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Genetic aspects of fertility traits in dairy cattle – review

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INTRODUCTION

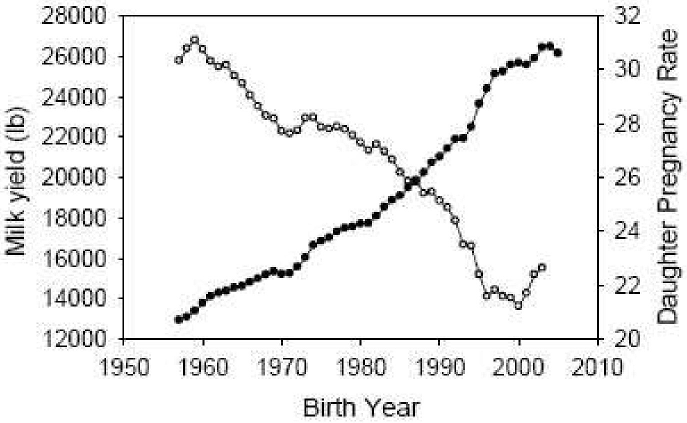
Fertility is considered a complex trait influenced by many physiological and disease-related variables. These is considerable scientific evidence to support the view that fertility performance is influenced by environment (E), genetics (G) and the interaction between G by E (GxE). Many hypothesis have been proposed to explain this including genetics, physiology, nutrition nad management, and these factors have been investigated at the animal, organ and celluar level at critical time points of the productive life of dairy cows (*Walsh et al.*, 2011).

It is largely known that, fertility in dairy cows strongly decreased over the last decades as milk production per cows has highly increased. Hence, the reproductive efficiency is became an high priority in all systems and it is considered higher in seasonal calving systems as the opportunity for cow to calve and become pregnant is time limited to ensure a calf per cow per year in synchrony with grass growth (*Dillon et al.,* 2006). Over the last 30 years, genetic selection for increased milk production, particularly within the North American Holstein-Friesian genotype, has been very successful. Between 1985 and 2003, the rate of phenotypic gain in milk production per cow per year has been 193 kg for the United States, 131 kg for the Netherlands, 35 kg for the New Zealand and 46 kg for Ireland (*Dillon et al.*, 2006). In Italy, the rate of the phenotypic gain in milk production per cow per year has been 112 kg in Holstein-Friesian with an average increase of the calving interval of 1.4 d per year (*Cassandro and Penasa*, 2010). Despite these countries having diverse production systems, genetic selection criteria and climatic conditions, they all report a sensible decline in reproductive performance during the same period inducing, in recent years, the emphasis within selection indices for Holstein-Friesian has shifted from predominantly production to funcional nonproduction traits associated with improved health and fertility (*Miglior et al.*, 2005).

Poor reproductive performace often leads to premature culling and decreased productive career of dairy cows. The association between the declines in fertility and milk production in the last decades, is evident in the Holstein population, as reported in *Figure 1* (*USDA-ARS AIPL*, 2007).

Figure 1

Trends in milk production and pregnancy rate by year of birth in the North American Holstein population (*USDA-ARS AIPL*, 2007)



However, there is now evidence that the phenotypic historical decline in fertility has reached a nadir and begun to improve "versus to zenit" (*Crowe*, 2008; *Norman et al.*, 2009).

Moreover, new research areas, as understanding genotype by environment interactions are crucial in determining the best health and management practices to achieve high levels of productive and reproductive efficiency. Recent studies have reported higher reproductive performance in high milk producing herds (herd average of > 10,000 kg milk production per lactation) than producing herds and concluded that this was likely due to better nutritional and reproductive management (*LeBlanc*, 2008).

Aim of this review, is primarily to review the effect and improving fertility through breeding strategies. This paper review the genetics aspects and strategies and their potential consequences affecting fertility in dairy cows.

