SIMULATION OF GENETIC CONTROL OF REPRODUCTION IN BEEF COWS. IV. WITHIN-HERD BREEDING VALUE ESTIMATION WITH PASTURE MATING

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ABSTRACT

Procedures for breeding value estimation for reproductive traits under pasture mating conditions were developed and tested using a computer simulation model of genetic control of bovine reproduction. The model generated annual calving rates (BCR) (0 or 1) and calving dates (CD) for each cow as a function of underlying genetic variation in two independent traits: single-service conception rate (CRG), which was indicative of the ability to conceive when estrus occurs, and postpartum interval (PPI) from calving to first estrus. Observed values for BCR and CD were shown to be complex, nonlinear functions of breeding values for ability to conceive (CRG) and for postpartum interval (PPI) and of the previous CD. Effects of CRG on BCR and CD were small at high values of CRG, but these effects increased as CRG declined. Effects of PPI on BCR and CD were small for cows that previously calved within the first 21 d of the calving season, but these effects increased for cows that calved after d 21. Previous CD had substantial nongenetic carryover effects on both BCR and CD. Unbiased estimates of CRG and PPI could not be derived in the absence of breeding information. However, CD were reasonably highly correlated with breeding values for ability to conceive, provided information on open cows was included in the evaluation. Calving dates were only weakly associated with breeding values for PPI, in part because of the relatively short mean PPI (70 d) that was simulated.

(Key Words: Beef Cattle, Reproduction, Simulation, Selection, Breeding Value.)

Introduction

Breeding value estimation for reproductive traits is not straightforward. Reproductive fitness can be defined as the ability of a cow to calve in each year, and fitness may be quantified in terms of actual calving dates (CD) such that females that calve early in the calving season are favored. Thus, the phenotypic measure of reproductive competency is discontinuous, and it is composed of a group of the most phenotypically undesirable females (open cows) and a second, larger group of females that may be stratified based on a set of apparently continuous CD. The apparent continuity of the CD scale is misleading, however, because the bovine estrous cycle dictates that females calving within any period of 21 ± 2 d may differ in CD only because of potentially random differences in the stage of their estrous cycle at the beginning of breeding. These and other factors make translation of measures of reproductive fitness from the phenotypic to the additive genetic, or breeding values, scale difficult.

Johnson and Notter (1987a) developed a stochastic simulation model of bovine reproduction to investigate the relationship between underlying genetic variation in reproductive potentials and resulting phenotypic expression of reproductive competency. The model was also used to develop unbiased breeding value estimation procedures for assumed underlying genetic variables (Notter and Johnson, 1987). However, those procedures required knowledge of breeding dates of individual females. This information is normally available only in herds using artificial insemination and is not part of the performance data collected by most beef cattle breed associations. With pasture mating, only information on frequency and date of calving is available for use in breeding value estimation. Thus, this study was designed to assess the suitability of such data for breeding value estimation for underlying reproductive traits.
Materials and Methods

Data. Reproductive data were simulated using the model of Johnson and Notter (1987a). Genetic variation in reproductive traits was assumed to arise from underlying, normally distributed genetic variation in two uncorrelated traits, postpartum interval (PPI) and potential to conceive when estrus occurs (CR). Phenotypic values for PPI were generated by summing normally distributed additive genetic and permanent environmental deviates with a temporary environmental deviate drawn from a skewed Pearson III gamma distribution. The resulting phenotypic distribution of PPI was skewed toward large PPI values. Phenotypic values for CR at each mating were derived as the sum of independent, normally distributed additive genetic, permanent environmental and temporary environmental deviates. Actual conception rates at each mating were derived by truncation of the resulting phenotypic distribution of CR values at a point corresponding to a mean single-service conception rate of 70%. Cows with values of CR above the truncation point were assumed to conceive; remaining cows did not conceive to the current mating.

A 63-d breeding season was assumed. The durations of the estrous cycle and of gestation were assumed constant at 21 and 276 d, respectively. These assumptions interacted with simulated phenotypic values for PPI and CR to define reproductive performance in the herd. Simulated reproductive outputs included date of first service, conception rate (0 or 1) at each service, number of services, overall annual calving rate (BCR; 0 or 1) for each cow, CD and PPI. A detailed description of the simulation procedures is given by Johnson and Notter (1987a).

