Genetics and Breeding for Fertility

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Abstract

Fertility as a fundamental trait in dairy breeding is under consideration for decades and gaining economic in recent years. As a complex trait it is difficult to be defined and recorded as well as to evaluate all contributing factors. Genetically it is influenced by male and female aspects of fertilization and conception and exhibits only low heritability. New developments in data recording and handling, advanced methodology in genetics and increasing computer power to evaluate sophisticated models resulted in new approaches in several countries. Problems connected to these efforts and strategies to overcome them are presented in a more general way via screening literature dealing with this topic. Most studies confirm that there is sufficient genetic variation in fertility for breeding purpose. It can be concluded that fertility should be accounted for in the selection index to prevent further deterioration in connection with strong selection for production traits. Nevertheless some research is left to be done to investigate carefully relationships between fertility and production, between male and female fertility, between fertility measurements in different parities and to derive appropriate economic weights which allows to optimize the overall genetic gain and to supply the breeders with the best rankings of sires and cows to achieve maximum benefit.

1. Introduction

There is no doubt that fertility is a fundamental trait from a breeders point as - in a more theoretical sense - it determines the contribution of an individual to the offspring in the next generation and thus gives the base for selection. However, fertility is not or poorly accounted for in most dairy cattle breeding programs. There are several reasons for it starting from difficulties in defining an appropriate trait which covers all aspects of fertility, problems in establishing efficient recording systems and uncertainties in modeling and evaluating it properly. In general, this reflects the fact that the whole process of reproduction is rather complex with numerous factors which have to act together to achieve a well developed zygote and finally a healthy offspring. In recent years some logistic and scientific progress concerning the critical points has been achieved and in connection with a changing economic situation of cattle breeders in the EU could lead to new assessment of functional traits in general and specifically of fertility traits relative to mainstream production traits. Additionally, fertility is second in culling statistics indicating the importance and need for improvement in practice. Despite these findings which seemingly favor a higher weight on fertility in breeding programs, three basic conditions have to be met to make sense of an inclusion of an additional trait in the selection index. First, the economic impact of the trait has to be sufficient, second, information about the trait of interest on candidates for selection or relatives thereof has to be available and third, the presence of a genetically determined variation of the trait in the population. Last not least, all possible consequences should be considered including ecological aspects or reaction of consumers which hardly can be covered in deriving economic weights. It is the intention of this paper to summarize attempts made so far to answer these important questions, to mention urgent points which should be solved and to outline some possible solutions.

2. Traits for fertility

Several aspects have to be considered in defining traits, especially if there are alternatives and if there might be different opinions what goal should be achieved. The whole reproduction complex has two consequences in dairy cattle. First and most important, offspring are produced for establishing the next breeding and producing generation (most females), animals who are not needed for breeding purposes can be used for beef production. Second, the ability for milking depends on reproduction and it is necessary to breed cows for maintenance of this ability. For decades dairy farmers were aiming for 'one calf per year' and this is true for dual purpose breeds whereas in pure dairy breeds it might be reasonable to prolong the calving interval due to difficulties in getting cows pregnant just at high level production and dry them despite high test-day results. Nevertheless there is no doubt that breeders want to have a healthy calf with minimum expenses in money and time. Another point is that there should be a easy and efficient way to record the trait and that information is available before selection. Furthermore fertility is based on both sexes which influence the process in different ways so that some compromise is necessary in finding a trait which is suited for male, e.g. capability of fertilization, and female, e.g. conception.

In all, there are three major possibilities how fertility can be measured. One would be to evaluate physiological characters like sperm quality in bulls and/or hormone levels of LH, FSH or progesterone in heifers or cows. Sperm quality is a matter of AI-stations and distributed semen is directly influenced via standardization, which has to be accounted for when analyzing paternal fertility. Hormone levels are expensive to be recorded so far and can hardly be seen as a practical trait but might get some impact as management tools if technology is improving. Besides this there is no way to cover male and female fertility together so that up to now little use is made of such measurements in a population-wide evaluation of fertility.

