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Additive genetic parameter estimates for heifer pregnancy and subsequent reproduction in Angus females[1,2]

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ABSTRACT: A primary objective of this study was to determine whether the binary traits heifer pregnancy (HP) and subsequent rebreeding (SR) were heritable in an experimental population of Angus cattle. A second objective was to determine the nature of the additive genetic relationships among HP, SR, and stayability (S(5 | 1)) in the same population. Heifer pregnancy was defined as the observation of a heifer conceiving and remaining pregnant to palpation at 120 d, given exposure during the breeding season. Subsequent rebreeding was defined as the observation of a 2-yr-old conceiving and remaining pregnant to palpation at 105 d, given pregnancy as a yearling and exposure during the breeding season. Stayability was defined as the probability of a female having at least five calves, given she becomes a dam as a 2 yr old. Data were analyzed using a maximum *a posteriori* probit threshold model to predict breeding values on the liability scale and Method $\Re$ procedures to estimate variance components in the determination of heritability (h^2). Additive genetic groups were used in determining the additive genetic relationships among these fertility traits. Additive genetic groups were formed on one trait's breeding values and used in the prediction of another trait's breeding values. Analyses yielded h^2 estimates that were out of the parameter space 8.5 and 46.3% for HP and SR, respectively, and 5.9% for the reestimation of S(5|1). The majority of point estimates outside the parameter space for SR converged toward 0, whereas those for HP and S(5|1) primarily converged toward 1. From the subsamples producing h^2 estimates within the parameter space, average h^2 for HP, SR, and S(5|1) were .21, .19, and .15, with standard deviations of .12, .14, and .08, respectively. The estimates of h^2 indicate that HP and S(5|1) were heritable and should respond favorably to selection; however, SR did not appear heritable due to the large number of subsamples producing h^2 estimates out of the parameter space. Fixed effect estimates for age of dam were significant for HP. From the analyses using additive genetic groups, the relationship among HP and S(5|1) appeared to be nonlinear. This potential nonlinear relationship seen between HP and S(5|1) indicates that selection for improved female fertility would be most effective by having predictions on both traits.

Key Words: Beef Cattle, Fertility, Genetic Parameters, Heritability, Pregnancy

Introduction

Efficient production in any species depends on the production of females, reproduction, and progeny growth (Dickerson, 1970). For a commercial cow/calf producer whose primary goal is to produce a live, healthy calf annually, no factor plays a more vital role than the reproductive fitness of females. Willham (1973) reported that, at the commercial level, reproduction was ten times as important as growth and twenty times greater than end-product attributes. Recently, Melton (1995) reported that the theoretical relative economic value of reproduction was 3.24 times greater than that of consumption attributes. Both emphasize the importance of reproduction to productivity at the commercial cow/calf level.

Improving reproductive performance depends on the reproductive fitness of replacement heifers, 2-yr-old cows, and the mature cow herd. Due to the large investment of time and resources associated with replacement heifer development, much of the success of an operation depends on getting heifers bred and calved by the age of 2 yr. This must then be followed with keeping them in the herd long enough to produce a minimum number of calves to cover their expenses and a share of those associated with cows that fall out of the herd early in their production life cycle. Therefore, it is important to select those heifers with higher genetic potential for

fertility that will breed early in their first season to calve as 2 yr olds and then continue to rebreed and calve early every year as mature females.

There were two primary objectives for this study pertaining to the improvement of female fertility in beef cattle. The first objective was to determine if heifer pregnancy and subsequent rebreeding were heritable traits in an experimental population of Angus cattle. The second objective was to determine the nature of the additive genetic relationships among heifer pregnancy, subsequent rebreeding, and stayability in the same experimental population of Angus cattle.

Materials and Methods

Data Source

Data for this study were obtained from the John E. Rouse Colorado State University Beef Improvement Center (**CSU BIC**), Saratoga, WY. The CSU BIC has an average elevation of 2,195 m and receives approximately 23 to 33 cm of annual precipitation, primarily as snow. The ranch consists of approximately 3,000 ha, including 320 ha of irrigated meadows, 400 ha of improved crested wheatgrass, and 2,280 ha of native sagebrush range (Schons et al., 1985; Schafer, 1987). Cattle are maintained on grass or meadows year round, with supplemental hay fed during winter months.

