GENETIC EVALUATION OF FEMALE REPRODUCTIVE PERFORMANCE

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INTRODUCTION

Fertility or reproductive performance is one of the most important components of production efficiency and genetic gain in beef production systems. It has been reported to be at least twice as important, economically, as production traits under a conventional cow-calf operation (Melton, 1995). A delay in conception due to poor fertility prolongs the calving interval, and causes a shift in calving pattern, which can lead to culling. However, reproductive traits in cattle are difficult to measure, report and interpret. This is particularly true for pasture mating situations, where information on females in extremely limited. In these situations, the only information readily available is whether or not a cow produces a calf, and when she calves.

Breeding value estimation for reproductive traits is difficult, in part because the expression of reproductive potential is often constrained by the management system. Reproductive data is of a complex nature, and is the culmination of many events that occur throughout the breeding season. Evaluation of genetic merit for reproduction requires information on the complete reproductive history of each animal, which is often unavailable. Thus, while genetic values for growth and carcass traits are reported in national genetic evaluations for most breeds, very few breeds report genetic values for fertility. In the past, correlated traits (such as scrotal circumference) have been used to indirectly select for female fertility. Currently, genetic values for three measures of female fertility are being reported in national genetic evaluations; days to calving, stayability and heifer pregnancy. The purpose of this paper is to review the suitability of these traits as measures of female reproductive performance, and to suggest improvements or modifications that could enhance the evaluation of fertility in national genetic evaluations.

REVIEW OF LITERATURE

Calving date/Days to calving

Calving interval has been used as the preferred measure of reproduction in dairy cattle. However, because a fixed breeding season is generally used in beef herds, calving interval has limited value as a selection criterion. Calving dates are generally available in field data, and their use requires minimal modification of existing performance programs. It is defined as the day of the year on which the cow calves, and allows comparison between cows when breeding is of the same duration, and starts on the same date. In early studies, calving date was found to be preferable to the alternative measure of calving interval. Later studies, which included the records of open cows in analyses, found calving date to be heritable, as well as having a clear economic interpretation.

In an early study, Bourdon and Brinks (1983) demonstrated the superiority of calving date over calving interval. In their study, calving interval was more susceptible to the bias caused by the use of a fixed breeding season, due to its strong dependence on previous calving date. In general, cows that calve early in the season will experience an ample postpartum period before the breeding season. As a rule, they will rebreed early, but are unable to register a subsequent calving interval of less than 365 days (Bourdon and Brinks, 1983). Cows that calve later in the season, however, have a shorter period between calving and breeding, and, therefore, the opportunity to record a shorter calving interval. In their study, calving interval decreased 0.86 days and calving date was delayed 0.11 days for each 1-day delay in previous calving date. The authors also noted that an additional advantage of calving date was its clearly identifiable economic value; calves born earlier in the calving season weigh more at weaning; while the economic interpretation of calving interval is difficult.

Numerous studies have addressed the issue of which parity should be used to measure calving date. Meacham and Notter (1987) used a sire model to estimate genetic parameters for calving date, calving interval and percent return using first and second calving records. All traits had a highly significant relationship with calving ease score recorded at first calving. Heritability estimates pooled across herds for calving interval, first and second calving dates and percent return were 0.04, 0.17, 0.07 and 0.11, respectively, and the estimated genetic correlation between first and second calving dates was 0.66. The authors noted that the lower heritability estimate for second calving date might reflect culling of open cows before the second calving, or real changes in the magnitude of genetic and environmental variation. The authors concluded that useful levels of genetic variation existed for first calving date, and that this trait could be used in sire selection as a measure of daughter's reproductive ability.

In order to make the best use of the data available for reproductive performance, information for open cows must be included in the evaluation. Notter (1988) noted that if data on open cows is ignored, the most genetically inferior, and possibly most informative, animals are ignored. Therefore, if sires differ markedly in the frequency of open daughters, consideration of open cows may be required to accurately estimate true sire difference in daughter's fertility.

