope for selection of fertility because traits such as calving to first service, services per conception, and days open could be used to predict the ability of the cows to conceive. Countries such as Ethiopia and The Netherlands have explored the use of reproductive performance records to estimate heritabilities and correlations for fertility traits (De Haer *et al.*, 2013; Zeleke *et al.*, 2016). The moderate to high positive genetic correlations observed in these studies suggest that improvement of one fertility trait is coupled with an improvement in another. A single fertility trait would not serve well for selection, thus various traits need to be

combined in an index for optimum genetic progress. More research is required to increase the availability of such information and to fill knowledge gaps, especially in South Africa.

Dairy cattle genetic evaluations have focused on production traits because they are easier to measure and are directly proportional to herd profitability, whereas fitness traits such as reproductive performance are difficult to define and record (Evans *et al.*, 1999; Pryce & Veerkamp, 2001; Miglior *et al.*, 2005). Consequently, effective selection tools for genetic improvement of reproductive traits were limited (Gutiérrez *et al.*, 2002). Milk yield has doubled in the past 40 years (Oltenucu & Broom, 2010). In the United States, the average milk production per cow over the period 1957 - 2007 increased by 5,9 kg, with 3,4 kg of this increase (or 56%) because of genetics (Van Raden, 2004). In South Africa, the Ayrshire breed has made remarkable genetic progress in production traits. Genetic increase of milk production per lactation has been recorded at 44.3 kg per year since 1983, butterfat production at 1.7 kg/year, and protein production at 1.4 kg/year (Mostert *et al.*, 2013). Even though proper management, good nutrition and environmental conditions contributed to the increased milk yields, genetics played a huge role because animals went through intensive genetic selection through the use of artificial insemination (AI) and worldwide distribution of semen from elite progeny-tested bulls (Oltenucu & Broom, 2010).

With increasing milk production, reproductive performance has been declining (Roxstroem *et al.*, 2001; Royal *et al.*, 2002; Pryce *et al.*, 2004; Oltenucu & Broom, 2010). Several studies on the genetic relationships between fertility and production traits found that correlations between milk yield and fertility traits were antagonistic and statistically significant (Grosshans *et al.*, 1997; Roxstroem *et al.*, 2001; Strucken *et al.*, 2012; Tenghe *et al.*, 2015). High positive genetic correlations between 305-day milk yield (MY) and CI showed that an increase in milk yield consequently prolonged CI (Table 4).

Table 4 Genetic correlations between 305-day milk yield and calving interval in various dairy breeds

Breed	Genetic correlation	Country	References
Holstein–Friesian	0.58	Australia	Haile-Mariam <i>et al.</i> , 2003
Holstein	0.69	South Africa	Makgahlela, <i>et al.</i> , 2007
Simmental	0.35	Turkey	Ulutas <i>et al.</i> , 2009
Holstein	0.59	Brazil	Toghiani, 2012
Brown Swiss	0.68	Turkey	Sahin <i>et al.</i> , 2014
Xinjiang Brown Cattle	0.47	China	Fu <i>et al.</i> , 2017
Girolando	0.59	Brazil	Canaza-Cayo <i>et al.</i> , 2017

In a sample of UK dairy cows that were monitored from 1975 to 1982 ($n = 2503$) and 1995 to 1998 ($n = 704$), calving rates to first service declined from 55.6% to 39.7% (Royal *et al.*, 2000). There is also evidence of an unfavourable relationship between milk production and oestrus behaviour with shorter oestrus periods (5.5 vs 11.1 hours) in high-producing cows (>40 kg per day) relative to low (<30 kg per day) (Lopez *et al.*, 2004). A study conducted in Poland showed that increased milk yield of first lactation cows (from $\leq 5\ 000$ kg to $>8\ 000$ kg) had a negative effect on their fertility in the first reproductive cycle, the CI calving increased from 378 to 517 days, the service period lengthened from 24 to 130 days, and the insemination interval increased from 1.63 to 3.44 (Sawa & Bogucki, 2011). In the USA, Lucy (2001) reported an increase in the number of AIs required for conception from 1.75 to more than 3 over 20 years. In South Africa, Makgahlela (2008) reported that the CI of Holstein cows increased from 386 in 1984 to 420 days in 2004. Increasing the interval between two calving dates reduces the number of calves born per herd/year. Reklewski *et al.* (2003) pointed out that the negative effect of high milk production on fertility may be because daily lactation yield peaks during the period that cows are more likely to conceive, that is, between 60 and 90 days of calving. The primary reason for reproductive disturbance is the aggravation of the negative energy balance, which leads to intense mobilisation of body fat reserves, thus increasing the incidence of metabolic and hormonal disorders and lengthening the period between calving and first oestrus after calving (Reklewski *et al.*, 2003).