The CSU BIC's breeding program emphasizes fertility, maternal ability, low pulmonary arterial pressure, and early growth while maintaining moderate mature size. A more detailed history of the ranch has been documented by Schons et al. (1985), Schafer (1987), and Schafer et al. (1990).

Heifer Management. Yearling heifers were managed separately from the cow herd. Heifers were examined and reproductive tract scores obtained 1 mo before the start of the breeding season. The reproductive tract scores suggest that most heifers were cycling or would be cycling by the start of the breeding season (Mathiews et al., 1995).

Heifers were synchronized using Syncro-Mate-B (Merial, Athens, GA) and were implanted to allow synchronized breeding the first of June each year. The yearling heifers were bred approximately 2 to 3 wk before the cows. One day following the AI breeding, animals were assigned to single-sire natural service cleanup pastures. Pregnancy examination via rectal palpation occurred 60 d after AI breeding and again at weaning (an approximately 120-d pregnancy observation), and nonpregnant and late-bred females were culled. Heifers were calved and managed after calving separately until their second breeding season.

Cow Management. Cows were maintained on grass throughout the year with supplemental hay fed during winter months. Two- and three-yr-old cows, thin cows, and older cows were managed separately during winter to ensure adequate energy balance.

As with the heifers, cows were synchronized with Syncro-Mate-B (Merial) and were implanted the second

week of June. Implants were removed from approximately one-half of the cows 9 d later and from the other half 10 d later. It was believed that essentially all cows were cycling at the initiation of the estrous synchronization protocol based on homosexual activity among the cows at pasture (Mathiews et al., 1995). Calves were removed at the time of implant removal to further promote cyclicity. Calves were returned to their dams following AI (48 h).

Cows were bred by AI approximately 12 h after estrus detection over a 2-d period. Those females not displaying estrus were time-inseminated approximately 54 h after implant removal. Similarly with the heifers, cows were placed into single-sire natural service cleanup pastures approximately 1 d after AI breeding. Pregnancy examination via rectal palpation occurred 60 d after AI breeding and at weaning (pregnancy observation at approximately ~105 d). Nonpregnant, late-bred, and a low number of thin, old cows were culled at weaning.

Heifer Pregnancy Analysis

Data Description. Heifer pregnancy was defined as the observation of a heifer conceiving and remaining pregnant to palpation, given exposure during the breeding season. Weaning palpation records were used in the analysis of heifer pregnancy and represented a 120-d pregnancy record. Pregnant heifers were coded as "1" and nonpregnant females were coded as "0."

Data included 1,326 records from heifers born in the years 1985 through 1993. Preliminary data editing removed 27 animals with no unique individual identification, pregnancy observation, cleanup sire identification, and(or) age of dam observation. The resulting heifer pregnancy data included 1,299 animals within 24 contemporary groups ranging in size from 45 to 64 heifers.

The average heifer pregnancy rate was 89.2%, with a high of 95.7% in 1990 and a low of 76.6% in 1991. The low pregnancy rate in 1991 reflected the use of the CSU BIC yearling heifers in a research project involving evaluation of Synovex-C (Fort Dodge Animal Health, Overland Park, KS) implant use on growth rate, pelvic measurements, and reproductive performance (Rusk, 1992).

Subsequent Rebreeding Analysis

Data Description. Subsequent rebreeding was defined as the observation of a 2 yr old conceiving and remaining pregnant to palpation, given pregnancy as a yearling and exposure during the breeding season. Two-year-old females were coded similarly to the heifers with rebred animals denoted by "1" and nonpregnant females by "0". As in the heifer pregnancy analysis, the weaning palpation record was used in the analysis but represented approximately a 105-d pregnancy observation in the 2-yr-old females.

After editing records with no unique individual cow identification and(or) rebreeding observation, data in-

cluded rebreeding pregnancy observations on 789 2 yr olds from the 1986 through 1994 breeding seasons. Further data removal for lack of within contemporary group variation reduced the number of usable subsequent rebreeding observations to 558 2 yr olds within 33 contemporary groups. The average rebreeding pregnancy rate was 91.9% over 9 yr. Rebreeding pregnancy rates have ranged from a minimum of 86.9% in 1987 to a maximum of 96.2% in 1990.

