ABSTRACT

Computer simulation was used to evaluate four selection strategies for reproductive success in beef cattle. The strategies were 1) no culling; 2) culling of nonpregnant heifers; 3) culling of nonpregnant heifers and cows nonpregnant twice; 4) culling all nonpregnant females. In addition, simulations were conducted utilizing method four for 20 yr, then changed to method three for an additional 20 yr. Cows were removed from the herd at age 10 if not previously culled. Because reproduction is a threshold character, an underlying normally distributed liability that influences whether or not a cow will produce a calf was assumed with a heritability estimate of .2, a mean of zero and a standard deviation of one. Regressions of breeding value for reproduction and calving rate on year of selection were calculated assuming initial calving rates of 80 and 90%. Linear and quadratic effects for breeding value were present for all selection methods at both initial rates. All primary breeding value regressions were different than that for no culling. At the 90% initial calving rate, methods three and four were different from method two. There were no differences among any regressions for calving rate. Progress for breeding value was more regular than for calving rate; maximum progress for breeding value in 40 yr was approximately .32 standard deviations for selection method four. Calving rate was more erratic, although calving rate increased approximately 7% as a result of 40 yr of selection using method four at the 80% initial calving rate. It appears that much of the improvement attained by any method of selection occurred in the first 20 yr. This result is logical because the initial herd was randomly generated and thus unselected. There was also little difference between selection method four over 40 yr compared with a method whereby the intensity of selection was reduced from method four to method three after 20 yr. These results suggest that occasional retention of a nonpregnant cow, although generally not economically feasible, will do little to influence the genetic composition of the herd, assuming that the cow has already produced at least one calf.

(Key Words: Calving Rate, Simulation, Reproduction, Selection, Beef Cattle.)

Introduction

Reproduction (production of a calf) in beef cattle has long been regarded as a lowly heritable trait and thus, it is not expected to respond rapidly to direct selection. Factors contributing to this low heritability include the trait's composite nature, the fact it is a threshold trait and the current reproductive rate (above 80% in most herds).

Threshold traits generally complicate genetic analysis somewhat, depending in part on the heritability and incidence of the trait. Threshold characters can be evaluated using methodology that assumes for the expressed trait an underlying phenotypic liability that has a unique heritability and is normally distributed (Lush et al., 1948; Dempster and Lerner, 1950; Falconer, 1981).

Even with the low estimated heritability of reproduction, many producers and researchers have been cautious about allowing nonpregnant cows to remain in the herd. Reasons given for this reluctance have largely been economic; however, concerns about the genetic impact of such decisions have frequently been voiced. Under situations in which keeping a nonpregnant cow could be justified economically, what effect would this have on the genetic composition of the herd?

The objectives of this study were to evaluate various selection strategies for reproduction in beef cows by computer simulation and to determine the genetic impact of a reduction in the intensity of selection.
Materials and Methods

Four strategies for culling of nonpregnant females were evaluated by computer simulation. The simulation program was written in BASIC for the IBM Personal Computer. The primary selection strategies were:

1) no culling of nonpregnant females,
2) culling of nonpregnant heifers only,
3) culling of nonpregnant heifers plus cows nonpregnant twice during their lifetime,
4) culling of all nonpregnant females.

The program allowed inputs for selection method, number of years of selection, initial calving rate, heritability of the trait and the maximum cow age. Provisions were also made for changing the selection method during the simulation. A random number seed allowed variable multiple simulations with identical input parameters.