DIRECT MEASUREMENT

An important direct measurnment of fertility is the pregnancy rate that measures how quickly cows become pregnant again after calving. It is defined as the percentange of nonpregnant cows that become pregnant during each 21-d period, because each eastrus cycle represents one chance for a cow to become pregnant. In recent years, many reproductive specialists have recommended this measure of reproductive success over the more traditional measure days open. Pregnancy rate calculations are more current, cows that do not become pregnant are included in calculations more easily, and larger rather than smaller values are desirable, simplifying selection by producers. Pregnancy rate can be calculated in function of voluntary waiting period and days open, as follow:

$$\text{Pregnancy rate} = 21/(\text{days open} - \text{voluntary waiting period} + 11)$$

where, voluntary waiting period is the initial phase of lactation during which no inseminations occur. The voluntary waiting period may vary across herds or seasons but would not affect genetic evaluations unless it differed for cows within the same herd-year-season. The constant factor of 11 centers the measure of possible conception within each 21-d time period such that cows conceiving during the firt 21-d period receive 100% credit on average and so on. As an example (assuming a voluntary waiting period of 60 d), a herd that averages 154 d open has a pregnancy rate of 20% while a herd averaging 133 days open has a pregnancy rate of 25%. Across the possible range of days open, this formula produces far from linear results (*Figure 2*).

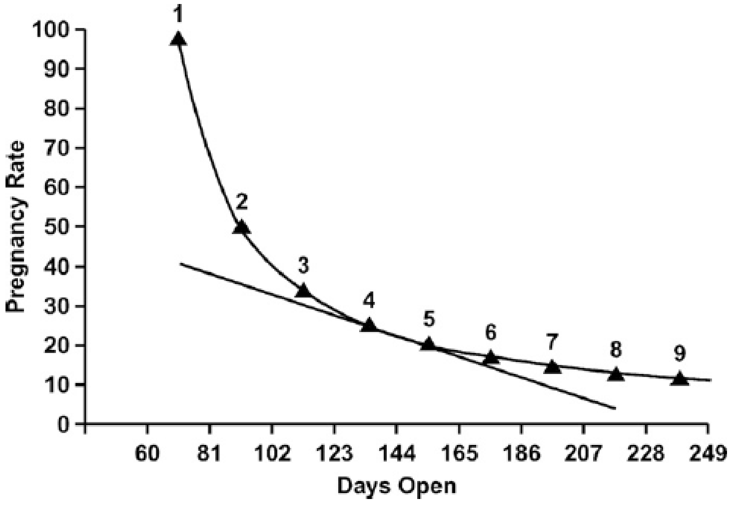
The genetic correlation between days open and pregnancy rate is estremely high (0.99) beacuse the only way to reduce days open is for cows to become pregnant at a faster rate. Knowing record on days open is it possible to transform data in pregnancy rate using this simple linear function, as reported by *VanRaden et al*. (2004):

$$\text{Pregnancy rate} = 0.25 \times (233 - \text{days open})$$

Reliable data on days open and on consequence on pregnancy rate is the most difficult aspect on using this direct measurment. Due to this, calving interval (CI), that is traditionally considered the main fertility indicator during the productive life of dairy cattle, might not be the most desirable direct measures of reproductive efficiency because of measures of CI are available only for cows that calve 2 or more times and not for females that do not calve and are culled. Moreover, CI is not an early measure of fertility and it is not an adequate selection tool for breeding organizations, which select bulls on the basis of the earliest information recorded on their female offspring. Consequently, indirect measurements of CI are more interesting for breeding programs based on improvement of fertility aspects.

Figure 2

Comparing nonlinear and linear trend from days open to pregnancy rate when a cow has one chance (numbered) to become pregnant during each 21-d cycle (*VanRaden et al.*, 2004)

