Genetic evaluation of male and female fertility

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ABSTRACT

Fertility is under consideration for decades and gaining economic importance in dairy breeding in recent years. As a complex trait it is difficult to define and to record as well as to evaluate all contributing factors. Genetically it is influenced by male and female effects of reproduction and exhibits only low heritability. New opportunities 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 possible solutions are presented in general and in more detail for the evaluation for fertility (NR90) as introduced in Germany. Results confirm that there is sufficient genetic variation for breeding purpose. It is concluded that fertility should be accounted for in the selection index according to ist economic weight to prevent further deteroriation in connection with selection for production traits. Future aspects and their possible consequences are discussed.

INTRODUCTION

There is no doubt that fertility is a fundamental trait as - in a more theoretical sense - it determines the contribution of an individual to the offspring in the next generation. In contrast to multiparious species, it is however not possible or at least not useful to measure fertility in cattle by litter size or number of offspring during lifetime and there is need for an appropiate definition. Furthermore, the whole process of reproduction is quite complex with numerous factors which have to act together to achieve a well developed zygote and finally a healthy offspring. From the genetic point of view, fertility can be looked at as a combined trait involving both male and female components of reproduction and in a very strict manner the embryo itself as well. As a low hertiable trait, little emphasis was set on fertility at all and research was then mainly focussed on male fertility. Changes in the economic situation of cattle breeders with quotas and already high levels on milk production as well as new developements in methodology which allowed more sophisticated models raised the interest in functional traits in the past few years. In culling statistics of most countries fertility is second behind low production indicating the need for improvement and a recent survey (Philipsson et al., 1994) clearly demonstrated the superiority of index selection including non production traits. In this paper we try to point out the difficulties in defining and analyzing reproduction traits more generally and introduce in some detail the actual genetic evaluation of male and female fertility in Germany.

MATERIAL AND METHODS

Fertility - trait definition

To approach the problems associated with fertility, it is worth to consider some aspects which led to the dequalifying expression 'secondary trait' used along with traits for health and calving ease. First, the economic importance is not obvious and farmers tend to prefer such traits where a revenue can be seen immediately, e.g. milk production. From a breeders point of view fertility is also self-selected with some respect and if necessary controlable by veterinarian means. Secondly, there exists no unique definition which would allow a commonly accepted selection strategy and recording schemes are often not available or not well established with respect to demands for analyzing the data. Thirdly, the heritability is low and fertility is more difficult to model so that also geneticists concentrated primiarily on production traits. Nearly all these aspects are anyhow conntected with the basic question of how to define fertility, especially for breeding purpose. As mentioned above fertility is a combined trait with male and female aspects and several 'subtraits' for both sexes. Male reproduction ability is characterized through semen quality such as sperm density, volume, foreward moving and anatomical factors, whereas female fertility is based on rate of uterus involution, onset of cyclicity after birth, sign of estrus among others. These subtraits interact in a very special way and result in a vital embryo in case of success. Therefore it seems quite logical to base the measurement of fertility on this positive event. Nevertheless there are several possibilities which can be used and should be discussed with respect to their possible application. As long as only male fertility was considered the number of inseminations per sucessful parity (insemination index) or the nonreturn rate was used. These were applied for the female fertility as well and in addition interval measures like calving interval, interval from calving to first AI or days open were introduced. The advantage of 'interval traits' is that they aim directly to the economic merit which is derived as additional costs per day of increase in calving interval in most cases. In Germany a economic weight of this trait of approximately 2 to 3 DM per day was calculated. On the other hand there are effects like interval from calving to first insemination which are influenced by the breeder, it is difficult to account for the number of inseminations, the trait is not defined for heifers and the information is available quite late especially for selection of test bulls. The numbers of inseminations per successful parity (insemination index) is critical as well 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. As a consequence, the nonreturn rate based on day 90 (NR90) was chosen as fertility trait in Germany. This choice also allowed some continuity in the evaluation as NR56 was the trait for male and NR90 for female fertility up to now. To avoid dependencies of successive inseminations, only the first insemination was used as an observation. Double inseminations within the first two days, often routinely applied by the breeders, were not judged as return events. Although none of the traits is perfect, we judged the NR90 as an appropriate measure to model male and female genetic effects.