In order to analyze threshold characters, one must make certain assumptions concerning the genetic control of such traits and the statistical methodology used. Problems are encountered using standard analytical procedures due to the binomial nature of threshold characters and the fact that the variance and mean are correlated (Lush et al., 1948). This problem becomes especially important as the threshold value becomes very small or very large (<.2 or >.8). Dempster and Lerner (1950) and Falconer (1981) have discussed these types of traits in light of an underlying liability that is normally distributed and can be evaluated with conventional methods and assumptions. This liability is both genetically and environmentally determined with a mean of zero and standard deviation of one. Additional information required for analysis is the truncation point on the normal curve or threshold at which the trait either occurs or does not occur. For most traits this is simply the incidence of the trait. This value is then converted to standard deviation units using the z scale of the standard normal curve. In the present simulation, this value was the starting point for calving rate for each herd, and subsequent changes were assumed to be due to genetic or random environmental effects. An initial 100-cow herd plus replacement heifers were randomly generated for each run with a breeding value standard deviation equal to \( \sqrt{h^2} \), where \( h^2 \) equals the heritability estimate of liability for reproduction. The age structure of the cow herd was determined using the age distribution reported by Greer et al. (1980). Once the simulation started, cows were either nonpregnant or produced calves, replacement heifers were moved into the cow herd and female calves (sex randomly determined) were kept for replacements based solely on number requirements. Breeding values of female calves were calculated as:

\[
\frac{1}{2} DBV + \frac{1}{2} SBV + (GSD \times RD \times \sqrt{.5}),
\]

where

- \( DBV \) = breeding value of the dam,
- \( SBV \) = breeding value of the sire,
- \( GSD \) = genetic standard deviation \( (\sqrt{h^2}) \),
- \( RD \) = standard normal deviate and \( (\sqrt{.5}) \) = Mendelian sampling variance.

A sire population (100 animals) was generated at the beginning of the simulation with a mean breeding value of zero. This population was then randomly sampled such that five sires were used for 2 yr and each sire was mated to an equal number of cows. The sampling was then repeated for each subsequent 2-yr period. The initial cow herd and the sires used had identical breeding values for each selection method.

Determination of a cow's calving status first required the calculation of her liability.

\[
Liability = BV + (ESD \times RD),
\]

where liability is a cow's value in standard deviation units for a given year,

- \( BV \) = cow's breeding value,
- \( ESD \) = environmental standard deviation \( (\sqrt{1-h^2}) \) and \( RD \) = standard normal deviate.

The concept of liability is based on the assumption that even though a character of a threshold nature either does or does not occur, it is determined by normally distributed genetic and environmental effects. The sum of these effects determine the liability for the character in question. Working in standard deviation units, it is then possible to determine whether or not the individual will exhibit the character.

The liability value calculated above was then compared with the initial truncation point and the phenotypic outcome (pregnancy) was determined by whether the liability value was above or below that point. Annual mean
breeding value and calving rate could then be determined. Once the simulation begins, the assumption is made that the threshold may move (because of a change in mean breeding value); however, the underlying biological determinant is fixed at the original point.

Heritability of liability was used in the simulation and was determined by probit transformation from the heritability of the observed trait to that on the underlying scale (Lush et al., 1948). The ratio of the two values is equal to \( z^2 \), where

\[
z = \frac{p(1-p)}{\text{height of the ordinate of the normal curve at the threshold point}} \quad \text{and} \quad p = \text{incidence of the trait.}
\]

At a reproductive rate of 80%, this transformation approximately doubles the heritability estimate. The uses and biases of this method have been discussed by a number of authors (Robertson and Lerner, 1949; Dempster and Lerner, 1950; Van Vleck, 1972; Rutledge, 1977; Gianola, 1979, 1980). In general, when predicting response to selection, the biases of this transformation are minimal, especially for traits that are lowly heritable. This methodology has been used by a number of authors when evaluating the inheritance of all or none traits (Robertson and Lerner, 1949; Johansson et al., 1974; Mikami and Fredeen, 1979; Kennedy and Moxley, 1980; Meijering, 1984).

Cows were culled from the herd based on selection strategy and on an age-dependent culling distribution (Greer et al., 1980). Culling other than that due to pregnancy status at each age was random and reflected primarily death loss or management practices and generally averaged 2 to 3% in younger age groups. No culling was done due to production; the assumption must therefore be made that production and reproduction are uncorrelated.

