

World Trends in Dairy Cow Fertility

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ABSTRACT: Although differences exist between breeds and countries, dairy cow fertility has generally declined since around 1980. However, for many countries, an improvement in phenotypic and genetic trends for female fertility has been observed from the early to mid 2000s largely as a consequence of introducing breeding values for fertility and increased emphasis on fertility in breeding objectives. However, for some countries, fertility is still deteriorating genetically. Barriers to genetic improvement include: 1) the low heritability of fertility - genomic selection tools have helped to increase the reliability of bull breeding values; 2) insufficient selection intensity on fertility as a consequence of economic drivers of milk production versus fertility; 3) a possible association between level of milk production and the genetic correlation of fertility and milk production and 4) the impact of inbreeding on reproductive performance and increased probability of lethal recessives arising.

Keywords: dairy cattle; fertility; genetic trend

Introduction

On-farm recording of fertility, health and longevity and consequently selection for these traits has been practiced in the Scandinavian countries for over 30 years (Heringstad et al. (2013)). For other countries it was not until the mid-1990s that serious attention was given to genetic improvement of fertility traits (Weigel (2006)). This probably occurred as a consequence of research documenting unfavorable genetic correlations between fertility traits and milk production traits (see the reviews of Pryce and Veerkamp (1999); Berry et al. (2014)) and observed reductions in fertility performance. For example, in a sample of UK dairy cows monitored between 1975–1982 ($n = 2503$) and 1995–1998 ($n = 704$) calving rate to first service reduced from 55.6% to 39.7% (Royal et al. (2000)). It became clear that the observed deterioration in fertility was partly genetic therefore requiring a genetic solution. Consequently, breeding programs have gradually been expanded to include fertility traits, with many also including longevity and measures of health (Miglior et al. (2005)).

Fertility is a trait of great importance to most dairy farmers. After all, lactation is dependent on parturition (i.e., reproduction). Variation exists however in the relative importance of fertility in national breeding objectives. In some countries, it is economically more valuable to produce extra milk rather than improve fertility, while in others there is a strong link between pasture production profiles

and milk lactation profiles. To optimize pasture usage, calving patterns need to align with the initiation of grass growth and therefore good fertility is essential.

Heritability estimates of traditional fertility traits are generally low (<0.1); these very low heritability estimates belie the fact that selection for fertility can lead to worthwhile changes, because the trait is highly variable (Pryce and Veerkamp (1999); Berry et al. (2014)).

The aims of this study were to: 1) quantify phenotypic and genetic trends in female fertility in international Holstein populations; 2) summarize the genetic correlation between milk production and fertility across different production environments.

World Holstein Friesian Federation Survey

In 2012 the World Holstein Friesian Federation contacted its member organizations to respond to a survey of the status of dairy cow fertility. The respondents were asked to provide means of the annual per cow values for the following traits: milk yield, milk protein yield and concentration, milk fat and concentration, calving interval, interval between calving and first insemination, non-return rate, number of AI per cow, number of cows, number of herds and fertility EBVs of bulls and cows. Respondents were also asked to provide information on the effect of genomic selection on reliability of bull proofs for: 1) young bulls (i.e., no daughters); 2) progeny-test, or 1st crop daughters, and 3) older bulls (2nd crop) with larger progeny groups.

Completed surveys were received from 17 respondents from a total of 16 countries (Argentina, Australia, Belgium, Canada, Croatia, Czech Republic, Finland, France, Germany, Ireland, Italy, the Netherlands, New Zealand, Switzerland the UK and the USA). Both the Swiss Holstein and Swiss Herdbooks responded on behalf of Switzerland.

Phenotypic Trends

Phenotypic trends for calving interval in 16 countries between 1990-1999 and 2000-2007 are shown in Table 1. Generally, the phenotypic trend in the 1990s shows greater deterioration (i.e. larger regression coefficients) than the 2000s. For several countries, phenotypic trends for calving interval have changed from being unfavorable (i.e. increasing) in the 1990s, to favorable (i.e. decreasing in the 2000s. The “world” trend for calving interval (Figure 1), which is the annual mean for calving interval from each

country, weighted by the number of cows contributing to each country mean, shows that phenotypic calving interval has plateaued around the year 2006 at 405.5 d. The weighted “world” mean deterioration between 1990 and 2000 was 1.25d/year. Assuming the phenotypic SD of calving interval is 59 days (from 9 studies reviewed by Berry et al. (2014)), then over 10 years (between 1990 and 1999), the decline has been approximately 0.2 phenotypic standard deviations, or 3.2% of the phenotypic mean in 1990. A polynomial fitted the “world” curve with an R^2 of 98%, tentatively suggests that phenotypically calving interval is starting to improve, although it will take some time to reach the level of calving interval observed in the early 2000s. The corresponding world trends for non-return rate is presented in Figure 2.