Stayability Analysis

Data Description. Stayability was defined as the probability of a female having at least five calves, given she becomes a dam as a 2 yr old (Snelling et al., 1995). Dams were assigned a "1" for a successful stayability observation and "0" if unsuccessful. Twins were counted as a single calving observation. Data included 3,109 dams born in the years 1958 through 1989. The average success rate for stayability of 37.7% agreed with earlier research performed on the same herd using data from animals born through 1986 (Snelling, 1994).

Statistical Procedures

Heifer pregnancy, subsequent rebreeding, and stayability were analyzed using a maximum *a posteriori* probit threshold model (Gianola and Foulley, 1983; Harville and Mee, 1984) in the prediction of animals' genetic merit on the underlying scale. In addition, Method $\Re$ (Reverter et al., 1994; Snelling et al., 1995) was used in the estimation of variance components for the three traits of interest. Single-trait analyses for heifer pregnancy, subsequent rebreeding, and stayability can be expressed using a univariate animal model as follows:

$$\mathbf{y}^* = \mathbf{X}\beta + \mathbf{Z}\mathbf{u} + \mathbf{e}$$

where

$$\text{var}\begin{bmatrix} \mathbf{u} \\ \mathbf{e} \end{bmatrix} = \begin{bmatrix} \mathbf{A}\sigma_{\mathbf{a}}^2 & \mathbf{0} \\ \mathbf{0} & \mathbf{I}\sigma_{\mathbf{e}}^2 \end{bmatrix}$$

and $\mathbf{y}^*$ = a vector of "pseudo observations" on the underlying scale for heifer pregnancy, subsequent rebreeding, or stayability; $\mathbf{X}$ and $\mathbf{Z}$ = known incidences relating pseudo observations in $\mathbf{y}^*$ to fixed and random effects, respectively; β = p × 1 vector of fixed effects, $\mathbf{u}$ = q × 1 vector of random additive genetic effects of animal on the underlying scale; $\mathbf{e}$ = vector of residual error; $\mathbf{A}$ = Wright's numerator relationship matrix of additive relationships among individuals; $\mathbf{I}$ = identity matrix; and $\sigma_{\mathbf{a}}^2$ and $\sigma_{\mathbf{e}}^2$ = additive and residual variance, respectively. In the probit threshold model, residual variance on the underlying scale is constrained to 1 (Gianola and Foulley, 1983; Harville and Mee, 1984). Threshold traits are characterized by an underlying continuous scale, which is observed by expression of the trait in

discrete categories. The observed category is dependent on an underlying phenotypic value relative to fixed thresholds (Falconer, 1989; Snelling, 1995).

The animal model for heifer pregnancy included the fixed effects of age of dam, contemporary group defined as birth year and cleanup service sire to account for pasture effects, and age as a covariate. Age of dam was coded according to BIF (1996). The animal model for subsequent rebreeding included the fixed effect of contemporary group defined as year of measure and cleanup service sire; however, age of dam and age effects were deleted. The fixed effect for the stayability animal model included birth year contemporary group. Random effects in all three single-trait analyses included the random additive genetic effect of animal and residual error.

Significance of age of dam and age fixed effects in the heifer pregnancy single-trait analysis was tested using procedures described by Boik et al. (1993), who developed computational methods of testing fixed effects using likelihood ratio F-tests. Such tests were deemed more powerful than alternative methods in testing for significance of fixed effects because of the distinction made between random and fixed effects, the inclusion of relationships among animals, and iterative algorithms used for solving the mixed-model equations. Probabilities of significance for F-tests for age of dam and age were obtained from SAS (1990) using the probability functions for the F-distribution. Prediction error variances were calculated using the diagonal of the inverse of the coefficient matrix.

Three generation pedigrees were implemented for each single-trait evaluation of variance components for heifer pregnancy, subsequent rebreeding, and stayability. The pedigree used in the estimation of breeding values following the determination of h^2 for each trait included all animals recorded for the CSU BIC herd. Table 1 summarizes the available pedigree structure for each single trait and breeding value estimation analyses.

Ninety-five percent confidence intervals were generated for h^2 estimates obtained from each single-trait analysis following procedures described by Mallinckrodt et al. (1997) for approximate confidence intervals of h^2 estimates from Method $\Re$.

Groups Analysis

In order to determine the nature of the potential relationship between heifer pregnancy and stayability, an animal model with additive genetic groups (Golden et al., 1994) was applied. Groups analysis is an alternative method for describing the additive genetic relationship between the two traits and avoids a computationally burdensome bivariate threshold analysis. More importantly, using additive genetic grouping this way can reveal a nonlinear additive genetic relationship between traits.