Three simulations with different random number seeds were made for each selection strategy. The results of each simulation were then averaged for analysis. Regressions of breeding value and calving rate on year of selection were calculated. Because the linear plus quadratic effects were significant for breeding value for all methods, the \( x \) values (year) were transformed by \( \log_{10} (x) \) in order that single linear coefficients could be tested. Differences between slopes of regression lines obtained using the different culling criteria were tested using Student's t-statistic (Steel and Torrie, 1980). Differences in mean breeding values and calving rate for each selection method were also tested by Student's t.

Results and Discussion

Mean breeding values and calving rates for each selection strategy over the 40-yr period are presented in table 1. Differences existed (\( P<.05 \)) among mean breeding values and mean calving rates for the four primary selection strategies at initial calving rates of 80%. Breeding values at the 90% initial calving rate also were different, while calving rates for methods two and three were the same. Increases in mean breeding values for methods two to four were greater (\( P<.05 \)) at the 80% initial calving rate than at the 90% rate. When selection method four (culling all nonpregnant females) was practiced for 20 yr and then selection method three was practiced for an additional 20 yr, such that a cow was culled after being nonpregnant twice, the only difference (\( P<.05 \)) compared with method four, was for mean breeding value at the 80% initial calving rate. Therefore, in general, reducing the intensity of selection had little effect.

The regression of breeding values on year was significant in all instances for both linear and quadratic effects. When testing differences among the linear coefficients of the \( \log_{10} \) transformed \( x \) values, method one at the 80 and 90% initial rates was different (\( P<.05 \)) from the other methods. The transformed linear regression for method two at the 90% rate was also different from the others (table 2). The quadratic effect present for all selection methods except method one appears due to a leveling off of response to selection in later years. For method one, the quadratic effect appears to be accounting for some of the up and down nature of response. Annual means for breeding value and calving rate at the 80% initial calving rate are presented in figures 1 and 2, respectively. Similar patterns were present at the 90% rate, although the magnitude of change was not as great at the higher initial rate. Regression coefficients for breeding value for methods two to four at the 80% initial rate were greater (\( P<.05 \)) than those at the 90% rate.

Additional selected runs using method four were performed to evaluate changes in assumptions or simulation parameters. When cows were removed from the herd after 15 yr rather
than after 10 yr, an increase in mean breeding value occurred at both initial rates, although neither was significant. This result is somewhat in conflict with selection theory, which generally dictates rapid generation turnover. However, this outcome is apparently due to the fact that only truly superior cows will remain in the herd until age 10. Therefore, postponing the culling of these individuals until age 15 allows them to continue to contribute this superiority to the herd rather than being replaced by a relatively unknown individual. This situation would only be expected to occur with lowly heritable traits, as well as those measured at a number of points. Production and management problems associated with age have been ignored in this study.

An additional run was also made using a heritability estimate of .5 and a 100-yr time span. During the first 20 yr, breeding value and calving rate increased much more rapidly than when a heritability of .2 was assumed. After 20 yr, regardless of heritability, enough progress had been made to reduce variability to the point that a leveling-off of response to selection occurred. This response would be expected as a 100% calving rate eventually was approached.