Table 1. Phenotypic means for milk yield and calving interval (CI) (2000-2007) and linear regressions (*b*) of calving interval on year of calving between 1990 and 1999 (1990s) and 2000 and 2007 (2000s).

Country	Milk (l)	CI (days)	<i>b</i> * (1990s)	<i>b</i> (2000s)
Argentina	7,255	455	1.88	-3.18
Australia	6,088	400		2.16
Belgium	7,397	408		1.36
Canada	9,615	418	1.22	0.88
Croatia	6,096	437	0.28	1.08
Czech Rep.	7,631	419	3.18	2.45
Finland	8,671	397	0.74	2.26
France	8,119	413		2.50
Germany	8,291	407	1.22	-0.64
Ireland	6,453	388	1.09	-0.62
Italy	10,826	434	1.61	0.34
Netherlands	8,755	412	1.69	0.22
New Zealand	4,088	369		0.20
Switzerland	7,219	405		1.14
UK	8,479	416		3.73
USA	11,333	424		-0.83

*Missing values are where incomplete data was provided for this time period.

The “world” trends for reproductive performance should be cautiously viewed as an indication of the future. The trends are weighted towards larger populations and therefore may not necessarily apply to all countries. Substantial variation in fertility performance and trends clearly exists among countries (Table 1). For example, calving interval tend to be longer in countries with greater cow milk production (Table 1). Where there were larger annual phenotypic gains in milk yield, there have also been larger changes in calving interval (i.e. regression of calving interval and milk yield on calving year from 2000 to 2007) (Figure 3).

Figure 1. Overall “world” phenotypic trend for calving interval, weighted by the number of reported cows in 16 countries that responded to the World Holstein Friesian Federation survey, the dotted line is a fitted polynomial (R^2 98%).

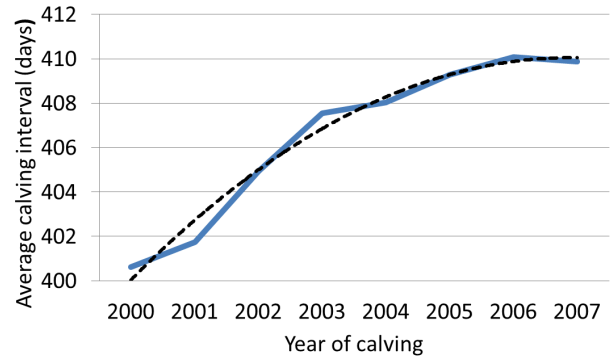


Figure 2. Overall “world” phenotypic trend for non-return rate, weighted by the number of reported cows in five countries that responded to the World Holstein Friesian Federation survey (Belgium, Germany, Italy, Netherlands, Switzerland), the dotted line is a fitted polynomial (R^2 75%).

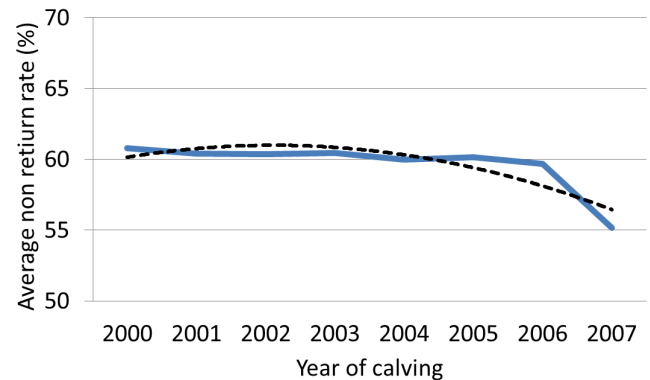
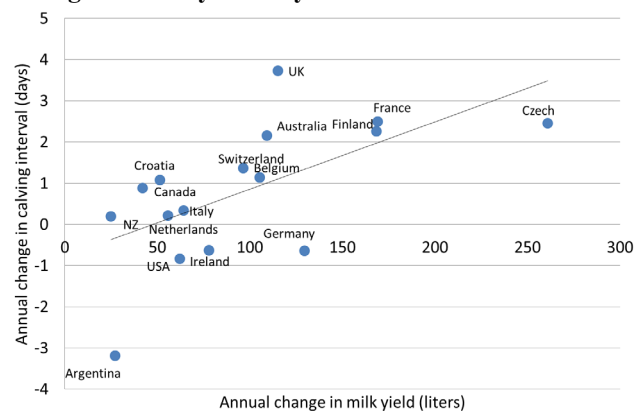