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Table 1. Available pedigree structure for heifer pregnancy (HP), subsequent rebreeding (SR), and stayability (S(5|1)) for both single-trait analyses of variance components and breeding value estimation (EBV)

Pedigree	No. animals	No. sires	No. dams	No. foundation animals	No. nonzero elements in A^{-1}
HP	2,048	130	1,080	549	11,598
SR	1,461	114	869	491	7,771
S(5|1)	3,726	119	1,847	2,095	16,534
EBV	20,445	226	4,592	10,412	97,767

Additive genetic groups and subsequent group equations were formed following procedures described by Westell et al. (1988) for each trait. Animals with at least one unknown parent (foundation animals) were assigned to genetic groups, representing low, intermediate, and high breeding values. In the first analysis, we included additive genetic groups for heifer pregnancy as a fixed effect in the prediction of estimated breeding values for stayability. In a second analysis, we included additive genetic groups of stayability as a fixed effect to predict estimated breeding values for heifer pregnancy. The animal model for the analysis of heifer pregnancy with stayability genetic group effects included the fixed effects of age of dam, contemporary group as defined previously in the single-trait analysis of heifer pregnancy, additive genetic group effect of stayability, and age as a covariate. The animal model for stayability with heifer pregnancy genetic group effects included the fixed effects of birth year contemporary group and additive genetic group effect of heifer pregnancy. Both group effect analyses included the random additive genetic effects of animal and residual error. The low additive genetic group in each analysis was constrained to zero. Predicted breeding value solutions on the underlying scale for each trait were obtained using a maximum *a posteriori* probit threshold model (Gianola and Foulley, 1983; Harville and Mee, 1984) using h^2 estimates from the single-trait analyses for each trait.

Results and Discussion

Heifer Pregnancy

The average and median h^2 estimates for heifer pregnancy were .21 (Table 2) and .20, respectively. Of the 200 subsamples obtained from Method $\Re$, only 183 produced point estimates of h^2 within the parameter space (Figure 1). Thus, the single-trait animal model for heifer pregnancy was inappropriate for the data 8.5% of the time.

Previous research of heifer fertility on the observed scale has included such measures as pregnancy, conception, and calving rates. Most have concluded that heifer fertility was lowly heritable and the response to selection would be minimal (Dearborn et al., 1973; Milagres et al., 1979; Koots et al., 1994); however, Hetzel et al. (1989) reported making large responses in selection for

fertility. Buddenberg et al. (1989) examined the h^2 of pregnancy on both the observed and underlying scales in Angus, Hereford, and Polled Hereford females bred to calve at 3 yr of age and raised under Ozark range conditions. For Angus, h^2 estimates were .17 and .34 on the observed and underlying scales, respectively. Heritability estimates for Hereford and Polled Hereford were .04 and .05 on the observed scale and .08 and .10 on the underlying scale, respectively. Their research suggested that the h^2 on the observed scale tended to be lower than h^2 estimated on the underlying scale.

The h^2 estimates for heifer pregnancy in this study were not different from more recent reports on heifer pregnancy and the use of threshold analytical procedures in the estimation of variance components. Snelling et al. (1996) obtained average h^2 estimates of .21 and .30 for linecross and Line 1 Herefords from Ft. Keogh Livestock and Range Research Laboratory in Miles City, MT. Furthermore, Evans et al. (1999) reported an h^2 estimate of .14 on the underlying scale for Hereford cattle from field data. Results from this study in conjunction with those from Snelling et al. (1996) and Evans et al. (1999) suggest that heifer pregnancy seems more heritable than previously reported, with higher estimates of h^2 likely being due to the use of more appropriate analytical procedures for categorical data.