In evaluating the implications of these results, one must keep in mind several factors. First, the threshold nature of the trait and its relatively high initial incidence (80%+) alter the typical way in which selection operates. While evaluating another threshold trait occurring at a low incidence, Mikami and Fredeen (1979) estimated that it would take 10 generations to reduce the incidence of cryptorchidism in pigs from 5 to 3% by direct selection, even with a heritability of .5. Management changes have been ignored in the present study; however, it should be obvious that with such a low heritability estimate, management will play a major role in altering reproductive performance. The degree of nonadditive genetic control of calving rate has also been ignored. The methodology used in this simulation assumes a narrow-sense heritability and does not take into account nonadditive variation. Therefore, improvement by the use of appropriate mating systems may well occur. Lastly, family selection may be useful to a certain degree. It may prove advantageous to increase the proportion of cows in the herd that are related to cow families known to be highly fertile. Unfortunately, the success of family selection is based in part on a high degree of relationship among family members.
<table>
<thead>
<tr>
<th>Selection method</th>
<th>Initial calving rate</th>
<th>Initial calving rate</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>80%</td>
<td>90%</td>
</tr>
<tr>
<td></td>
<td>Breeding value</td>
<td>Breeding value (log_{10} (x))</td>
</tr>
<tr>
<td></td>
<td>b₁</td>
<td>b₂</td>
</tr>
<tr>
<td>No culling</td>
<td>.0096</td>
<td>.00019</td>
</tr>
<tr>
<td>Nonpregnant heifers</td>
<td>.0186</td>
<td>-.00028</td>
</tr>
<tr>
<td>Nonpregnant heifers plus cows open</td>
<td>.0193</td>
<td>-.00034</td>
</tr>
<tr>
<td>twice</td>
<td>.0206</td>
<td>-.00032</td>
</tr>
<tr>
<td>Any nonpregnant female</td>
<td>.0282</td>
<td>-.00037</td>
</tr>
<tr>
<td>Reduction of selection intensity&lt;sup&gt;b&lt;/sup&gt;</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

<sup>a</sup>Breeding value polynomial regressions using x + x² and regressions using log_{10} (x).

<sup>b</sup>Changing from method four to method three after 20 yr.

<sup>c,d,e</sup>Coefficients in the same column with different superscripts differ (P<.05).

<sup>f</sup>Coefficient differs from that of method four (P<.05).

TABLE 2. REGRESSION COEFFICIENTS FOR BREEDING VALUES<sup>a</sup> AND CALVING RATE BY SELECTION METHOD
Figure 1. Yearly breeding values by selection method (standard deviation units, 80% initial calving rate).

Figure 2. Yearly calving rates by selection method (percentage, 80% initial calving rate).
and large family size. Neither of these factors is particularly applicable to cattle.

Interpretation of these results points out several things. Logically, genetic selection would not be expected to make dramatic increases in a trait when performance already is high. Also, assuming heritability of a trait is constant for each age group, culling of nonpregnant heifers may tend to remove the genetically inferior animals early. Culling nonpregnant heifers in the 80% group accounted for the largest proportion of improvement obtained for both breeding value and calving rate when going from one selection method to the next. This indicates that while further progress was achieved with each increase in selection intensity, the greatest single increase was obtained through the culling of nonpregnant heifers. This response was not the same at the 90% rate (table 1). Inskeep et al. (1961) concluded there was little genetic relationship between heifer and cow fertility. Janson (1980) found a phenotypic correlation of zero between heifer fertility and pregnancy rate the following year, but a genetic correlation of .6. This author concluded that there was similar genetic control of both heifer and cow fertility; however, due to a low phenotypic correlation and low heritability estimates, the environmental effects likely were different.

Much of the improvement attained by any method occurred in the first 20 yr of selection. Because the base herds were randomly generated with a mean of zero and a standard deviation of one, this base population should be considered unselected. This is not normally the case in an actual herd and therefore, the simulation probably reflects greater progress than would actually be realized. After 20 yr, a large proportion of the very inferior animals have been removed. Also calving rate has increased toward 100%, thus reducing the selection differential. Both of these factors would account for the response in breeding value attained.

A reduction in intensity of selection from method four to three after 20 yr (method five) resulted in little difference in progress between methods four and five for the subsequent 20 yr (figure 3). By culling nonpregnant heifers, elimination of genetically inferior animals from a reproductive standpoint was achieved. Keeping a cow that was nonpregnant but had calved as a
heifer did little to change the response. The simulation indicated that keeping such a cow, if economics warrant, will have little effect on the genetic composition of the herd. While this is not recommended as general policy, the short-term influence would likely be minimal. This study has also ignored possible contributions to herd fertility via sire selection, as well as selection of females based on the component factors affecting reproduction.

**Literature Cited**