Figure 3. Annual increase in milk yield versus change in calving interval by country from 2000 to 2007.



Genetic Trends

Mean annual cow EBVs/PTAs by birth year for female fertility were converted to genetic standard deviation units using the genetic standard deviations of EBVs/PTAs obtained from the genetic evaluation units of each country. Only Holstein populations greater than 50,000 cows were included. Where necessary the sign of some country EBVs/PTAs was changed so that positive values reflected superior fertility.

The base that each country expresses fertility EBVs varies, which presents a challenge in illustrating genetic trends in a comparable way. Also, the definition of the fertility trait reported may vary by country. Furthermore, for Germany, Italy and the Netherlands EBVs were only provided for cows born up until 2009, so there may not have been sufficient time for a nadir to be observed in the cow population. For Canada, only breeding values for female fertility for cows born since 1997 were available, so the results are not included in Table 2.

The time-point when the genetic trend changed from being unfavorable to favorable was approximated by calculating the derivative of a 2nd order polynomial fitted to cow EBVs against year of birth. Genetic trends before and after the nadir (where observed) were calculated, as linear regressions and a “world” genetic trend calculated by weighting the number of cows contributing to each regression.

Table 2. Genetic trend (linear regression; *b*) of female fertility of cows born between 1990-2000 expressed in genetic SDs of EBVs. For countries with a visible nadir, the year and genetic trend in genetic SDs in the last 5 years of data provided *b* (post-nadir).

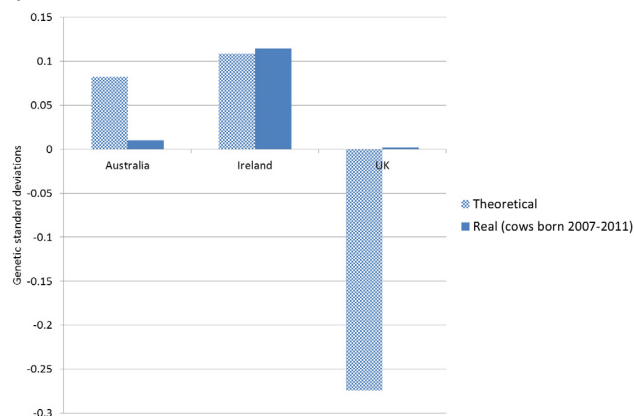
	<i>b</i>		Nadir (year)
	1990-2000	post-nadir	
Australia	-0.08	0.01	2005
Belgium	-0.11		
Finland	-0.04	0.01	2007
Germany	-0.11		
Ireland	-0.17	0.13	2003
Italy	-0.15		
Netherlands	-0.11		
New Zealand	-0.05	0.02	2001
UK	-0.10		
USA	-0.10	0.11	2003
“World”	-0.09		

Between 1990-2000, the “world” annual rate of genetic deterioration was approximately -0.09 genetic SDs in fertility EBVs and ranged between -0.17 and -0.04 (Table 2). However, genetic merit for fertility in many countries has started to improve in the early part of the 21st century. In Australia, Ireland, New Zealand and the USA the nadir, calculated from the derivative of fitted polynomials, was between 2001 and 2005. For all other countries, the nadir was either not within the bounds of the data, or no clear nadir was observed. Interestingly, in some cases the nadir occurred before the introduction of fertility

breeding values. This could have arisen due to: 1) selection on another correlated traits, such as longevity (VanRaden et al. (2004)), or 2) because it coincided with widespread use of several bulls that had positive fertility breeding values or 3) culling for poor fertility by farmers.