Fixed-effect solutions for age of dam and age on the probability and underlying scales, their associated

Table 2. Number of random 50% subsamples, h^2, standard deviation (SD), standard error of the mean h^2 (SE), and 95% confidence interval (CI) for heifer pregnancy (HP), subsequent rebreeding (SR), and stayability (S(5|1))

Trait	No. subsamples	h^2	SD	SE	CI
HP[a]	200	.27	.24	.017	.000 to .671
	183	.21	.12	.009	.059 to .440
SR[b]	162	.12	.17	.013	.000 to .395
	87	.19	.14	.015	.018 to .495
S(5|1)[c]	118	.14	.09	.008	.001 to .288
	111	.15	.08	.008	.036 to .304

[a]Of the 200 subsamples obtained from Method $\Re$, 183 produced point estimates of h^2 within the parameter space.
[b]Of the 162 subsamples obtained from Method $\Re$, 87 produced point estimates of h^2 within the parameter space.
[c]Of the 118 subsamples obtained from Method $\Re$, 111 produced point estimates of h^2 within the parameter space.
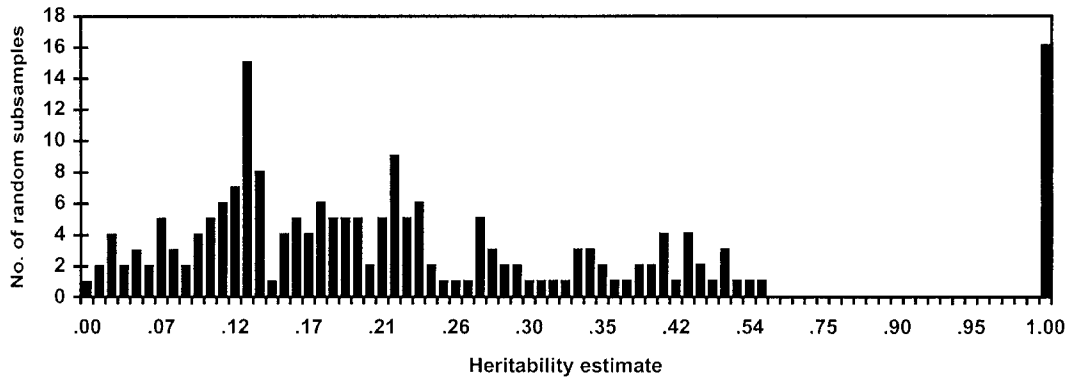
Figure 1. Heritability estimates for yearling Angus heifer pregnancy.

standard deviations, and *P*-values are presented in Table 3. The fixed effect of age of dam was significant; however, the effect of age did not appear to be a significant factor in determining whether a heifer became pregnant or not. Heifers out of 4-yr-old dams were 14% less likely to become and remain pregnant to 120 d compared with heifers out of mature dams. Snelling et al. (1996) and Evans et al. (1999) both reported significant age of dam effects on the probability of becoming pregnant. Snelling et al. (1996) reported linecross Hereford heifers out of younger dams had lower probabilities of pregnancy compared with those of older dams; however, in Line 1 Herefords, heifers out of 3 yr olds had lower probabilities of becoming pregnant vs heifers out of dams belonging to other age groups. Evans et al. (1999) reported heifers out of 2-yr-old dams were 10% less likely to conceive and remain pregnant than heifers out of mature cows. Evans et al. (1999) further reported a significant age effect, citing a 10% advantage in probability of pregnancy for every 20 d earlier a heifer was born in the calving season.

Estimated breeding values expressed as percent probabilities were obtained for heifer pregnancy using

Table 3. Estimates of age of dam (AOD) and age effects on heifer pregnancy on both the percent probability (% probability) and underlying scales (MAP) with corresponding standard deviations (SD) and *P*-values

Effect	% probability	MAP	SD (MAP)	$P > F$
		AOD, yr		
2	−7.15	−.180	.197	.00
3	−5.57	−.140	.162	
4	−14.28	−.366	.168	
5–9	.00	.000	.000	
10	25.27	.683	.449	
11	−11.02	−.280	.341	
12	9.41	.238	.413	
13+	−6.50	−.164	.281	
		Age, d		
	.11	.003	.004	.14

the average h^2 of .21. The average estimated breeding value for all animals in the pedigree, for sires, and their range were .14, .09, and −23.87 to 20.02, respectively. There appears to be adequate variation among animals for heifer pregnancy in the CSU BIC herd to make selection decisions for the purpose of promoting higher reproductive rates among replacement heifers.

Subsequent Rebreeding

The average and median h^2 estimates for subsequent rebreeding were .19 (Table 2) and .02, respectively. Of the 162 subsamples, only 87 produced point estimates for subsequent rebreeding h^2 within the parameter space (Figure 2), which is at least in part due to the small number of subsequent rebreeding observations available for analysis and the 50% repeated subsampling procedure of Method ℜ.