Notter and Johnson (1988) obtained genetic parameter estimates for calving date with records for open cows included in the analysis using simulated data. They proposed a procedure using threshold theory to calculate penalties for open cows. Observed calving dates (CD) for cows that calved were transformed as $W = \ln(CD+1)$ to normalize the data, and calving dates for open cows were projected by considering cows that didn't calve to represent the upper tail of a truncated normal distribution of the transformed calving date. The authors found no carryover effects of prior calving date in cows calving within the first 21 days of the breeding season, but for cows calving after day 21, each 1-day increase in calving date was associated with an increase of 0.69

days in the next calving date. Adjustment for previous calving performance in this study reduced repeatability estimates of calving date from 0.26 to 0.24, while heritability estimates remained constant at 0.125, and the correlation between actual and adjusted calving date was 0.95. The authors suggested these results indicate that even though significant transient environmental effects existed between adjacent calving dates, adjustment for these effects didn’t greatly affect overall rankings of females. Correlations between mean calving date and ability to conceive were found to be consistently higher for actual calving date than for the transformed data. The authors also found that selection against late calving was more effective than selection for early calving in identifying cows with genetic potential to conceive. The authors concluded that under pasture mating, unbiased estimates of ability to conceive cannot be obtained, but selection based on observed calving date yielded acceptable estimates, provided that open cows were included in the evaluation.

Buddenberg et al. (1990) compared estimates of variance components obtained from excluding and including records of open cows. Open cows were assigned a value based on the projected mean calving date of the open cows in an unrestricted breeding season, as described by Notter and Johnson (1988). Data were transformed as outlined by Notter and Johnson (1988), and the projected mean calving date for open cows was then obtained separately for each year based on the actual data and percentages of open cows for that year. Heritability estimates were obtained as paternal half-sib correlations. In general, the proportion of variance due to service sire and sire of dam increased when open cows were included in the analysis. Heritability estimates (open records excluded) for first-calf, second-calf and mature animals were 0.20, 0.04 and 0.03, respectively. The corresponding estimates for open records included were 0.39, 0.13 and 0.00, respectively, and confirmed that estimates from data excluding open cows are biased downward. The authors suggested that the lower heritability estimates for older animals was most likely the result of culling open cows each year. Service sire was the largest source of variation in calving date in both data sets, and sire of dam accounted for only a small portion (<10%) of variation. As a result of culling open cows, variation associated with service sire and sires of dams generally decreased with age. The authors concluded that attention should be given to selection against late calving date of first-calf heifers, and that the advantages of this selection would be lower birth weights, less dystocia and more recovery time between calving and breeding.

Days to calving has been investigated by researchers in Australia, and gives the same information as calving date when the cows to be compared went into breeding on the same day. Meyer et al. (1990) compared calving rate, number of calves, calving success and days to calving as measures of reproductive performance in Australian beef cattle. Calving rate was defined as the number of calves a cow produced divided by the number of opportunities to do so; calving success was scored as 0 (non-calver) and 1(calver); and days to calving was calculated as the difference in days between the beginning of the breeding season and calving date, for each breeding season. Cows not calving were assigned a predicted value, derived from threshold theory, as suggested by Notter and Johnson (1988). Days to calving was analyzed both as observed, and transformed to logarithmic values, while calving success was analyzed without adjustment for the categorical nature of the trait. Heritability estimates for calving rate for Zebu crosses, Herefords and Angus were 0.17, 0.07 and 0.02, respectively. Heritability estimates for days to calving for Zebu crosses, Herefords and Angus were 0.09, 0.05 and 0.08, respectively. Transformation to log scale had practically no effect on estimates or on the predicted difference between calvers and non-calvers. Heritability estimates for calving success for Zebu crosses, Herefords and Angus were 0.08, 0.08 and 0.02, respectively. The authors concluded that days to calving appeared the most suitable trait for incorporation into genetic evaluation, as it is readily measurable under pasture conditions, and allows information on all cows to be included in the analysis. As well, the authors noted that the expected deviation of the distribution from normality for this trait would be considerably less than for other traits considered, which would allow the application of standard methods of genetic evaluation for analyses.