Methods

In contrast to continuous traits, the NR90 with its outcome 0 and 1 belongs to the categorial traits and the assumptions analyzing these by linear methodology are not fulfilled. 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 categorial 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. MISZTAL et al. (1989) pointed out that a threshold model requests a factor of three up to five of CPU-time in comparison to a linear model. Because of the low heritability and moderate frequencies of NR90 it was decided to choose the linear approach for the genetic evaluation of fertility in Germany. Additional runtime costs for routine evaluation were also considered to be to high compared to the expected additional benefit up to now. 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.

Models and genetic parameters

Models for genetic evaluation of any trait should account for all genetic and systematic (non genetic) effects influencing the outcome. However, it is often quite difficult first to explore all factors and second to record them correctly. Moreover, they have to be definded 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. In Germany, for example, the herd size is moderate and there are good reasons to account for herd effects as close as possible. So it was decided to consider the fertility of heifers and cows with second and later parities as the same trait to achieve large enough subcells. On the other hand it might make sense in countries with a better a herd structure to establish a multitrait model. The most important non genetic effects are herd (82%), lactation number (8%), interval from calving to first insemination (3%), technician (2%), age at first insemination (2%), month (2%) and year (1%). The figures in brackets estimated by Distl and Kräusslich (1986) show the proportion of the whole non genetic variance explained by the factors and are in accordance to most investigations found in literature. In evaluation models, where male and female fertility are incorporated jointly, two genetic effects, the sire representing the paternal and the dam for the maternal genetic effect have to be included, respectively. Numerous estimates for heritabilities of male and female fertility can be found in literature (see Weller and Ron, 1994) indicating low values in the range from 0.01 to 0.05 and it was decided to take 0.02. The genetic correlation between male and female fertility is not quite clear and literature estimates vary from slightly positive to slightly negative correlations. Preliminary analyses (REML) of our own material with the appropriate evaluation model resulted in an average correlation of -0.2 with a high variability among the subdatasets. As a compromise, a negative correlation of -0.1 between the paternal and the maternal effects was assumed in the genetic evaluations so far. Since consecutive service periods of a cow were taken as repeated measures, a permanent cow effect was added to the model with an assumed variance equal to .15 of the phenotypic variance. Finally, the following model was chosen for the evaluation of fertility:

$$y_f = h*y + s + l + a + r + a_p + a_m + u_p + e$$

where y_f is the return event (0 or 1), **h*y** the herd*year, s the season, **l** the number of the following lactation (8 and greater were set to 8), **a** the age of heifers at first insemination, **r** the time interval from calving to first insemination (cows), $\mathbf{a_p}$ the paternal genetic effect of the sire, $\mathbf{a_m}$ the maternal genetic effect of the cow and $\mathbf{u_p}$ the permanent environmental effect of the cow.

Instead of the usual herdclass*year*season comparisons used in dairy trait evaluation in Germany herd*year classes were introduced to correct for the herd effect as close as possible. The reasons were that special management means of breeders (estrus observation, double insemination, prophylactic medical treatment) differ very strongly among herds and would influence such sensitive traits enormously, whereas a meaningful criterion for the assignement to herdclasses is difficult to define. Additionally, as the inseminator is closely confounded with the herd it is possible to neglect it as an separate effect which anyhow would be difficult to define due to the registration practice in Germany.

Data

Starting in 1985 all inseminations of a cow within a service period were recorded electronically by AI stations in Bavaria. Based on the first insemination it was checked wether a following insemination was recorded within the next 90 days and in case of a return the trait (NR90) was set to 0 else to 1. Double inseminations within the first two days were not regarded as a return event. This resulted in some 7 million observations which were combined with data for milk evaluation and double checked with respect to pedigree information as well as birth and calving dates. Heifers with an age at first insemination less than 13 or more than 26 month were excluded and comparable limits were set for ages of first inseminations within parities. Additionally, data were not accepted if the interval from calving to first inseminations was below 25 or over 200 days. Cows involved in embryo transfers were neglected as well. After editing some 6.5 million observations from 2.7 million cows in 309.000 herd*year classes remained for evaluation. The overall NR90 in German Fleckvieh was 61.7%.

Computations

Mixed model methodology was applied to solve the equation system resulting from the model described above. The numerator relationship matrix among all animals allowed the evaluation of paternal effects for cows and maternal effects for sires as well as to account for the genetic correlation between these two effects. Some 3.7 mio. animals and 2.7 permanent effects in combination with the fixed factors resulted in an equation system of dimension 10.3 million.