Previous h^2 estimates of rebreeding rate ranged from 0 in Hereford cattle to .18 in Angus females when estimated on the observed scale (Buddenberg et al., 1989); however, transformation to the underlying scale via probit transformation increased the h^2 in Angus females to .32. Recent research by Snelling et al. (1996) supports Buddenberg et al. (1989), finding h^2 of .002 and .01 for linecross and Line 1 Herefords, respectively, on the observed scale vs h^2 of .17 and .49 on the underlying scale using threshold procedures for variance component estimation. Although subsequent rebreeding appears to be heritable in Hereford and Angus cattle (Buddenberg et al., 1989; Snelling et al., 1996), it is difficult to conclude that subsequent rebreeding is heritable in the CSU BIC Angus female population, with approximately half of the subsamples failing to produce h^2 estimates within the parameter space. Rebreeding success of 2 yr olds appears to be due to circumstances and conditions, physical and(or) environmental, that have yet to be quantified in this population.

Stayability Analysis

The average and median h^2 estimates (Table 2) for stayability were .15 and .14, respectively. The analysis
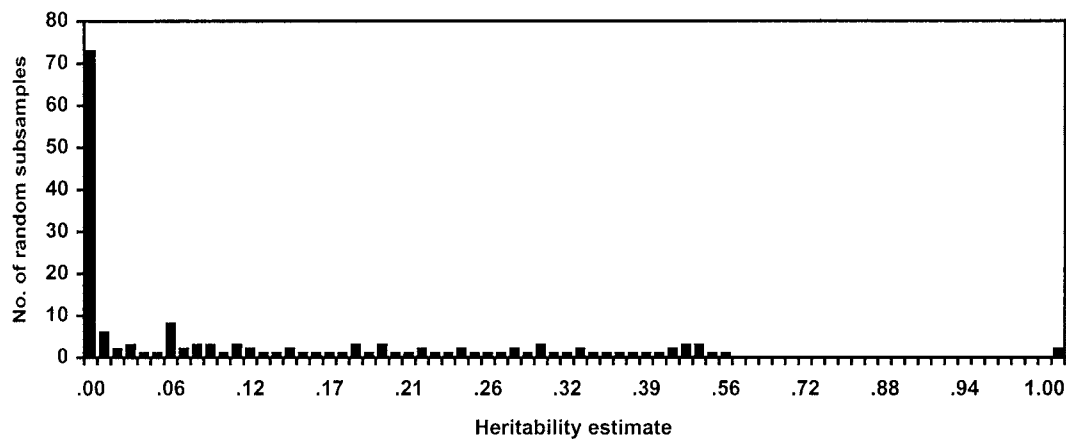
Figure 2. Heritability estimates for subsequent rebreeding in Angus 2 yr olds.

of stayability yielded estimates of h^2 out of the parameter space 5.9% of the time (Figure 3).

Snelling et al. (1995) first estimated h^2 for stayability in the same herd, representing females born through 1986. Using animal model Method $\mathfrak{R}$ and animal model marginal maximum likelihood, Snelling and coworkers obtained h^2 for stayability of .23 and .14. Our estimate of stayability is slightly lower than that reported previously for the same herd; however, the h^2 estimate of .23 for stayability is the mean estimate from Method $\mathfrak{R}$ of five usable subsamples. Heritability estimates from this study agree with those obtained in Red Angus field data (Snelling et al., 1995). Results obtained here along with those of Snelling et al. (1995) suggest that stayability is heritable in this population.

Genetic predictions were obtained using the average h^2 estimate of .15. The average EBV for all animals, for sires only, and their range were 3.62, 5.33, and −15.91 to 33.83, respectively. There appears to be adequate variation in EBV to make selection decisions toward improving the stayability in the CSU BIC herd.