Johnston and Bunter (1996) demonstrated that days to calving, as defined by Meyer et al. (1990), was also a suitable measure of reproductive performance in a large field data set. Cows with open records were assigned a projected value on a within breeding management group basis. The highest days to calving record within each breeding management group was identified, and a constant number of days (21 days) were added to this record to generate the projected value for all non-calvers. The procedure proposed by Notter and Johnson (1988) to create penalty records was also considered. However, the procedure was deemed unsuitable because some of the predicted days to calving records for non-calvers were less than actual days to calving records. Calving success, scored as 0 (non-calvers) and 1 (calvers), was included in a bivariate analysis with days to calving, and was analyzed without any adjustment for the categorical nature of the trait. The genetic correlation estimate between the traits was –0.97, and the authors concluded that selecting for days to calving would be the same as selecting for calving success, with the added benefit of being able to distinguish between early and late calvers. Heritability estimates for days to calving in the first and second parities were 0.10 and 0.11, respectively, while repeatability and heritability estimates of 0.25 and 0.12 were obtained for a repeatability model. The genetic correlation between days to calving in the first and second parities was 0.85, supporting the use of a repeatability model. Genetic correlations between days to calving in the first parity and growth traits were generally unfavorable but not significantly different from zero, and thus the authors concluded that direct selection on reduced days to calving would be required to improve the trait.

Once a trait has been deemed suitable for incorporation into national genetic evaluations, the nature of the relationship between the trait and other traits is of primary interest. Meyer et al. (1991) used a subset of the data used by Meyer et al. (1990) to investigate covariances between days to calving, growth traits and male fertility traits. A weak but consistently favorable association (-0.30) was found between scrotal circumference and days to calving, while serving capacity and days to calving were found to be unrelated in this study. There seemed to be little favorable genetic association between growth and female fertility in the temperate breeds. Estimates of the genetic correlations were larger in Zebu crosses for yearling (-0.36) and weaning weight (-0.66). The authors failed to find any unfavorable genetic correlations between growth and days to calving, and concluded that joint selection for fertility and growth should improve genetic potential in both.

Rege and Famula (1993) studied factors affecting calving date in USA field data. They found that animals which as heifers calved in the first 21 days of the calving season had lower average subsequent calving dates, and gave birth to calves which were weaned earlier and had significantly heavier yearling weights than those that calved after the 42nd day of the season. Also, animals that calved late as heifers proceeded to calve later than initial early calvers in subsequent parities. Repeatability of calving date was estimated at 0.23, and heritability at 0.16. Genetic correlations between calving date and birth weight (-0.30), weaning weight (-0.05), postweaning gain (-0.64) and yearling weight (-0.60) were generally favorable. The nature of the relationship between calving date and maternal breeding value (BV) was also studied, with an increase in maternal BV associated with a delay in calving date. The authors suggested that there is an optimum level of milk production above which reproduction is jeopardized. Moreover, calving date of younger cows was more adversely affected by high maternal BV than was calving date of older cows, and late calving was associated more with high than with low milk production potential. The authors found that early initial calvers were superior to their late counterparts in subsequent reproductive performance. They concluded that since heifer calvings aren't constrained by a previous calving; most heifers are bred and have the opportunity to calve early; differences in heifer performance are good indicators of genetic differences in calving date.

The study by Johnston and Bunter (1996) investigated the relationship between calving success and days to calving, but was unable to account for the categorical nature of calving success, due to computational limitations. Johnston et al. (2001) estimated the nature of the relationship between days to calving and calving success, using a new analytical procedure that accounted for the categorical nature of calving success. Days to calving and calving success were defined as described by Johnston and Bunter (1996), and only records from the first parity were retained for analysis for both traits. In addition, calving success records were only used from breeding management groups where variation existed, so that calving success records were removed for all animals in breeding management groups where all cows calved. Variance components were estimated using the Bayesian approach via the Gibbs sampler. Heritability estimates for days to calving and calving success (on the underlying scale) were 0.12 and 0.04, respectively, and the genetic correlation estimate between the two traits was –0.66. The authors suggested that, based on these results, selection for reduced days to calving would result in correlated increases in calving success. The correlation between estimated breeding values (EBV) for both traits was –0.96, indicating that shorter days to calving was favorably associated with an increased probability of a successful calving. The regression coefficient for days to calving EBV was –0.6 percent success/day. Thus, for each 1-day shorter days to calving EBV, there was a 0.6% increase in calving success EBV. The authors concluded that, from a selection point of view, days to calving and calving success are genetically similar, with the former having a higher heritability.