Although realized responses can quantify changes that have happened in the past, selection index theory can be used to model future selection responses. Predicted responses to selection were calculated using national indexes (APR, EBI and PLI) for Australia, Ireland and the UK respectively and are previously presented in the study of Berry et al. (2014). Selection candidates were assumed to be progeny test bulls, with 75 daughters, and yearly gains were calculated based on a 0.22 standard deviations change in the aggregate index (Rendel and Robertson (1950)). Theoretical responses to selection on the UK PLI show that genetic merit for calving interval is predicted to deteriorate through selection on this index (Figure 4) because it is not economically advantageous to halt this deterioration given the underlying assumptions used in the calculation of the economic weightings. However, the realized genetic gain in UK cows (Figure 4) is close to zero, showing that actual selection decisions differ from predictions. In fact, the average EBV/PTAs for fertility in the top 100 UK bulls ranked on APR, EBI and PLI (Australia, Ireland and UK) are 0.47, 0.66 and 0.39 genetic standard deviations more than cows born in 2011, so there are good opportunities to improve fertility through selection.

Figure 4. Selection response predicted through selection on APR (Australia), EBI (Ireland) and PLI (UK) and realized genetic gain for cows born between 2007 and 2011



Another question that is frequently asked, is what proportion of the phenotypic trend is genetic? VanRaden et al. (2004) reported that 40% of the phenotypic decline observed in the USA was due to genetics. Comparing the genetic and phenotypic trend in Ireland between 1980 and 2010 reported by Berry et al. (2014) it can be concluded that 64% of the phenotypic decline in calving interval in Ireland was due to genetics.

Genetic Correlations and Responses to Selection

One of the reasons why there are inconsistencies in realized responses to selection could be because of the variation in

emphasis on fertility among national breeding objectives. Most breeding objectives are complex and include many traits each weighted by their respective economic value, although in some circumstances the weights may be derived by desired gains or other means rather than economics.

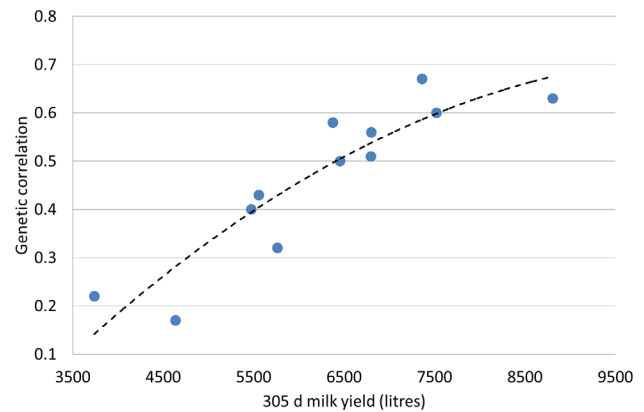
A popular way to compare selection indexes is percentage emphasis on traits (calculated using the index weight and genetic standard deviation); while this approach works well within a country and can be used to monitor changes in the index over time, it is a meaningless way to compare selection indexes between countries or to understand the outcome of selecting on an index. This is because the emphasis on a trait does not necessarily correlate with the selection response as it does not account for heritability and covariances between traits.

A selection index can be used to calculate responses to selection, as this will account for all the (co)variances between traits and the economic values applied to each trait. For illustration purposes, this can be done using two traits with varying genetic correlations between them. In the meta-analysis of published genetic correlations between performance and reproductive performance (Berry et al. (2014)), the pooled mean of the genetic correlation between calving interval and protein was 0.5 and between calving interval and milk yield was 0.46. When the genetic correlation between reproductive performance and milk production was assumed to be 0.50 and bulls had large progeny groups, then at least 33% of the emphasis (or half the emphasis placed on yield) within the breeding goal would need to be placed on reproductive performance to halt any deterioration in fertility. The minimum emphasis on reproductive performance required to halt any deterioration when the genetic correlation with milk production was 0.3 was 23% (or 30% of the emphasis on milk yield).

In environments where the genetic correlation between reproductive performance and milk yield is strong, then more emphasis is required on fertility to prevent deterioration in this trait, depending on other traits that are in the breeding goal. In a simple 2 trait index, if the emphasis on fertility was 23% and the genetic correlation between reproductive performance and milk production was 0.5, then obviously reproductive performance would decline, so quite a different outcome to holding reproductive performance steady.