Another group of fertility traits is related to various time periods with the underlying assumption that farmers want to get their cows pregnant as soon as possible after calving. Commonly used are calving intervals (CI), intervals from calving to first (CFI) or last (CFL, days open) insemination, intervals between first and last insemination (service period) and intervals between successive inseminations. The variety shows that their is no unique interval measurement that is clearly preferable. The calving interval which might be considered as the most straightforward on what farmers aim at has some major drawbacks (Hansen, 1979): first, there are two calvings necessary to get the information, which is to late in comparison to milk traits, and second there are no records available for heifers or first infertile cows with the consequence of possible bias through selection. Interval traits related to last insemination implicitly assume that the cow has finally conceived and are exposed to biases through culling and bulls for natural service. CFI on the other side can be recorded comparatively easy and is early available but heavily influenced by the breeders and at least in high producing breeds it can be doubted that short CFI are desirable. The advantage of these characters is that they are continuously distributed and directly connected to the economic goal.

A third category of fertility traits might be denoted as 'success' traits. The most important among them are non-return-rates (NR) where it is checked whether a cow/heifer returns after the first insemination within a given period which alters from 30 to 130 days with emphasis on NR56 and NR90, number of inseminations per service period / conception / calving and conception rate after first calving. Their advantage is that they are available quite early and are related to efforts made to get a cow pregnant. On the other hand they are at least categorical traits and therefore require a more sophisticated analysis from the theoretical point of view . Further problems are the uncertainty whether a cow got really pregnant (culling, natural service bull, later insemination) and how to deal routinely double inseminations for management reasons. The traits based on numbers of inseminations per successful parity are critical as successive inseminations can hardly be considered as independent observations, breeders may choose 'fertile' sires for the second and latter inseminations and eventually sires for natural insemination are used. The problems are often connected with the payment system, where second and third inseminations are free and correct management decisions of breeders may cause serious difficulties for genetic evaluation.

In general it can be stated, that most researchers in literature prefer the one or another success trait although their heritabilities are comparatively low. An efficient system for matching AI-information with milk recording data is precondition for such trait definitions and must be improved continuously. New methods of pregnancy testing via ultrasound or hormonal tests should substantially improve the quality of data.

3. Relationships among fertility traits

Heritabilities of fertility traits are generally low which is mainly due to the complexity of the trait as mentioned above starting from defining to recording the trait and analyzing it in a proper way accounting for all factors. Numerous of estimates are published ranging from zero to at most 0.05 for NR, conception rates or numbers of inseminations. Somewhat higher estimates in the range from 0.05 to 0.15 can be found for interval measurements throughout the literature. It is not unexpected that differences between breeds are reported but due to the high standard errors no clear tendency can be stated. Heritabilities vary slightly over parities with some indication, that higher parities show higher estimates (Jansen, 1986; Jansen et al., 1987; Van Arendonk et al., 1989; Weller, 1989; Marti and Funk, 1994) with exception of heifer fertility which had higher values. However, in cases were female and male fertility is compared it seems that female heritability is larger (Jansen, 1986).

Intense investigations of genetic relationships between fertility measurements were conducted by Janson (1980) and Janson and Andreasson (1981). NR after 28/56/168 days matched quite well (r_g from .66 to .93) but NR28 and number of insemination per service period was only correlated with 0.6. NR-measures and CFI were even worse or practically uncorrelated, once more indicating problems connected with CFI. This was confirmed by small correlations between CFI and CLI and actually a value of zero for CFI and FLI. Correlations for heifers (only success traits) were in the same direction but in most cases somewhat more strength. Hoeckstra et al. (1994) recently conducted a similar study in Dutch Black and White and found analogous results. Dependencies between male (direct) and female (maternal) fertility are not yet investigated intensely. Jansen (1986) found strong varying relationships for different parities, reaching from -0.9 for heifers to 0.2 in parity 3. Hansen (1979) concluded negative correlations when investigating NR56 of bulls with CI of their daughters. Considering the different preconditions of bull and cows fertility and lack of hard evidence it can be concluded that no or a small negative correlation might exist and should be taken in analysis where both effects are included.

A major concern of evaluating fertility traits is whether different parities can be considered as the same trait. Differences in heritabilities indicate a varying amount of genetic determination of the trait but need not necessarily conclude on different traits. Genetic correlations estimated by Jansen et al. (1987) tend to the conclusion that cow fertility is the same trait regardless of parity but that heifer and cow fertility might be genetically determined in different ways which is in agreement with physiological findings.