Data set 2 of Johnson and Notter (1987b) was used to investigate breeding value estimation procedures with pasture mating. Simulated data included records on 100 herds of 50 cows each. Cows in each herd were sired by five bulls (10 daughters/bull). Records were simulated for six calf crops; all cows were assumed to be cycling (i.e., postpubertal) at the start of the first breeding season. Assumed values of heritability and repeatability for both CR (on the binomial scale) and PPI were .15 and .20, respectively. Genetic and environmental variance components for the data were given by Johnson and Notter (1987b). The same data set was used by Notter and Johnson (1987) to investigate breeding value estimation procedures with known breeding dates.

Breeding Value Estimation. To mimic pasture mating conditions, only data on annual BCR and CD were used to estimate breeding values for PPI and CR. These data are insufficient to allow theoretical derivation of breeding value estimation procedures equivalent to those derived by Notter and Johnson (1987) with known breeding dates. Instead, linear and quadratic relationships between phenotypic measures and underlying breeding values were investigated, and accuracies of derived breeding value estimates for PPI and CR were compared with those obtained by Notter and Johnson (1987).

Results and Discussion

Effects of Breeding Values for Calving Rate and Postpartum Interval on Calving Performance. Before attempting breeding value estimation for CR and PPI from observed calving data, underlying relationships between genetic variables and simulated values of BCR and CD were investigated using simulated data. Models were fitted separately for first calving (for which no previous calving data were available) and for the subsequent five calvings. For first calving, the model included both linear and quadratic effects of breeding values for CR (CRG) and PPI (PPIG). As expected, only linear and quadratic effects of CRG were significant. Observed relationships were:

\[ \text{BCR} = 0.967 + 0.178 \text{CRG} - 0.170 \text{CRG}^2 \]  
\[ \text{R}^2 = 0.17 \]

\[ \text{CD} = 16.99 - 7.96 \text{CRG} + 1.86 \text{CRG}^2 \]  
\[ \text{R}^2 = 0.08 \]

Thus, the effect of improving CRG was largest at low values of CRG and decreased as CRG increased.

For later calvings, the model included fixed effects of year of calving and of nursing status (lactating or dry) at the start of breeding; continuous linear and quadratic effects of CRG, PPIG and prior calving date (PD) for nursing cows; interaction effects between nursing status and linear and quadratic effects of CRG and PPIG; and interaction effects between the linear effect of PD and the linear effects of CRG and PPIG for nursing cows. All effects were significant for BCR except those for year, overall effects of nursing status and the interaction of the quadratic effect of PPIG with nursing status. The final model (\( \text{R}^2 = 0.16 \)) was:
BCR = \( .949 + .154 \text{CRG} - .0023 \text{PPIG} \\
- .0024 \text{PD} - .120 \text{CRG}^2 \\
- .00071 \text{PPIG}^2 + .000081 \text{PD}^2 \\
+ .0019 \text{CRG} \cdot \text{PD} - .00014 \text{PPIG} \cdot \text{PD} 
\)
for nursing cows and:

BCR = \( .959 + .204 \text{CRG} - .0002 \text{PPIG} \\
- .174 \text{CRG}^2 - .000089 \text{PPIG}^2 
\)
for dry cows.

For CD, all effects were significant except those for year, the quadratic effect of PPIG and the interaction effects of nursing status with quadratic effects of both CRG and PPIG. The resulting model (\( R^2 = .16 \)) was:

CD = \( 19.46 - 6.54 \text{CRG} + .21 \text{PPIG} + .271 \text{PD} \\
- 1.99 \text{CRG}^2 + .0043 \text{PPIG}^2 + .0075 \text{PD}^2 \\
+ .066 \text{CRG} \cdot \text{PD} + .011 \text{PPIG} \cdot \text{PD} 
\)
for nursing cows, and:

CD = \( 17.25 - 9.33 \text{CRG} + .015 \text{PPIG} \\
+ 1.14 \text{CRG}^2 + .0003 \text{PPIG}^2 
\)
for dry cows.