Genetic Groups

Three additive genetic groups formed on heifer pregnancy estimated breeding values were used in the analysis of stayability (Figure 4). Differences, based on a minimum of two standard deviations, exist between the three heifer pregnancy additive genetic groups, providing evidence for the existence of a nonlinear relationship between heifer pregnancy and stayability. The difference between the middle and the high heifer pregnancy genetic groups suggests higher heifer fertility appeared favorably related to higher sustained fertility. Lesmeister et al. (1973) reported that heifers with the ability to conceive earlier in their first breeding season calve earlier and wean more calves compared with females breeding later in the breeding season. They tended to continue conceiving earlier in the breeding season and calving earlier through subsequent years. The difference between the low heifer pregnancy group and the middle heifer pregnancy group suggests diminishing returns in stayability beyond the given thresh-
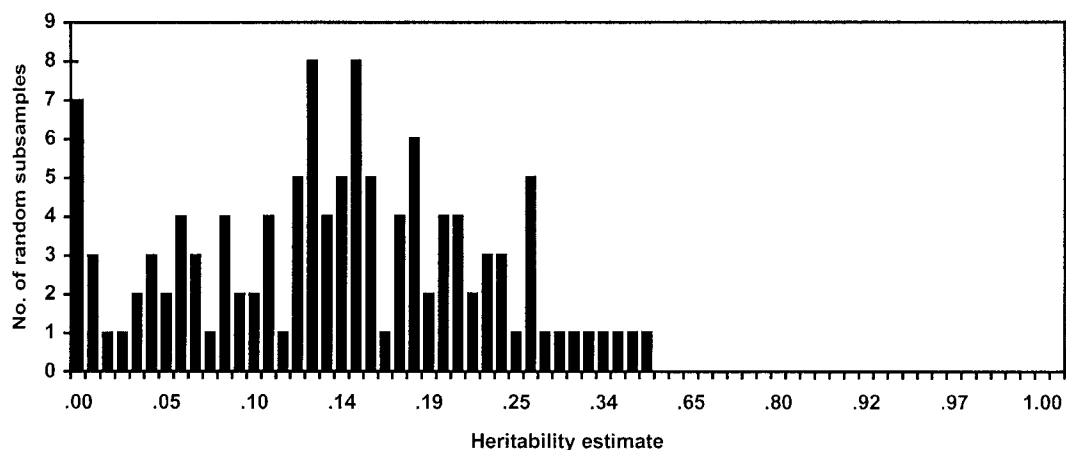

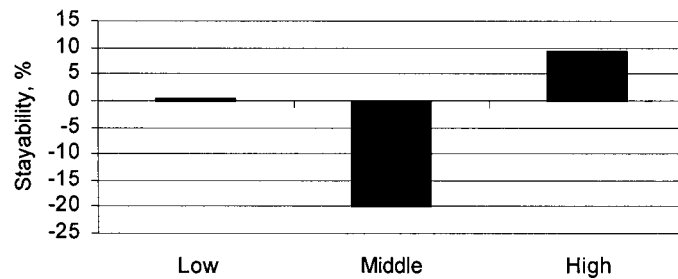**Figure 3.** Heritability estimates for stayability in Angus females.

Figure 4. Additive genetic group solutions of low, middle, and high heifer pregnancy on stayability expressed as a deviation from the low heifer pregnancy genetic group.

old. The CSU BIC's previous culling practices may lend evidence for understanding the relationship between heifer pregnancy and stayability. Before 1986, selection favored bulls and cows with genetic potential for growth. Bulls were selected on the basis of their weaning performance, their dam's record, and 120-d gain test performance. Replacement heifers were selected on the basis of their own performance as well as their dam's record. Furthermore, cows were culled primarily on the basis of their calves' weaning weight records, with additional females being culled for structural soundness and pregnancy status in the fall. Genetic trends were positive for weaning weight, postweaning gain, yearling weight, and milk from the late 1950s to 1986 and were .26, .41, .67, and .14 kg/yr (Schafer, 1987). The stayability solutions for the heifer pregnancy additive genetic groups may reflect selection processes before implementing the current practice of culling all nonpregnant females at weaning, regardless of their calves' performance records.

An additional analysis was performed fitting three additive genetic groups formed on stayability estimated breeding value in the genetic prediction of heifer pregnancy. The standard deviations for this particular group's analysis were relatively high; stayability genetic group differences were not significantly different from zero and may have been due random chance.

Implications

More appropriate analytical techniques have made possible more accurate prediction of genetic merit for reproductive traits. As such technology is applied, producers will have the tools to place direct selection on the economically important traits of female reproduction. Incorporating heifer pregnancy probability expected progeny difference into national cattle evaluations would allow producers to select sires with daughters having high additive genetic potentials for pregnancy at first breeding. A few breed associations have incorporated stayability expected progeny difference into national cattle evaluations, seeing its benefits in improving the reproductive lifespan of females through sire selection. Using these probability expected progeny differences along with proper nutrition and management would promote favorable responses in female fertility.

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