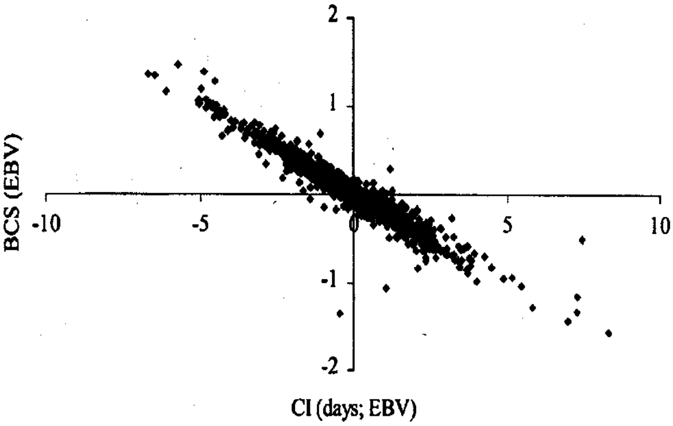


INDIRECT MEASUREMENT

One of the most interesting indirect measures of reproductive performance is the body condition score (BCS). Most studies on the relationships between BCS and fertility traits have been carried out (*Pryce et al.*, 2000, 2001; *Dal Zotto et al.*, 2007). Indeed, *Dal Zotto et al.* (2007), estimated a genetic correlation between BCS and CI of -0.35, indicating a moderately negative genetic association for these traits. *Pryce et al.* (2000), plotted BCS estimated breeding values versus CI estimated breeding values for 3,770 sires showing a strong linear realtionship (*Figure 3*). Therefore, cows that are thinner are more likely to have a longer CI. It is likely that cows are mobilizing body tissue to substain milk production, so BCS or BCS change is likely to be closely related to energy balance. Cows in negative energy balance, particularly in early lactation, may be yielding milk at the expense of reproduction. Hence, condition score has the potential to be used in breeding programmes. Genetic differences in the shape of the profile of depletion of reserves in early to peak lactation followed by recovery during the rest of the lactation may help to identify animals most suitable for improving fertility. Also, a flatter lactation curve may be a way of avoiding short-term nutrient deficits in dairy herds (*Pryce et al.*, 2004).

Figure 3

Estimated breeding values (EBV) of BCS versus calving interval (CI) for sires obtained from univariate analyses (*Pryce et al.*, 2000)



As already mentioned, the fertility trait is very complex and it is for this reason that to improve the estimation accuracy of the index in Italy (*Biffani*, 2008) was proposed an aggregate index based on direct and indirect correlated traits. This approach not only allows to take into account the complexity of the fertility trait but also improves, increasing the reliability of the index. Since February 2006 for the Italian Holstein is available an aggregate index for fertility, whose goal is to improve the conception to first service. This index is obtained by analyzing multi-trait, ie including 3 directly traits, related to fertility (calving interval, calving-first insemination interval and non-return rate at 56 days), and 2 indirect traits (milk production and BCS). *Table 1* shows the 5 traits used and their relative weight in the index aggregate itself. The weights assigned to each individual trait are not random, but depend on the genetic relationship between the traits themselves, and above all depend on the relationship that exists between them and the goal of the index: the conception rate at first service. Using these 5 traits there is an average increase of the reliability of almost 7%. The increase is mainly due to the greater amount of information available, but also to the contribution of two traits, milk and BCS, which have a heritability greater than that of the classic traits related to fertility.

Table 1

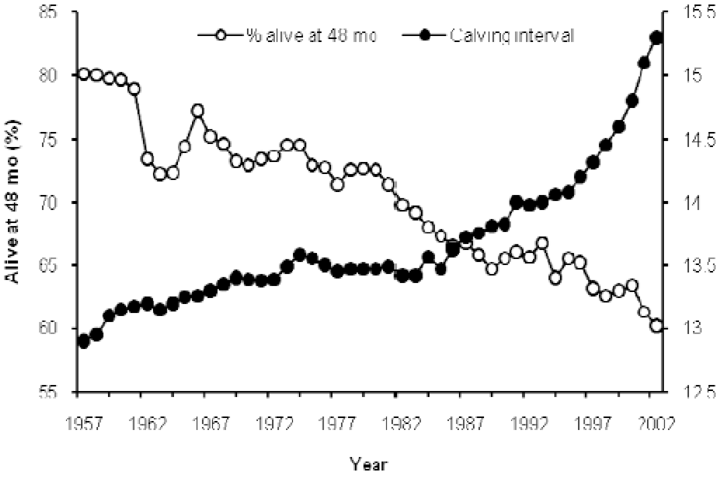
Traits included in the index aggregate fertility and their relative importance (*Biffani*, 2008)

Trait	Relative emphasis, %
Calving interval	51
Non return rate at 56d	17
Calving to 1st insemination	16
Milk yield, kg of 305d at mature equivalent	9
Body condition score	7

Moreover, improving fertility will also allow to avoid a reducing on longevity as reported by *Oltenacu and Broom* (2010). In *Figure 4* are shown the association between the declines in fertility, that reflected in increased calving interval, and decrease in longevity, measured by the proportion of cows still alive at 48 months of age (stayability) in Holstein cows in the north-eastern United States, from 1957 to 2002. Poor reproductive performance often leads to premature culling and decreased longevity of dairy cows.