Success or failure of dairy farming depends to a greater extent on the farmer's or breeder's management skills and practices, together with market factors, environmental factors, and the herd genetic composition. Overall, dairy herd health and nutrition are primary determinants of fertility. The feeding level of

young animals affects the age at which they reach puberty, whereas in mature animals inadequate nutrition reduces the production of ova, which can result in failure to conceive (Shortle, 2014). A negative energy balance normally occurs during early lactation because feed intake is low, whereas milk production is greater as the cows are transitioning. These cause the animal to use body reserves to overcome the energy deficit (Ibtisham *et al.*, 2018). Formulating diets to meet the requirements of the cow while avoiding over-consumption of energy may improve the outcomes of the transition period and lead to improved fertility (Cardoso, 2017).

Body condition score (BCS) is a good herd management tool with which to check the body reserves and energy status of cattle. Because good health, milk production, fertility and fitness depend on a good BCS, it should not be less than 2 to 2.5 and should be the same at drying off and at calving (Garnsworthy, 2007). Body condition score has a direct effect on the fertility of dairy cattle. Carvalho *et al.* (2014) showed that cows that maintained BCS from calving to 21 days after calving had higher pregnancy per AI at 40 days (83.5%) than those that lost BCS (25.1%) in the same period. Klopčič *et al.* (2011) noted that animals that stay in good condition during the first part of lactation show shorter calving intervals. Kadarmideen (2004) showed that BCS has favourable genetic correlations with fertility traits (-0.35 with days to first service) and that the genetic merit for BCS increases the genetic merit for lactation somatic cell score (SCS). Through selection of BCS and SCS, an opportunity for indirect selection of resistance to mastitis is provided, because SCS in milk has a genetic correlation of about 70% with clinical mastitis (Kadarmideen & Pryce, 2001). Body condition score is detrimental to post-partum health (Markusfeld *et al.*, 1997), in which cows in poor condition at drying off were at greater risk of having retained placentas, and cows that lost more body condition during the dry period suffered more from retained placenta and metritis. A well-balanced ration is recommended throughout the stages of a producing dairy cow to avoid the negative effects caused by poor nutrition.

Successful reproduction is the result of a chain of events, including resumption of oestrous cycles post-partum, the development and ovulation of a healthy oocyte, fertilisation, embryo development, implantation in the uterus, maintenance of pregnancy and parturition (Garnsworthy *et al.*, 2008).

The main behavioural sign of an oestrous period is standing to be mounted, which is used to determine the correct time to inseminate. However, this traditional way of detecting cows is unsatisfactory (Van Eerdenburg *et al.*, 1996). Moreover, in high-yielding herds, the percentage of cows that display standing to be mounted by other cows has decreased. A study by Roelofs *et al.* (2005b) showed that only 58% of cows were observed in standing oestrus, leaving it more difficult to detect oestrus. As a result, submission rate to AI would decrease and lead to reduced reproductive efficiency (Crowe *et al.*, 2018). However, the use of a combination of signs of oestrus and heat detection aids has a positive association with reproductive efficiency (Cowen *et al.*, 1998; Rao *et al.*, 2013). Other methods of detection and quantifying oestrus have been recommended, such as pedometers (Roelofs *et al.*, 2005a) and electronic activity tags (Lovendahl & Chagunda, 2010).

A healthy dairy cow should release its first dominant follicle at around 15 days post-partum, although it may not show typical heat behavioural signs during first ovulation. This 'silent oestrus' is thought to be the result of high oestradiol (E2) concentrations of foetal origin at the end of gestation, which induces 'refractoriness' in the hypothalamus to E2 at the first postpartum ovulation (Boer *et al.*, 2010). However, behavioural signs will be present at the subsequent oestrus owing to the effect of the corpus luteum produced after the first ovulation, which provides the progesterone (P₄) that removes the refractory state.

The percentage of cows that become pregnant from first postpartum insemination has declined from 55.6% to 39.7%, which was attributed to an increase in the proportion of cows exhibiting atypical ovarian hormone patterns from 32% to 44% (Royal *et al.*, 2000). Atypical ovarian hormone patterns, such as extended anoestrus or prolonged high progesterone concentrations often require pharmacological interventions before normal cycles can be resumed (Pring *et al.*, 2012). The delay of normal patterns of early resumption of ovulation in high-yielding Holstein-type cows may be owing to the effects of severe negative energy balance, dystocia, retained placental membranes and uterine infections (Crowe *et al.*, 2014). The key to optimising the resumption of ovulation in dairy cows is appropriate pre-calving nutrition and management so that the cows calve down in optimal body condition (BCS of 2.75 to 3.0) with postpartum body condition loss restricted to 0.5 BCS units (Crowe *et al.*, 2014). This would ensure that cows would become inseminated shortly after calving and conceive earlier, resulting in shorter calving intervals.