4. Relationships to other traits

The relation of fertility and production traits is a major concern in dairy cattle breeding. Although there is some indication that there are negative relationships as stated by Jansen (1985) when comparing conception rates and culling reasons of Holsteins with Black and White which originated from the same base population the results are ambiguous with prevailing antagonistic relations. It seems that relationships depend on several factors, whereof the trait definition is one of the most important. Especially traits based on intervals from calving to time of insemination, e.g. first insemination (CFI) show unfavorable correlations to production traits of 0.3 to 0.5 throughout the literature (Everett et al., 1966; Hansen, 1978; Berger et al., 1980; Weller, 1989). Relationships of fertility traits like conception rate, NRR or number of inseminations are neither clear, several studies found correlations around zero (Hansen et al., 1979; Rothchild et al., 1979; Raheja et al., 1989; Moore et al.,1990;) whereas others stated a negative relation (Gaillard et al., 1974; Oltenacu et al., 1991; Weller and Eszra, 1997). These conflicting results indicate that investigators should be very cautious in designing and analyzing experiments. It can be questioned whether interval measures are best suited for such analyses as there are non genetic effects like later insemination or more chances on high producing cows compared to herdmates which force a unfavorable relation. Such management tools might be justified from a breeders point of view but demonstrate once more that interval traits have disadvantages in practical application. A final answer to the question of genetic antagonism between production and fertility traits can hardly be thought without a deeper knowledge on physiology, e.g. the hormonal interplay during lactation and reproduction (Gorski, 1979).

5. Further genetic aspects

Assumptions of linear methodology are not fulfilled in a strict sense when analyzing 'success' traits like NR after first insemination with its possible outcome 0 and 1. To overcome these problems the threshold concept with an underlying variable was introduced quite early by Wright (1934) and extended by Falconer (1965). Gianola (1982) and Gianola and Foulley (1983) developed a threshold model for sire evaluation of categorical data with some analogy to MME. Although linear models are theoretically not justified, several investigations on field data (Weller et al., 1988; Hagger and Hofer, 1989) as well as simulation studies (Meijering and Gianola, 1985) showed that there is only very little difference in using linear versus threshold methodology. Hoeschele (1989) carried out intensive simulation studies for all-or-none traits, which resulted in a nominal superiority of the threshold concept only for extreme categories and high heritabilities. This was confirmed by Weller and Ron (1992), who found correlation greater .99 for random effect solutions between a linear and a threshold model when analyzing the conception rate in Israeli Holsteins. Nevertheless, there remains an open field for animal geneticists to introduce the threshold concept in animal models, especially when two animals and their relationships have to be accounted for.

Fitness traits like fertility exhibit in general only a small additive genetic variance but might have some genetic variation due to dominance and epistatic effects. Falconer (1989) cites several examples in experimental animals and heterosis effects are already used in animal breeding when improving fertility traits like e.g. crosses of laying hens for numbers of eggs and hybrid programs to increase litter size in swine. Although it is known that cross bred in dairy and beef cattle are superior in reproduction systematic investigations are scarce. Hoeschele (1991) analyzed HF in the US and found considerable dominance variance components at least as large as the additive one and some indication for a substantial additive x additive component. Accordingly, there was a negative effect of inbreeding on fertility with prolongation of interval measurements of about three days for 25% inbred animals. Fürst and Sölkner (1994) also estimated a dominance component for CI as large as the additive variance and even a higher impact of additive x additive interactions. Increases of 2.3 and 0.7 in days open per 1% inbreeding were estimated by Hermas et al. (1987) and Beckett et al. (1979), respectively. Some more studies are necessary to get a clear insight how genes play together to come up with strategies to use non-additive effects. Advances in biotechnology and molecular genetics might allow breeding designs which are not possible up to now.