Figure 4

Average calving interval and proportion of cow salive at 48 months of age over time for Holstein cows in the north-eastern United States (*Oltenacu and* Broom, 2010)



GENETIC PARAMETERS

For many years, due to low heritability values, there was a perception that genetics could not contribute to the improvements in fertility traits. Therefore, if genetics contributed indirectly to deterioration in fertility, then genetics can also contribute to its improvement.

The heritability of traditional fertility measures across different countries and breeds of cattle tend to be less than 5% (*Pryce and Veerkamp*, 2001). In *Table 2* are shown the heritability values of different fertility traits used in different countries (www.interbull.org, 2014).

Table 2

Heritabilies of fertility traits used in different countries (www.interbull.org, 2014)

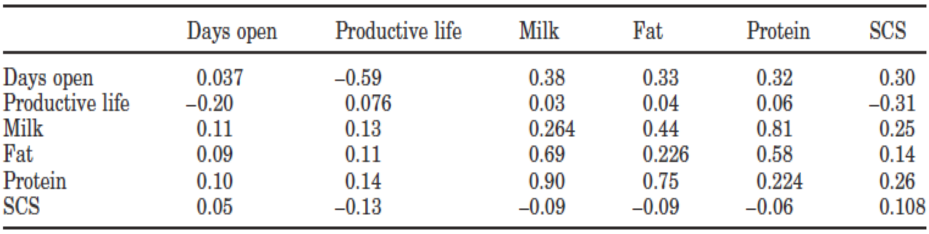
Country	Fertility trait	Heritability
USA	Pregnancy rate	0.04
Francia	Conception rate	0.02
Svizzera	Non return rate at 56d	0.01
	Calving to 1st insemination	0.04
Norvegia	Non return rate at 56d	0.01
Olanda	Non return rate at 56d	0.02
	Calving to 1st insemination	0.06
Israele	Conception rate	0.03
Irlanda	Calving interval	0.04
Finalandia	Days open	0.04
Danimarca	Non return rate at 56d	0.01
	Calving to last insemination	0.02
Germania-Austria	Non return rate at 90d	0.02
Svezia	N. of inseminations	0.03
	Calving to 1st insemination	0.04
Inghilterra	Calving interval	0.05
	N. of insemiantions for conception	0.03
	Non return rate at 56d	0.02

The implications of low heritability is that we need to collect fertility data on a large population of animals to achieve high reliability of genetic proofs, compared to higher heritability traits such as milk production. In general, as an example, with 200 daughters, a dairy bull has an expected reliability for calving interval of almost 80%; 80% reliability for milk yield is achievable, on average, with just 30 daughters for milk production.

In *Table 3*, are shown genetic and phenotypic correlations and heritabilities for yield traits, days open and productive life (*VanRaden et al.*, 2004). Yield traits had higher heritabilities than fertility traits and showed an antagonist correlation among them.

Table 3

Genetic parameters (heritabilities on diagonal, genetic correlations above diagonal, and phenotypic correlations below diagonal) for first-lactation traits and productive life of Holstein (*VanRaden et al.*, 2004)

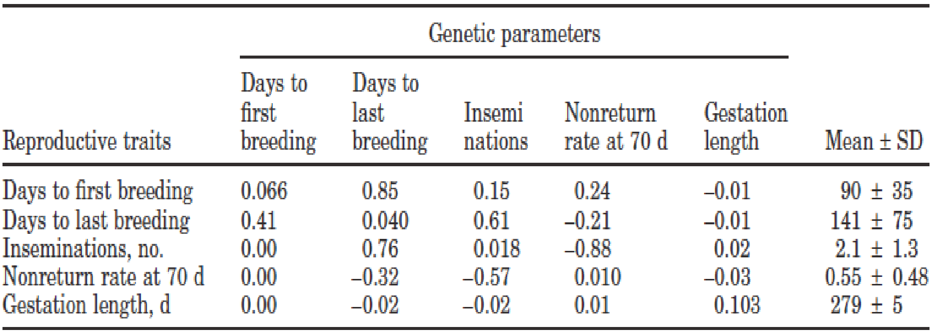


	Days open	Productive life	Milk	Fat	Protein	SCS
Days open	0.037	–0.59	0.38	0.33	0.32	0.30
Productive life	–0.20	0.076	0.03	0.04	0.06	–0.31
Milk	0.11	0.13	0.264	0.44	0.81	0.25
Fat	0.09	0.11	0.69	0.226	0.58	0.14
Protein	0.10	0.14	0.90	0.75	0.224	0.26
SCS	0.05	–0.13	–0.09	–0.09	–0.06	0.108