Solutions were calculated by iterating on the data without explicitly forming the mixed model equations as suggested by SCHAEFFER and KENNEDY (1986) and MISZTAL and GIANOLA (1987) using second order Jacobi. This strategy was the best fit to the available computer resources with a maximum of 210 MB CPU-storage. High efficency of input/output was reached by reading binary files into buffers. Time requirements for the solution were roughly 15 min CPU per iteration (55% I/O) on an IBM 3090 mainframe. Convergence was reached after about 90 iterations.

RESULTS

Fixed effects

As several fixed effects were included in the model restrictions were necessary which was achieved by setting average effects to zero. The influence of the month of insemination on NR90 is positive in summer with 2% above average and negative in winter. The number of parity showed a strong impact on NR90 with an estimate of 14% above average for heifers, a value of about zero for the second service period and nearly linear decreasing effects of the latter parities up to -6% for cows with 8 and more service periods. An increase of the NR90 was found for age of insemination from 12 to 20 month with a constant effect of this factor up to 26 month. Apart from herd*year effects the strongest influence is exhibited by the time interval from calving to first insemination. Starting from -20% for a period of 25 days there is a rapid increase to -3% at an interval length of 50 days and further a moderate increase to +10% with 200 days.

Genetic effects

The standard deviations of the estimated breeding values for the paternal (maternal) effects were 0.04 (0.05) for sire and 0.02 (0.03) for cows, respectively. The distribution of the breeding values followed closely a normal distribution however with some asymmetry at the lower tail indicating a comparatively high proportion of animals with breeding values in the range of -.10 to -.20. These results are in accordance with most studies on this field and clearly demonstrate that there is some variation available to improve fertility genetically. Genetic trends were estimated averaging the breeding values of the cow population per year. In German Fleckvieh it seems not justified to interprete the figures found as a positive or negative trend for either male or female fertility, whereas in Braunvieh a slightly but steadily deterioration of .25% per year is obvious in maternal breeding values for NR90. Correlations between the breeding values of the aniamal model and the former sire model, which was applied within each AI-center separately since 1986, were 92% for the paternal and not more than 70% for the maternal effects, respectively. The first figure is quite similar to the correlation of breeeding values between the animal and sire models in dairy traits. The relatively low correlation for the maternal breeding values is not unexpected due to the changes in trait definition (no consecutive insemination within service period), fixed effects (no herdclass) and methodology.

DISCUSSION

It is surely beyond our scope to present an optimal solution for such a complex trait which is discussed and worked at for decades. Nonetheless, new aspects in trait definition and recording, possibilities to store and handle huge amounts of data and developements in methodology allow new approaches to improve fertility. It was pointed out that all of these aspects interact with each other, unfortunately sometimes in an antagonistic way at least in application, e.g. sophisticated methodology with genetic models and amount of data. Definitions of interval measurements are strongly influenced by breeders and not available in case of heifers or failure of conception. The nonreturn rate is therefore of some advantage especially when analyzing male and female fertility jointly and used in most countries. Considering successive inseminations within a service period as repeated observations is critical as these are not independent, well performing animals do have less observations in average and treatments in later inseminations may differ among cows according to their dairy traits. The question whether NR is the same trait in heifers and cows is not clearly answered and contrary opinions can be found in literature. Starting or resuming the female reproduction may be influenced by different genes and more research is necessary to estimate genetic correlations and eventually evaluate possible benefits of a multitrait model. Some effort should be made to improve the quality of data, possibly by routinely conducted pregnancy tests or by registering the culling reasons carefully and including them in the recording system. Data recording in huge test herds might be of advantage with this respect but it can be doubted whether the results are valid for the average managed herd. Test herds might however be useful to record subtraits and genetic markers which might be genetically determined by major genes such as cystic ovaries, gonadal hypoplasia or chromosome abberations (see Philipsson, 1981). The decision for linear or threshold models will greatly depend on whether it is possible to evaluate large amount of data with models accounting for all genetic and systematic factors by the theoretically justified methodology even in routine work. That will also depend on breeding organizations, e.g. which expenses they are willing to pay for the evaluation of fertility which is furtheron connected to the weight of this trait in the total merit index. Some research is necessary to get the appropriate economic weight but there is no doubt that fertility should be included in the breeding goal as there is sufficient genetic variation to improve both male and female reproduction.

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