In fact substantial variation exists in published genetic correlation estimates between fertility and milk production and it seems reasonable to hypothesize that these may vary across production environments or countries. Using only the studies included in the meta-analysis by Berry et al (2014) that reported 305 day milk yield means and genetic correlations with calving interval used, there appears to be a relationship between the genetic correlation of milk and reproduction and the reported mean milk yield of the study (Figure 5). Increasing yield by 1,000 liters increased the genetic correlation by around 0.1. The fertility trait chosen was calving interval, as there are more published genetic correlations for this trait than others (Berry et al., 2014).

Figure 5. Published genetic correlations between calving interval and 305 d milk yield against milk yield, the polynomial regression (dotted line) fitted with an R^2 of 83%



Published genetic correlation estimates between milk production and calving interval were stronger in high production environments (Figure 5). There are several possible explanations for this: 1) genotype-by-environment interactions exist for fertility traits, this has been observed in milk production traits and may influence correlations between traits as well. So, if the genetic variance in one trait is not expressed fully, then this may affect the covariance with another trait; 2) higher genetic merit cows for milk production experience more metabolic stress than their lower genetic merit counterparts because their feed intake does not cover nutritional demands, increasing the genetic correlation in high yielding environments; 3) there is potential bias in the data, as good fertility is relatively important in seasonal production systems and these often have lower average yields. Conversely, high yielding cows with long calving intervals may be better tolerated in high production systems where good fertility is not of such great importance.

Calving interval is often viewed as a poor selection criterion choice because it is censored i.e. the least fertile cows fail to re-calve which could add to the bias, especially if higher yielding cows are more likely to be given more chances to conceive. However, it is also the trait that has most observations because it requires only calving dates to calculate it rather than mating dates.

Unfortunately, there are far fewer studies that present genetic correlations between milk production and other reproductive traits, especially over the range of milk yields shown in Figure 5. For example, there were only 6 studies that estimated the genetic correlation between milk yield and non-return rate in the review of Berry et al. (2014) and no clear trend could be observed.

Genetic Evaluations

To help arrest the global genetic decline in fertility, international breeding values for fertility have been calculated by Interbull since 2007. In February 2014, 22 countries provided fertility data to Interbull for international bull evaluation for at least one breed. Within country, the most popular measures of fertility were non-return rates; for

example 56 day non-return rates, although some, such as the Walloon region of Belgium use 90 day non-return rates. A number of countries have developed methodologies to improve the accuracy of selection for fertility by including various predictors of fertility. For example, the UK model includes days to first service, the interval from calving to conception, and two measures of the cow's ability to conceive (Wall et al. (2003)). In Germany, 5 fertility traits are used: interval from first to successful insemination and non-return rate to 56 d of heifers, and interval from calving to first insemination, non-return rate to 56 d, and interval first to successful insemination of cows (Liu et al. (2008)).

Despite a considerable amount of effort invested into improving the accuracy of genetic evaluations for fertility and the fact that the weightings assigned to fertility in breeding objectives have increased, progress using conventional selection criteria is often still limited due to insufficient fertility data, especially mating and pregnancy records (Sun and Su (2012)). The accuracy of EBVs and the length of time for accurate traditional EBVs to be achieved through progeny test programs have meant slower progress than is now possible with genomics. Not all countries meet the requirements to have their fertility data included in Interbull evaluations and there is evidence that genotype x environment (GxE) interactions may limit the utility of fertility proofs derived in other countries especially where the definitions of fertility between countries are very different. For example the Interbull correlation for cow's ability to conceive, or trait "C2" between breeding values/PTAs for bulls from Australia is highest with South Africa (0.88) and Ireland (0.87) and lowest with Switzerland (0.26), demonstrating that the trait definition of fertility is different in each country and that there is also likely to be GxE. For example, calving interval is used to predict breeding values in Ireland and Australia, while in Switzerland the trait is 56 non-return rate. To disentangle GxE from trait definition, a study would be required to calculate the genetic correlation of the same measure of fertility for cows in the datasets of each country.

Genomics

Genomic selection has had a dramatic effect on the reliability of breeding values for animals without records or progeny. In Table 3, the increase in reliability for bulls without progeny ranged between 18% and 38%. The impact of genomics on reliability is, as expected, less for bulls with progeny, with very little advantage for bulls with large progeny groups (2nd crop). Including genomics in fertility evaluations will increase the accuracy of selection and therefore potentially speed up the rate of genetic progress in fertility, especially for bulls with either no or few progeny.