Effects of CRG on BCR and CD are shown in figures 1 and 2. Large quadratic effects of CRG were evident for both traits. Calving rates (figure 1) were only slightly influenced by CRG for individuals that were above average in CRG, but a much stronger relationship was observed for individuals that were below average. Interaction effects involving CRG and PD were small, but a major environmental influence of PD on subsequent BCR was observed, especially at low values of CRG. Effects of CRG on BCR were somewhat larger for dry cows than for nursing cows, but the overall pattern of response was similar.

Effects of CRG on CD (figure 2) were again largest at low values of CRG and decreased as CRG increased. The relationship between CRG and CD was reasonably consistent across PD, but major nongenetic effects of PD were observed. These results suggest that effects of CRG on calving performance are largest at low values of CRG but are much reduced at values above the mean.

Effects of PPIG on BCR and CD are shown in figures 3 and 4. Effects of PPIG were clearly nonlinear and interacted strongly with PD. Effects of PPIG on both BCR and subsequent CD were minimal for cows calving within the first 21 d of the previous calving season, but they were much larger for late calvers and at high (undesirable) values of PPIG. Apparently, cows that were dry or that calved within the first 21 d of the calving season had sufficient time to reinitiate cycling before the next breeding, so that PPIG was not an important influence on subsequent calving performance.

Results in figures 1 through 4 suggest that CD are a complex function of CRG, PPIG and previous reproductive history. In particular, phenotypic carryover effects among calvings appear large and may need to be considered in breeding value estimation. Also, information on both BCR and CD must be combined to allow optimum use of available data.

Adjustment of Calving Data for Nongenetic Effects of Previous Calving Date. Information on BCR and CD was combined in a manner analogous to that used by Notter and Johnson (1987) for first CD. Observed CD for cows that calved were transformed as \( W = \ln(\text{CD} + 1) \) to normalize the data; CD for open cows were...
projected by considering cows that did not calve to represent the upper tail of a truncated normal distribution of transformed CD. This procedure allowed all calving information to be expressed on the CD scale. In yr 1, an average of 7.7% of the cows did not calve, and their projected mean CD was d 72. In subsequent years, an average of 10.6% of the cows did not calve, and their projected mean CD was d 84.

Phenotypic carryover effects of previous calvings were studied by comparing performance in adjacent and nonadjacent years. Figure 5 shows the relationship between adjacent (yr 2 and 3) CD for cows that calved in both years. The relationship was not linear; effects of PD were small for cows that had calved by d 21, but they were much larger for cows that calved after d 21. This relationship presumably includes truly permanent cow effects of genotypic and permanent environmental origin, as well as transient environmental effects generated at the previous calving. These transient effects could be postulated to be largest for adjacent calvings and to become progressively less important in more-distant future calvings. This hypothesis is supported by the observed relationship between CD in yr 2 and yr 6 (figure 5). The relationship is less strong than that between CD in yr 2 and yr 3 and has no obvious discontinuities. Adjustment of current calving data for nongentic effects of previous calving performance should correct for transient environmental effects only and should not remove differences arising from genetic differences among cows. Factors to allow such an adjustment can be derived by comparing the relationships between calving performance in progressively more-distant pairs of years to that between pairs of calvings that are distant enough that transient effects of the earlier calving on later performance can be assumed to be trivial.

To attempt to derive appropriate adjustment factors for effects of previous calving performance, cows were categorized at yr 2 into four groups: 1) cows that did not calve, 2) cows that calved, but whose calves died before the start of breeding, 3) cows that calved within the first 21 d of the calving season (early calvers) and 4) cows that calved after d 21 (late calvers). In the simulation model, cows in the first two groups were always assumed to be cycling at the start of breeding. Calving dates (including projected CD for open cows) in yr 3 and 6 were calculated for each group defined in yr 2 (table 1). In addition, CD in yr 3 and 6 for cows in the last two groups were adjusted by linear regression to a CD of d 21 in yr 2. For yr 3 data, regression coefficients were calculated separately for cows that calved before and after
TABLE 1. ESTIMATES OF CARRYOVER ENVIRONMENTAL EFFECTS ON CALVING DATE (CD) BETWEEN ADJACENT CALVINGS