6. Non-genetic factors - environmental effects

To get unbiased estimates in genetic evaluation it is a precondition that all genetic and systematic (non genetic) effects influencing the outcome are accounted for. However, it is often quite difficult first to explore all factors and second to record them correctly. Moreover, they have to be defined in a way that they also allow statistically satisfying comparisons of the effects which are aimed at. It is therefore a demanding task to find a compromise which meets all requirements This effort is also closely connected to the structure of the data and the trait definition. Nearly all models for fertility found in literature include herd, year and season effects. There are numerous investigations which indicate advantages of a more specific time factor, e.g. month, on the one hand but there is also evidence for interactions between these factors. Depending on herd sizes several compromises were applied in differnt countries, ranging from h*y*s interactions to h*y or y*s interactions with the remaining factor as cross classification. As long as different parities are considered as the same trait this factor has to be included as well, in general a decreasing fertility in higher parities can be observed. In case that these measurements are not taken as traits, time intervals from calving to first insemination for cows or age at calving for heifers have to be corrected for, these are mostly modeled in different age classes, clearly showing an improvement in fertility with increasing time but also indicating problems for extreme duration. The impact of technicians and AI-studs is included in various investigations (Janson et al., 1980; Jansen et al., 1985; Hansen, 1979) but requires intense and careful recording and is often closely confounded with herd effects. In cases of crossbreeding were heterosis might be expected or only female fertility is evaluated a correction for grading or mated sire groups are included in the model.

7. Possibilities for breeding

Considering most of the research done on this field there is little doubt that fertility is deteriorating due to emphasis put on production traits for the last few decades. This might even be disguised by veterinarian and management means which are routinely applied nowadays. It can be questioned whether it is possible or useful to improve male fertility as sperm quality of each ejaculate is separately judged and can be manipulated to a great extent (Hansen 1979). However, it is well known that several bulls fail completely at AI-studs on the one hand and that on the other hand there is no evidence for a close relationship between sperm quality and practical fertility traits. Thus it looks reasonable to cull less fertile bulls (bad sperm donation performance) and include their breeding values for fertility into the selection index. Although small genetic changes will improve fertility only on a long term immediate effects on bull selection are to be expected (Syrstad, 1981). Significant differences in sire strains evaluated by Weller (1989) could also be utilized for improvement on the short term.

Nevertheless there is some agreement across scientists working on this field that female fertility should be focussed at. The negative correlation to production traits requires an inclusion of fertility into selection indices to prevent further deterioration especially in very high producing herds (Hodel et al., 1995). Reliable estimates for breeding values for female fertility of bulls could be achieved if number of progeny testing is increased, e.g. accuracies of 0.8 are to be expected for progeny groups of 200. Consequent use of animal model evaluation considering male and female fertility simultaneously results in breeding values for cows with accuracies up to 0.35 which at least on average allows substantial genetic gain, e.g. when selecting cows or bull dams purely based on fertility (Averdunk, 1994). Philipsson (1981) also stated that culling of cows because of poor fertility alone is no guarantee for improvement. Antagonistic relationship to milk with an expected decrease of 3% per generation however cannot be accepted on the long run. As cuts in genetic gain on production traits might be refused by breeders it should be evaluated what increase in testing capacity is necessary to maintain production gain without deteriorating fertility.

8. Conclusions - future prospects

There is no doubt that fertility should be improved. Critics due to incorporation of fertility into breeding goals should be replied that we do not only need fertile animals but animals at all to have a base for selection. Of course, a correct weight should be put on reproduction and other functional traits and effects on production which look to be antagonistic should be considered seriously. In this sense, Philipsson et al. (1994) clearly demonstrated the superiority of index selection including non production traits. The question of the correct weight might be most difficult due to unknown economic situations at the time when today’s breeding decisions get relevant. There is sufficient genetic variation for breeding purpose but all possibilities should be used to exploit it optimally. New aspects in trait definition and recording, possibilities to store, combine and handle huge amounts of data and developments in methodology will allow more efficient ways to improve fertility and should be applied consequently. In progeny testing larger progeny groups are desirable and it is to check what costs are involved to increase group size to an extent that selection on fertility is possible without loosing in production traits. Advances in QTL-detection and application of pre-selection on test bulls might be one future objective to achieve this. It should be clearly stated that some efforts have to be undertaken to change the current situation which requires collaboration of farmers, AI-studs, research institutes and breeding industry.

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