Regions of the genome with large effects on female reproductive performance (more specifically embryonic death) have been detected. VanRaden et al. (2011) documented the existence of haplotypes that had a high population frequency in the population but that did not exist in the homozygous state. The effects are only observed in mating related individuals that share the same lethal haplotype. In fact, significant effects on calving rate were observed between matings of carrier sires and

daughters of carrier sires, confirming that the haplotypes harbour embryonic lethal mutations (VanRaden et al. (2011); Fritz et al. (2013)). Recently, in Holstein, Montbeliarde and Normande cattle, Fritz et al. (2013) identified 34 candidate haplotypes ($p < 10^{-4}$) including Brachyspina, CVM, HH1 and HH3 previously reported by VanRaden et al. (2011) and three novel mutations that had effects on protein structure. A deletion carried by 13%, 23% and 32% of Danish, Swedish and Finnish red cattle appears to be responsible for embryonic mortality, but has a favorable effect on milk production (Kadri et al. (2014)). The impact of these mutations are likely to increase as inbreeding increases in intensively selected cattle breeds, which is why controlling these mutations using mating plans is becoming more important.

Table 3. Change in reliability (%) from genomics of fertility (fert) and production traits in young sires, progeny test (PT) sires and 2nd crop sires.

Country	Sire Group	Fert	Production
Australia	Young	22	35
	PT	10	13
	2nd Crop	1	0
Canada	Young	27	33
	PT	10	2
	2nd Crop	2	0
D/S/F	Young	28	33
France	PT	24	21
Germany	Young	18	42
Italy	Young	38	34
	PT	20	3
	2nd Crop	17	1
Switzerland	Young	1-5	10-20
UK	Young	29	34
	PT	17	3
	2nd Crop	~0	~0

GWAS have already been used to identify QTL with large effect on fertility and some promising candidates have been found (e.g. Pimentel et al. (2010); Sahana et al. (2010)). Whole genome sequencing is likely to improve the resolution and detection of causative mutations of these candidate SNP. While new mutations are likely to be identified, the challenge will be to apply this knowledge into practical applications.

New approaches, such as RNAseq in conjunction with GWAS can also help to improve the genetic control of complex traits, such as fertility. Recently Moore et al. (2014) found 560 differentially expressed genes in the corpus luteum of Irish cows with high and low genetic merit for fertility of which SNP associated with 211 and 175 genes were previously identified by 2 independent GWAS studies (in Australia and Europe).

Non-additive Effects

The rate of inbreeding in most dairy populations is increasing, with estimates in Holsteins typically being +0.20% per annum (e.g. Kearney et al., (2004)), while higher estimates have been published for other breeds

(Melka et al. (2013)). The average increase in calving interval or days open, for example in the female progeny resulting from the mating of two non-inbred half-sibs in Holsteins, is estimated to be between 1.2 days and 8.8 days (Wall et al. (2005); McParland et al. (2007)). For a rate of inbreeding of +0.2%/year, the effect of inbreeding on calving interval could range between 0.02d and 0.14d, which is 1% to 8.5% of the world phenotypic decline observed between 2000 and 2006 (Figure 1b). Therefore non-additive genetic effects may be contributing to the observed decline in fertility.

Over the last 20 years crossbreeding has been advocated as a potential solution for the decline in dairy cow fertility as lower yielding breeds may possess superior fertility and crossing them to higher yielding breeds can also result in heterosis (e.g. Heins et al. (2008)). However, with the exception of New Zealand, there has been reluctance in the dairy industry to adopt crossbreeding. In New Zealand, the overall profitability of the crossbred is superior to either Jersey or Holstein (Lopez-Villalobos et al. (2000)). In other countries, the breeding goal and economic climate may make crossbreeding less attractive.

Conclusions

The well documented deterioration in dairy cow fertility is starting to recover, with genetic and phenotypic trends in many countries improving since the early to mid-2000s. Barriers to genetic improvement include: 1) the low heritability of fertility - genomic selection tools have helped to increase the reliability of bull proofs; 2) insufficient selection intensity on fertility as a consequence of economic drivers of milk production versus fertility; 3) a possible association between level of milk production and the genetic correlation of fertility and milk production and 4) the impact of inbreeding on reproductive performance and increased probability of lethal recessives arising.

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