<table>
<thead>
<tr>
<th>Item</th>
<th>Third calving</th>
<th>Sixth calving</th>
<th>Environmental effecta</th>
</tr>
</thead>
<tbody>
<tr>
<td>Mean CD for cows that weaned calves at the second calvingb, d</td>
<td>23.3 ± .8</td>
<td>25.5 ± .4</td>
<td></td>
</tr>
<tr>
<td>Deviation from the mean for:</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Open cows, d</td>
<td>12.5 ± 1.4</td>
<td>17.8 ± 1.1</td>
<td>−5.3 ± 1.8</td>
</tr>
<tr>
<td>Dry, calving cowsc, d</td>
<td>−2.5 ± 1.4</td>
<td>−1.2 ± 1.2</td>
<td>−1.3 ± 1.8</td>
</tr>
<tr>
<td>Regression on second calving date for:</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Early calversd, d/d</td>
<td>.16 ± .07</td>
<td>.20 ± .02</td>
<td>−.03 ± .08</td>
</tr>
<tr>
<td>Late calvers, d/d</td>
<td>.88 ± .05</td>
<td>.20 ± .02</td>
<td>.69 ± .06</td>
</tr>
</tbody>
</table>

aDifference between values at third and sixth calvings.

bAdjusted to a mean second calving date of d 21.
cCows that calved, but whose calves died.
dCalved within the first 21 d of the calving season.

d 21 in yr 2. A single regression coefficient was used for both groups in yr 6 (see figure 5).

Cows that were open in yr 2 calved 12.5 d later in yr 3 and 17.8 d later in yr 6 than cows that calved at d 21 in yr 2 (table 1). The difference between these values (−5.3 d) is the reduction in subsequent CD attributable to transient carryover effects in the nonlactating cow. Cows that calved but did not nurse calves in yr 2 calved an average of 2.5 d earlier in yr 3 and 1.2 d earlier in yr 6. The differences between these values (−1.3 d) is also an estimate of transient carryover effects in nonlactating cows. Although the difference between these estimates approached significance (P<.10), their average value of −3.3 d was used to adjust subsequent CD of nonlactating cows.

For cows that calved early (before d 22) in yr 2, effects of second CD on third CD (.16 d/d) did not differ from those observed at sixth calving (.20 d/d), suggesting no transient carryover effects of PD in cows calving within the first 21 d. However, for cows that calved after d 21, effects of PD were much larger in yr 3 (.88 d/d) than in yr 6. Thus, for cows calving after d 21, each 1-d increase in CD was associated with a transient environmental increase of .69 d in the next CD.

Adjustment of CD for carryover environmental effects of the previous calving was accomplished by adding 3.3 d to CD of cows that did not lactate in the previous year, and by regressing current CD of late calving cows from the previous year to a d=21 PD. Calving dates of cows that calved before d 21 in the previous year were not adjusted. Adjustment factors may be underestimated if transient environmental effects generated in yr 2 are still present in yr 6. Also, the data were not adjusted for transient effects expressed in nonadjacent years. Relationships of calving performance in yr 2 to performance in yr 4 and 5 were similar to those observed for yr 6, and suggested that transient environmental effects were primarily expressed in adjacent years.

Adjustment for previous calving performance reduced the phenotypic variance of CD by 5.3% (from 412 to 390 d2) and reduced the repeatability of CD from .26 to .24. Heritability remained unchanged at .125, and the correlation between actual and adjusted CD was .95. Thus, even though significant transient environmental effects existed between adjacent CD, adjustment for these effects did not greatly affect overall rankings of cows for CD.

Correlations of Calving Date with Breeding Values for Ability to Conceive and Postpartum Interval. Correlations of mean CD (including projected CD for open cows) with CRG over time are shown in figure 6 (line III-A). Adjustment for transient effect of previous CD improved the correlation between CD and CRG by at most .01, suggesting little benefit from
skewed phenotypic distribution and the greater accuracy associated with late calving resulted in an essentially linear relationship between untransformed mean CD and CRG. However, the relationship shown by line III-A still required projection of mean CD for open cows based on transformed data. Correlations based on mean CD were only about .05 lower than those arising from the multistage selection model proposed by Notter and Johnson (1987) (line II-E in figure 6). However, if information on cows that did not calve was excluded from the data (line III-C in figure 6), the correlation between CRG and mean CD was considerably reduced, especially in yr 1.