Various methods have been used to incorporate records of open cows in the analysis of calving date and days to calving (Notter and Johnson, 1988; Johnston and Bunter, 1996). An alternative approach would be to use survival analysis to evaluate reproductive traits. Such analyses could model days to calving with a hazard rate or probability of calving past time t, given the individual has not calved prior to t. Studies in dairy cattle have shown that survival analysis is useful for evaluating longevity (Ducrocq, 1994) and fertility traits such as days open (Eicker et al., 1996) but little research has been undertaken using the survival model for analysis of beef fertility traits. Although survival analyses offer several advantages over the linear model, e.g., better statistical modeling of censored data, the high computational requirements associated with applying these non-linear analyses hinders their use with an animal model and large data sets. Despite this drawback, survival analysis offers the potential for better evaluation of fertility traits in beef cattle in the future.

Stayability

Another trait of primary interest to the beef industry is the length of the productive life of females, sometimes termed “stayability”. Snelling et al. (1995) conducted within-herd genetic analyses of stayability, where traits considered were probabilities of a female having 2,5,8 and 11 calves, given that she calved once. The number of calves born to each dam was used to assign binary stayability observations to dams old enough to have had the required number of calves, coded as 1 (success) and 0 (failure). Observations of failure on culled cows not yet old enough to have had the required number of calves were not used. Three variations of nonlinear procedures for mixed-model analysis of binary data were used to estimate variances and predict genetic merit; animal and sire model marginal maximum likelihood, and animal model Method R, with only the former yielding heritability estimates for all traits in all herds. The heritability estimates for probability of having 2,5,8 and 11 calves, given that she calved once, were 0.09, 0.11, 0.07 and 0.20, respectively, for herd one, and 0.02, 0.14, 0.09 and 0.07, respectively, for herd two. Comparing accuracies of the 4 traits, the predictions for probability of having 5 calves, given that she calved once, had the highest mean accuracy in both herds. The authors concluded that this result, along with higher heritability estimates, offset the greater number of records available at earlier ages.

Van der Westhuizen et al. (2001) estimated variance components for stayability, longevity and calving success, and investigated the nature of the relationship between the traits using a sire model. Stayability was defined as the probability of an animal surviving to a specific age (36, 48, 60, 72 and 84 months), given the opportunity to reach that age, and coded as 1 (cow survived) and 0 (last record). Calving success was coded as 1 (successful calving) and 0 (otherwise), and longevity was calculated from the age at which the last data set was recorded. Variance components and genetic values were obtained using GFCAT, a set of programs for the analysis of “mixed” model threshold models. Heritability estimates for stayability at 36, 48, 60, 72 and 84 months of age were 0.06, 0.10, 0.06, 0.03 and 0.11, respectively. Heritability estimates for calving success and longevity were 0.03 and 0.08, respectively. Product-moment correlations between stayability at different ages were found to be low, and the authors concluded that there would be little to no improvement in level of stayability when selection was applied at another level. In general, they concluded that heritability estimates and correlations between traits were of such a low magnitude that selection for these characteristics would result in limited genetic improvement, and also indicated that sires had little influence on the stayability, longevity or calving success of their daughters. However, the authors did not address whether these results would hold for evaluation under the animal model.

Heifer pregnancy

Evans et al. (1999) evaluated the feasibility of producing expected progeny differences (EPD) for heifer pregnancy using yearling bull scrotal circumference and yearling heifer pregnancy observations. Heifer pregnancy was defined as the observation that a heifer conceives and remains pregnant to palpation, given that she was exposed at breeding, and scored as 1 (successful pregnancy) and 0 (failure to maintain pregnancy up to 120 days). Heifer pregnancy was analyzed using a maximum *a posteriori* probit threshold model to predict BV on the underlying scale, while variance components were estimated using Method R. Age of dam and age of heifer had significant effects on heifer pregnancy; heifers from 2-year-old dams were 10% less likely to conceive and remain pregnant than heifers born from mature dams, and for every 20-day increase in heifer age, there was a corresponding 10% increase in the probability a heifer will conceive and remain pregnant. The heritability estimate for heifer pregnancy was 0.138, and the estimate of the genetic correlation between heifer pregnancy and scrotal circumference was not significantly different from zero. The authors concluded that heifer pregnancy data could be used to develop BV for heifer pregnancy.