Correlations, means, standard deviation and heritabilities for reproductive traits of Holstein are provided in *Table 4*. These results supports days to first breeding is an important component of fertility days to last breeding were more genetically correlates with days to first breeding (0.85) than with number of inseminations (0.61) or nonreturn rate (-0.21). At the contrary, gestation length contributes very little to the variance of calving interval. Therefore, for genetic evaluation, traits as days to first and last breeding, nonreturn rate seem to be more promising for predicting the fertility genetic index.

Table 4

Genetic parameters (heritabilities on diagonal, genetic correlations above diagonal, and phenotypic correlations below diagonal), means, and SD for Holstein reproductive traits



	Genetic parameters					
Reproductive traits	Days to first breeding	Days to last breeding	Insemi nations	Nonreturn rate at 70 d	Gestation length	Mean ± SD
Days to first breeding	0.066	0.85	0.15	0.24	–0.01	90 ± 35
Days to last breeding	0.41	0.040	0.61	–0.21	–0.01	141 ± 75
Inseminations, no.	0.00	0.76	0.018	–0.88	0.02	2.1 ± 1.3
Nonreturn rate at 70 d	0.00	–0.32	–0.57	0.010	–0.03	0.55 ± 0.48
Gestation length, d	0.00	–0.02	–0.02	0.01	0.103	279 ± 5

GENETIC EVALUATION

Accurate genetic evaluations for fertility requires exploitable genetic variation to exist. More importantly routine access to accurate data on sufficient numbers of animals to generate accurate estimates of genetic merit is required. Due to the known genetic antagonism between milk yield and fertility (*Berry et al.*, 2011) some of the genetic evalutations include milk yield as a predictor of fertility. However, the new fertility traits generated and recorded in many countries, such as the number of days from calving to first service, pregnancy rates during particular periods of the breeding season and calving rates within a pre-defined period of the calving season, body condition score, as indirect measurement, were very useful to improve estimated breeding values for fertility. Due to this worldwide situation, the fertility traits is included in the overall breeding indexes in many countries and their relative weight, as percentage of total merit indexes, ranges from 0 to 18,5% (*Minery et al*., 2008; *Canavesi*, 2009). In *Table* 5, are reported the relative emphasis on fertility and traits as percentage of total merit indexes of the most important countries in Holstein Friesian that are involved in the international genetic evaluation and in the worldwide semen market. *Minery et al*. (2008) showed that in comparing with previous years, there is a general increase of weight on fertility in the recent years, associated with a decrease of emphasis on the production traits.

Table 5

Relative emphasis (%) on fertility and other production, type and functional traits as percentage of total merit index (*Minery et* al., 2008; *Canavesi*, 2009

Country	**% of Total Merit Index**						
	Yield	**Type**	**Longevity**	**Somatic Cells Count**	**Fertility**	**Calving**	**Others**
United States (TPI)	45	29	10	5	8	3	-
Germany (RZG)	45	15	20	7	10	3	-
Netherlands (NVI)	40	27	8	9	16	-	-
France (ISU)	50	12,5	12,5	12,5	12,5	-	-
Canada (LPI)	51	27,2	6,8	5	10	-	-
Italy (PFT)	49	23	8	10	10	-	-
DFS* (S-Index)	34	16	6	14	9	6	15
New Zealand (BW)	61	18	5	7	9	-	-
Great Britain (PLI)	45,2	9,7	21,1	5,5	18,5	-	-

*Denmark, Finland, Sweden

The variety of traits considered in national fertility evaluation is continuously increasing. In recent years, fertility has regularly increased in total merit indexes in all countries and this trend can be considered a positive aspect to improve the fertility performances of dairy cows; at the contrary, the risk of using similar total merit indexes among countries is to increase the inbreeding. Inbreeding results from the mating of related individuals and it is also increasing within highly selected cattle population. In US, Holstein breed has rate of inbreeding of 0.2% per year (*Thompson et al*., 2000) correpsonding to an “effective” population size (*Ne*) of 50. Low *Ne* causes inbreeding and loss of genetic variation in a population. The current *Ne* of 50 in the US Holstein is lower than required to maintain genetic diversity in a population, but the decrease in *Ne* of Holstein and other dairy breeds is a recent phenomenon so little genetic variance has been lost to date.