Advancements in genotyping by sequencing technologies have facilitated the identification of single nucleotide polymorphisms (SNPs), which provide additional data for use in genetic evaluations of animals. Genomic selection identifies genetically superior selection candidates based on breeding values predicted as the sum of allele substitution effects of thousands of genome-wide SNP markers from the reference populations with phenotypes and genotypes (Meuwissen *et al.*, 2001; Goddard, 2009). This allows early selection of young animals without phenotypic information, and reduces the generation interval, thus accelerating the rate of genetic improvement. High genetic gains can be achieved through using young

animals without performance records as parents for the next generation (De Roos *et al.*, 2011; Buch *et al.*, 2012). Several statistical models have been developed for genomic evaluations, categorised mainly into best linear unbiased prediction (BLUP) approaches, which assume normally distributed SNP effects with equal variance, and Bayesian algorithms, which assume unequal variance of SNP effects (Meuwissen *et al.*, 2001; Van Raden, 2008). In multi-step genomic best linear unbiased prediction (GBLUP), the SNP effects are estimated and summed to obtain direct genomic values or are used to build a genomic relationship matrix that simply replaces the pedigree-derived numerator relationship matrix (Habier *et al.*, 2007, Van Raden, 2008). Using the selection index approach, the estimated direct genomic values would subsequently be blended with EBV, weighted by their reliabilities to obtain genomic breeding values (GEBV). The purpose of blending is to recover ancestral information from the EBV (Van Raden *et al.*, 2009). In the single-step GBLUP or unified approach, the pedigree and genomic information are combined into a single relationship matrix, which then enters the mixed-model equations to obtain GEBV for both genotyped and ungenotyped animals (Misztal *et al.*, 2009; Christensen & Lund, 2010). Genomic selection will be especially important for low heritable complex traits that have been difficult and expensive to measure such as fertility, disease and meat quality. The reliabilities of GEBV were found to be considerably greater than those of conventional parent averages (PA). For example, VanRaden *et al.* (2009) reported an expected genomic reliability of 63% for 26 traits, which was double the reliability of 27% for PA. Su *et al.* (2010) reported reliability of 55% averaged over 18 traits, which was close to double the reliability of 29% achieved for PA. A genomic breeding scheme was shown to be superior to a conventional breeding scheme, even in small dairy cattle populations (Thomassen *et al.*, 2014).

The cost of genotyping is a limiting factor in the adoption of genomic selection in developing countries such as South Africa. However, the cost of genotyping can be countered by greater saving costs because of the elimination of PT and additional annual monetary genetic gain owing to the reduction of generation intervals in genomic breeding programmes (GBP). This was shown in the study by König *et al.* (2009), in which a distinct economic advantage in discounted profit was found for all scenarios of GBP in the range of factor 1.36 to 2.59. The cost effectiveness of genomic selection compared with progeny testing was supported by Kariuki *et al.* (2017) in their gross margins study for PT and genomic selection (GS) schemes. This highlights that the GS breeding scheme is economically viable for developing countries because the higher the margin, the more effective company management in generating revenue for each unit of cost. Shortening the generation interval can also be achieved through the combined use of marker assisted selection and germ-line manipulations, known as velogenetics, which allows efficient introgression of mapped economic trait loci between genetic backgrounds (Georges & Massey, 1991). Through the process of velogenetics, Holstein calves have already been born from oocytes aspirated from eight-month-old females that were fertilised *in vitro* by the sperm of 10-month-old bulls (Taylor, 2016). Imputation algorithms can be applied to derive high-density genotypes from low-density genotypes, thereby increasing the size of the reference population (Calus *et al.*, 2014). The loss in accuracy of GEBV estimated from imputed genotypes is reported to be between 0% and 45% (Habier *et al.*, 2009; Weigel *et al.*, 2010). Imputation could be used to deduce missing genotypes and would be helpful in increasing the large reference populations that are needed for accurate genomic selection (Weng *et al.*, 2012). The low cost of genotyping would result in a large number of candidates being screened, hence increasing selection intensity. The shift towards genomic selection could be economically feasible for South Africa in improving low heritable traits such as fertility. However, genomic selection is not a 'silver bullet'. The need to have appropriate measures for female fertility remains the cornerstone of the much articulated gains in genomic selection.

Conclusion

The declining trend in fertility is being reversed by its inclusion in multi-trait selection indices, together with production and other functional traits. Fertility traits have been reported to have reasonable additive genetic variation, which shows that improvements are possible through genetic selection, despite low heritability estimates for individual traits. Several countries have already constructed multi-trait selection indices to select for all traits of economic importance, including fertility. Genomic selection is a promising opportunity for accelerating genetic improvement of complex traits such as fertility. Several countries have implemented genomic selection and demonstrated its potential in accelerating the rate of genetic improvement and the cost benefits. Successful implementation of additional fertility traits in genetic improvement programmes of South African dairy cattle would be dependent on whole-herd reporting and on cattle breeders optimising the use of technologies to improve the current state of female fertility.

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Authors' Contributions

RDK designed and drafted the manuscript, MLM drafted the manuscript, and CJCM and KD critically evaluated the manuscript.

Conflict of Interest Declaration

Authors declare that they have no conflicts of interest.

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