Doyle et al. (2000) investigated the nature of additive genetic relationships between heifer pregnancy, subsequent rebreeding and stayability. Heifer pregnancy was defined as described by Evans et al. (1999), and stayability as described by Snelling et al. (1995). Subsequent rebreeding was defined as the observation of a 2-year-old conceiving and remaining pregnant to palpation, given pregnancy as a yearling and exposure during the breeding season, and was coded as 1 (rebred animals) and 0 (non-pregnant females). All traits were analyzed using a maximum *a posteriori* probit threshold model to predict genetic merit on the underlying scale, while Method R was used to estimate variance components. The average heritability estimates for heifer pregnancy, subsequent rebreeding and stayability were 0.21, 0.19 and 0.15, respectively. The authors noted that, for the trait of subsequent rebreeding, only 87 of the 162 sub-samples produced point estimates within the parameter space, which they attributed in part to the small number of observations available, and the 50% repeated sub-sampling procedure of Method R. Three additive genetic groups formed on heifer pregnancy estimated BV (low, intermediate and high) were used in the analysis of stayability. The authors found differences between these groups, providing evidence for the existence of a nonlinear relationship between heifer pregnancy and stayability. The authors concluded that the difference found between the middle and high heifer pregnancy genetic groups suggested higher heifer fertility appeared favorably related to higher sustained fertility. In conclusion, the authors noted that heifer pregnancy and stayability were heritable and should respond favorably to selection, however subsequent rebreeding did not appear to be heritable. It should be noted, however, that variance components were estimated using Method R, which is not recommended for use with small data sets, as in this study. Thus, no conclusions regarding heritability of the traits can be made, and further research in this area is necessary

Other measures

Calving rate is an alternative measure of reproductive performance that has received attention by researchers. Ponzoni (1992) compared the merits of calving rate and calving day in the context of a comprehensive breeding objective. Calving day in this study was analogous to calving date, and calving rate was defined as the number of calves born per cow present in the herd. In this study, reproductive rate made the greatest contribution to genetic gain in economic units, regardless of which of the 2 traits was in the breeding objective. Genetic gain in reproductive rate and total gain in economic units were greater when calving rate was included in the breeding objective. This result was attributed to the greater phenotypic variance of calving rate under the economic and genetic assumptions made in this study. However, Ponzoni (1992) concluded that from a genetic point of view, the difference between using calving rate or calving day would be small, compared with the effect of completely ignoring reproduction.

While from a genetic point of view, calving rate, as defined by Ponzoni (1992), may be superior to calving date, from a production perspective, calving rate and calving success have some of the same deficiencies as calving interval. Both measures are historic, and do not indicate when cows calve in the calving season. Calving rate as defined by Meyer et al. (1990), can only be used after a number of calvings have taken place, and, thus, can't be used directly on heifers as a measure of future production.

Another potential trait for selection is pregnancy rate, as it has been shown that pregnancy rate measured in the first parity is the same trait as lifetime pregnancy rate. Morris and Cullen (1994) estimated genetic correlations between pubertal traits of males or females and lifetime pregnancy rate. Yearling pregnancy rate was considered normal, and coded as 1 (success) and 0 (failure). Lifetime pregnancy rate was calculated as the number of pregnancies divided by number of mating years, up to the fifth mating year. Heritability estimates for yearling and lifetime pregnancy rate and calving date were 0.04, 0.04 and 0.04, respectively. The phenotypic and genetic correlations between yearling and lifetime pregnancy rate were 0.84 and 0.92, respectively, indicating that they are the same trait. Genetic correlations of standardized age at first estrus with yearling or lifetime pregnancy rate were all negative and, hence, desirable in direction. For scrotal circumference, genetic correlation estimates with yearling and lifetime pregnancy rate were 0.53 and 0.34, respectively. From this study it appears that pubertal traits are favorably correlated with lifetime pregnancy rate.