However, inbreeding is not currently a serious problem, but if it continues to rise it will become a real problem in the next future. Inbreeding has three major undesirable effects. It causes inbreeding depression, including an increase in the incidence of abonmalities caused by recessive alleles, loss of genetic variance an random drift in the population means. Inbreeding depression reduces the value of many traits, articularly those related to fitness, such as fertility, ability to remain healthy, and other traits indirectly affecting welfare.

CROSSBREEDING STRATEGY

As alternative strategy at selection for pure breed and, at risk of inbreeding, is the crossbreeding. The crossbreeding has gained considerable acceptance and uptake on the strength of sound scientific results. Fundamentally a successful crossbreeding strategy aims to introduce favourable genes from another breed (breeding programme) that has been selected more strongly for traits of interest, to remove the negative effects associated with inbreeding depression, and to capitalise on heterosis or hybrid vigour. Several research studies were conducted to evaluate the effect of crossbreeding strategy on fertility performances. Much of the benefit is attributed to substantial improvements in cow fertility, indicating that crossbreeding can provide a “quick fix” solution to many of the repercussions of past selection on milk production alone.

Prendiville (2009) showed large differences in fertility performance between Jersey×Holstein-Friesian crossbred cows compared with both groups of purebred cows (Holstein-Friesian and Jersey). Averaged over the first five years, the pregnancy rate to first service of the Holstein-Friesian was 47 per cent, but the Jersey×Holstein-Friesian crossbred was markedly superior at 62 per cent. The six week in-calf rate was 56 per cent for the Holstein-Friesian and 70 per cent for the Jersey×Holstein-Friesian crossbreds. The 13 week in-calf rate of 90 per cent for the Jersey×Holstein-Friesian crossbreds was eight percentage units superior to the Holstein-Friesian. The fertility performance of the purebred Jersey was no better than that of the Holstein-Friesian. This leads to the conclusion that the superior performance of the Jersey crossbred cows is largely attributable to hybrid vigour. Again, productivity was not compromised with the crossbred cows compared to the Holstein-Friesian cows.

An economic analysis conducted in 2009 (base milk price of 27 c/l, and cull and calf values reflective of that time; Prendiville, 2009) estimated superior profit (per lactation) for the Norwegian Red×Holstein-Friesian and Jersey×Holstein-Friesian cows of +€130, and +€180, respectively, compared to the pure Holstein-Friesian cows. This equates to almost €13,000 and €18,000 more profit annually in a 100 cow herd for Norwegian Red crossbreds and Jersey crossbreds, respectively.

Heterosis, or hybrid vigour, is a form of non-additive genetic variation that is not ‘passed on’ through generations. Heterosis, however, is maintained to varying degrees in advanced generations of crossbreeding. As far as a long term strategy is concerned, three options exist. These are as follows:

I. Two-way crossbreeding. This entails mating the F1 cow to a sire of one of the parent breeds used initially. In the short term, heterosis will be reduced but over time averages 66.6 per cent.

II. Three way crossing. Simply use a high estimated breeding index (EBI) sire of a third breed. When the F1 cow is mated to a sire of a third breed, hybrid vigour is maintained at close to 100 per cent. Then revert back to using high EBI Holstein-Friesian sires. With the reintroduction of sires from the same three breeds again in subsequent generations the heterosis levels out at 85.7 per cent.

III. Synthetic crossing. This involves the use of F1 or crossbred bulls. In the long term a new (synthetic) breed is produced. Heterosis in this strategy is reduced to 50 per cent initially and is reduced gradually with time.