Correlations between mean CD (with projected CD for open cows and without adjustment for previous CD) and PPIG across years are shown in figure 7 (line III-T). Correlations based on CD alone were considerably lower than those that used breeding information (Notter and Johnson, 1987; lines II-A and II-Z). Also, calving data for estimation of PPIG would not be available until the second calving.

Figure 6. Correlations of breeding value for calving rate (CRG) with mean calving date over six calvings with (III-A) and without (III-C) inclusion of projected calving dates for open cows. Correlations of actual and estimated values for CRG for a categorical trait, multistage selection model with known breeding dates (Notter and Johnson, 1987) are given for comparison (II-E).

Figure 7. Correlations of breeding value for postpartum interval (PPIG) with mean calving date over six calvings including (III-T) or excluding (III-C) cows that were not nursing calves at the start of breeding. Correlations of PPIG with actual postpartum interval (Notter and Johnson, 1987) with (II-Z) or without (II-A) use of a normalizing transformation are given for comparison. Data are first available at second calving for III-T and III-C but near first calving for II-Z and II-A.

The adjustment procedure. Correlations were consistently higher for actual CD than for logarithmically transformed dates. This result is in conflict with that observed for PPI by Notter and Johnson (1987), who reported that normalization of skewed phenotypic values for PPI improved the correlation between PPI and PPIG. This discrepancy was apparently associated with the higher accuracy of breeding value estimation in late calvers (Notter and Johnson, 1987), such that the skewed CD distribution was more consistent with this increasing accuracy. Relationships between CRG and CD (either transformed or actual) were not linear in any year, but the extent of the nonlinearity was small for actual CD (for example, CRG = .59 - .026 CD + .000058 CD² in yr 6). Apparently the interplay of the...
Correlations between mean CD and PPIG could be improved somewhat by exclusion of records of females that were not lactating at the beginning of breeding and whose subsequent CD were not influenced by their PPIG (line III-C in figure 7). However, the increase in correlation from this edit was small compared with that obtainable from a knowledge of breeding dates. No improvement in estimation of PPIG was realized from adjustment for environmental carryover effects of previous CD.

Thus, in the simulated data, CD were only weakly related to PPIG. This result is primarily a reflection of the relatively low simulated mean value of PPI (70 d). As indicated in figures 3 and 4, effects of PPIG on CD would be expected to increase in data sets with a higher mean PPI.

Symmetry of Selection Response. As noted in figures 1 through 4, CD is a complex function of CRG, PPIG and carryover effects of the previous calving. As such, responses to selection for CD will likely be nonlinear and may vary with the nature of the selection. To assess possible asymmetry in selection response, mean values of CRG and PPIG were calculated for the 10% of the cows in the simulated data having the highest and lowest mean CD after six calvings. Selection responses in PPIG were essentially symmetric. Mean values for PPIG were \(-1.41 \pm .33\) d for early calvers and \(1.65 \pm .35\) d for late calvers. In contrast, selection responses in CRG were not symmetric (P<.01). Means for CRG were \(.39 \pm .02\) for early calvers and \(-.66 \pm .02\) for late calvers. Thus, selection against late calving was more effective in identifying cows with low CRG when compared with the effectiveness of increasing CRG by selection for early calving.

Conclusions

For herds using artificial insemination within a fixed breeding season, observed breeding and calving dates appear to provide sufficient information for breeding value estimation for ability to conceive. The categorical nature of expression of fertility and the multistage selection implicit in cows that require several services to conceive must be considered, but the theoretical basis to do this exists (Notter and Johnson, 1987).

With pasture breeding, only overall fertility rates and CD are available for breeding value estimation. In such cases, unbiased estimates of CRG cannot be obtained (at least given the assumptions of the simulation). However, selection based on observed CD yielded acceptable estimates of CRG, provided open cows were included in the evaluation.

Effects of PPIG on realized reproductive outputs were dependent on the assumed mean value for PPI. For the relatively short PPI simulated in this study, the impact of PPIG was small, and selection on CD would have relatively little impact on PPIG.

In general, the results of this study suggest some potential for use of calving information to estimate breeding values for reproductive traits. However, the implementation of such procedures will require development of more highly detailed performance recording schemes to obtain the necessary information.

Literature Cited