Morris et al. (2000) estimated genetic parameters for age at first estrus, calving date and pregnancy rates using experimental data. Heritabilities for standardized age at first estrus and calving date were 0.27 and 0.09, respectively. Genetic correlations of standardized age at first estrus with calving date and pregnancy rate were 0.57 and –0.36, respectively. The pregnancy rate for the line selected for reduced age at puberty was 5% higher than the line selected for increased age at puberty, and the mean calving date was 3 days earlier. Thus, the authors concluded that selecting for reduced age at puberty leads to earlier calving dates and higher pregnancy rates in beef females.

Researchers have also attempted to identify physiological parameters, such as endocrine factors, that are related to fertility, and are heritable. Mialon et al. (2000) found a favorable genetic correlation between age at puberty and postpartum intervals in experimental data. The length of postpartum anoestrus was estimated based on weekly blood progesterone assays and on twice daily detection of estrus behavior. Estimates of heritability and repeatability for the interval from calving to first observed estrus were 0.12 and 0.38, respectively. Corresponding values for the interval from calving to the first positive progesterone test were 0.35 and 0.60, respectively. The genetic and phenotypic correlations between the two measures of postpartum interval were 0.98 and 0.65, respectively. The genetic relationships between postpartum intervals and body weight and body condition score at time of calving were negative; cows that were genetically heavier at calving with more body reserves had shorter postpartum intervals. A favorable positive genetic correlation between age at puberty and postpartum intervals was found, in that heifers which were younger at puberty also had shorter postpartum intervals. While the favorable relationships of the postpartum intervals with weight at calving and age at puberty may benefit beef producers, it is unlikely that direct selection on either trait will be possible, due to the difficulty in measuring both traits outside of experimental populations.

Age at first calving has also been studied as a potential measure of reproductive performance. A reduced age at first calving would increase the number of calves born in the herd. An advantage of this measure is that it can be computed without the need for additional data, as the birth date of the cow and her first calving are generally known. The biggest disadvantages are that it only represents one component in the reproductive life of a cow, and that it is only recorded in heifers. Furthermore, in a variable seasonal environment, age at first calving reflects management decisions to a greater extent than genetic merit. Bourdon and Brinks (1982) reported a low heritability estimate (0.07) for age at first calving, and favorable correlations with growth traits.

CONCLUSIONS AND IMPLICATIONS TO GENETIC IMPROVEMENT OF BEEF CATTLE

Reproduction is a complex trait, and, hence, there are many different measures of reproductive performance. Some of the more popular alternative measures include age at first estrus, age at first breeding, calving rate and pregnancy rate. While many researchers have identified these measures to be heritable, they are not widely used for several reasons. Some measures are historic, and fail to provide an indication of when cows calve in the calving season (calving and pregnancy rates), while others are heavily influenced by management (age at first calving). Other measurements cannot be measured feasibly in field data (postpartum intervals).

The traits of calving date and days to calving have been identified as suitable measures of reproductive performance. They are heritable traits, and allow producers to distinguish between early and late calvers in their herds. However, past studies have generally used records from the first and second parities. Thus further research to ascertain whether these results can be extrapolated for the entire reproductive life of the female is needed. As well, the method of prediction of records for open cows needs further refinement. The alternative approach of using survival analysis should be investigated in the future.

The trait of heifer pregnancy is currently used in genetic evaluation. However, it fails to identify when an individual will calve in the calving season, thus should be included along with some measure of calving date. As well, the relationship between heifer pregnancy and lifetime productivity, or stayability, has not been clearly defined. Further research to properly quantify this relationship is needed.

While several measures of reproductive performance are currently being incorporated into national genetic evaluation, further refinement is still needed. Given the nature of reproductive records, it is unlikely that one individual measure will be able to completely predict reproductive performance. Most likely several measures will need to be used together. The main limitations to genetic evaluation of fertility in the past, and currently, are the lack of records available from field data. The adoption of whole-herd reporting schemes by herds will help to alleviate this problem. In conclusion, there is much potential to make improvements to the evaluation of female reproductive performance of beef cattle in the future.

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