The results presented strongly suggest that both Jersey×Holstein-Friesian and Norwegian Red×Holstein-Friesian can play a fundamental role as a part of a crossbreeding strategy to increase health and fertility without compromising production on dairy farms. For selection among breeds to be useful, an accurate across-breed genetic evaluation is vital and of large interesting in the future.

FUTURE RESEARCH IN GENETICS OF FERTILITY

Interaction of genetics and environment aspects (GxE) is an important field of the future research, as animals tend to adapt to the environment they are selected in, it is likely that selection for increased yield may also lead to environmental sensitivity. Harris and *Winkelman* (2000) and *Verkerk et al.* (2000) reported significant differences between cows of New Zealand origin and those of North American origin for conception rate, services per conception, and days to first service. These studies indicate that the negative genetic correlations between production, fertility and health in modern dairy cows, already large when producing in an intensive production enviroment, are even larger when cows are producing in a less intensive production environment. Therefore, the increase in negative genetic correlation between production and fitness traits in less favourable environments is indicative of a decline in adaptability associated with selection for increased yield in the modern dairy cows.

Another, important field of the present and future research is the genomic selection, already available in many highly selected dairy cattle populations. Simulation studies (*Veerkmap and Beerda*, 2007) have shown that genomic selection improves the accuracy of selecting juvenile animals compared with traditional breeding methods and compared with selection using information from a few genes or QTL only. Research in the areas genomics and proteomics promise to make genetic selection even more effective. The genomic and proteomics technologies combined with the bioinformatics tools that support the interpretation of gene functioning and protein expression facilitate an exciting starting point for the development of new management strategies and tools for the improvement of reproductive performance. Another promising research area is the expanding genomic selection to alternative breed sires and genotyping of crossbred cows producing in many environments. Required, however, is a very large database of animals; the larger the database the greater the improvement in accuracy from genomic selection.

Access to genomic information on individual animals can also be useful in predicting crossbred performance resulting from a given mating or identifying mates that are complementary. Calving interval is an accumulation of different individual fertility traits including the duration from calving to first ovulation, the intensity and duration of oestrus expression, the ability to conceive and maintain pregnancy to first service, and gestation length. Faster genetic gain will be achievable if selection were to be undertaken on improving all of the individual traits individually. Also, minimising the influence of management and recording errors (i.e., improved ability of individual farmers to detect oestrus, better record keeping, etc.) can also increase the heritability and therefore increase genetic gain, assuming routine access to the new traits is also available to identify the genetically elite animals.

CONCLUSIONS

Fertility in dairy cows during the last decades is globally decreasing with increasing levels of production. Future strategies to improve dairy cow fertility are needed for the benefit of the dairy industry and for cow welfare and should be based upon an integrative approach of these events.

Selection for high production reduces fertility and the reproductive traits have shown to be less heritable and more variable than production or type traits. However, fertility is partly controlled by animal genetics and this is well known and proven, hence animal fertility can be improved through genetics. The tools, as total merit indexes and selected bulls are available in many countries to identify genetically elite animals for fertility, without compromising other performance traits.

Across-breed genetic evaluations seem to be an interesting opportunity to select the genetically elite animals, irrespective of breed. Breed complementarity and heterosis, obtainable through crossbreeding, can provide an additional gain in performance, particularly in relation to fertility. An optimal breeding program should form an integral part of a strategy at individual herd and international level to increase farm profit through improving herd fertility without compromising other performance traits. An important field of the present and future research is the genomic selection, already available in many highly selected dairy cattle populations. A promising research areas are the studies on the GxE interaction and the genomic selection to alternative breed sires and genotyping of crossbred cows producing in many environments.

In conclusion, if infertility is a major cause of elimination of the cows and the very high cost, the strong selective pressure for the production of milk around the world has led to a sharp decline in reproductive efficiency in the breeding of dairy cows. However, from the genetic point of view the fertility is more variable of the type and the production, and the selection is possible, while expecting a genetic progress slow. Several countries are selecting for fertility, either by using direct measurements (eg pregnancy rate) and indirectly (eg BCS) and farmers have at their disposal bulls evaluated for these traits. New research frontiers, as the genomic selection and proteomic analyses could help the breeder, which must still continue to record all inseminations and, in general, all the reproductive events. The timely and proper recording of data in fertility leads to archives to analyze high-quality and you can have the most reliable breeding values, maximizing the genetic progress.

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