SIMULATION OF GENETIC CONTROL OF REPRODUCTION IN BEEF COWS

by

Maribeth Hepp

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APPROVED:

D. R. Notter, Chairman

R. E. Pearson

T. J. Marlowe

M. L. McGilliard

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TABLE OF CONTENTS

LIST OF TABLES

table page

LIST OF FIGURES

INTRODUCTION

Normal efficiency in reproduction is of great economic importance in beef cattle populations since the number of calves weaned per herd is of primary interest. Within a herd, the cost per calf weaned is strongly dependent upon the percentage calf crop weaned.

An understanding of the factors that affect the heritability and repeatability of reproductive traits and the relationship between reproduction and production is needed so that cattle breeders may determine the effectiveness of selection for reproduction, the best selection method to follow and the relative emphasis to place on reproduction and other traits of economic importance. Traditional measures of reproductive ability have been found to possess little or no genetic variation due in part to automatic selection for fertility; animals of low fertility produce fewer offspring.

The objectives of this study were

1. to simulate cow reproduction through the use of principal reproductive traits,
2. to investigate the impact of different levels of genetic variation and culling on the estimates of heritability and repeatability for resulting

reproductive traits, and

3. to estimate the genetic and environmental correlations between resulting reproductive traits and actual weaning weight.

REVIEW OF LITERATURE

Theoretical Aspects

There are many characters of biological interest or economic importance which vary in a discontinuous manner but are not inherited in a simple Mendelian manner. Characters of this sort appear at first to be outside the range of traditional quantitative genetics; yet when they are subjected to genetic analysis they are found to be inherited in the same way as continuously varying characters.

Problems with binomial data. Data of an all-or-none nature are such that observations must fall into one or the other of two mutually exclusive classes; that of the presence of the character and that of the absence of the character. The actually observed variance in binomial data is correlated with the mean ($\mu = np$; $\sigma^2 = npq$: where n is population size, p is the percent presence of the character and $q = 1 - p$). Hence the variance becomes very small when the percentage in either class approaches zero (Lush et al., 1948; Robertson and Lerner, 1949). This relationship, unlike the situation of normally distributed characteristics, makes the directly observed estimates of heritability depend in part upon the average incidence of the all-or-none trait.

Dempster and Lerner (1950) define the p scale as the binomial phenotypic expression of a trait. There are three basic problems associated with the p scale for determination of heritabilities and computations of genetic gains expected from selection. The first of these is that serious inaccuracies may result because genetic variation which may be completely additive for the underlying variate may lose this property on the p scale. Since the limiting genotypic values are 0 and 1, it is highly unlikely that a given gene substitution would have the same effect near these limits as in the middle of the range. Secondly, the environmental variance of the underlying variate may be independent of the mean genotypic value, but this property may be lost on the p scale. This result is apparent from the fact that environmental variance on the p scale, which is the total variance for any fixed genotype, is equal to p(1-p), where p is the probability of ones. Finally, the categorical nature of the p scale may obscure the finer degrees of measurable variation. All of these circumstances reduce to some extent the utility of the degree of heritability determined on the p scale. Therefore, correction for the average incidence should be performed before any comparisons can be made between heritabilities in different populations.

Probit transformation of heritability. Lush et al. (1948) were the first of several authors to research the transformation of binomial data to Bliss' "probit" scale. The assumptions for this transformation are: there is an underlying variate whose value is the sum of a normally distributed genetic component and an independent normally distributed environmental component; the binomial character is present in all those individuals, and only those, in which the underlying variate exceeds a certain threshold value; and gene substitutions have individually small and strictly additive effects on the underlying variate (Dempster and Lerner, 1950).

Heritability on the actually observed scale can be transformed into the genetically more accurate heritability on the probit scale by the equation

$$h_N^2 = \frac{h^2 p(1-p)}{Z^2}$$

where p is the fraction of those that express the character and z is the height of the ordinate at the point which truncates p of the area of the normal curve (Lush et al., 1948; Robertson and Lerner, 1949; Dempster and Lerner, 1950). The probit transformation makes the genetic variance independent of p (Robertson and Lerner, 1949).

This transformation for binomial heritability can be extended to the case where the expression of the character is a response in one of several mutually exclusive and exhaustive categories (Gianola, 1979). This was done not only for the case where the genetic and environmental distributions were assumed normal but also when they were assumed exponential. Even in the exponential case, the threshold values could not be calculated without knowledge of heritability of the underlying scale.

The transformation of heritability will not be applicable if the variation of the underlying distribution (σ_x^2) is large (Robertson and Lerner, 1949). Because of the interaction introduced by the change from a binomial to a normal scale, $p(1-p)/z^2$ is no longer an accurage measure of the total variance. There is not an a priori limit to σ_x^2 and therefore the transformed heritability could be greater than one.

Probit transformation may be satisfactory for the purpose of comparing heritability values, but it was not apparent how it could be used for devising optimum selection indexes nor for computing expected rates of genetic gain (Dempster and Lerner, 1950). The conditions under which serious errors were likely to result from the use of the convenient binomial phenotypic scale (p scale) and the nature and the magnitude of such errors were investigated. The estimates of genetic gain calculated on the basis of binomial heritability determinations constituted good approximations of the gain that should actually be achieved if the heritability of the underlying trait was moderately low and the character incidence is not too close to zero or unity. Under other conditions the genetic gain may be largely over- or under-estimated. For instance, the actual rate of gain in the selection for a rare character may be more than twice that calculated on the basis of p scale heritabilities. On the other hand, in the case of characters that are already very frequent in the population the rate of gain is likely to be somewhat less than that calculated, but the discrepancy is small except when heritability on the underlying scale is high or the incidence is very close to zero or unity (Dempster and Lerner, 1950; Van Vleck, 1972).

Under some circumstances, gains could be achieved at a much greater rate if classification of the phenotype could be made on a graduated rather than on an all-or-none basis. When strong selection was applied in favor of a very common character or when selection was weak for a rare character, selection on the all-or-none basis was inefficient (Dempster and Lerner, 1950).

Actual vs theoretical heritability. Van Vleck (1972) and Olausson and Ronningen (1978) analyzed simulated data to determine significant differences between actual heritability estimates and theoretical values based on heritability transformation.

Over all thresholds and heritabilities that were simulated, parent-offspring heritability estimates exceeded theoretical estimates by more than did paternal sib estimates (Van Vleck, 1972). In general, the location of the threshold was found to have a greater effect on the difference of the parent-offspring estimates from theoretical than on the paternal sib difference from theoretical. The average pattern for this difference was similar in both cases, though. There was greater under-estimation by theory at low frequencies of the trait than of frequencies near 50%. Similarly, the average estimates exceeded the theoretical by more for high true heritability than for low heritability by both methods, although the differences were greater for the parent-offspring method. These differences from theory were expected and were suggested to be due to the introduction of nonadditive genetic variance due to the change in scale from the normal to the binomial distribution (Robertson and Lerner, 1949; Van Vleck, 1972).

Estimating heritability for data on the underlying normal scale by multiplying the binomial heritability by $p(1-p)/z^2$ appears to be a reasonable approach for the paternal sib method (Van Vleck, 1972; Olausson and Ronningen, 1978. The validity of this approach is more doubtful for the parent-progeny method especially when only a small proportion of the population has the character (Van Vleck, 1972).

The genetic correlation between two traits, the one all-or-none and the other normally distributed, can be estimated by the half-sib correlation method in the ordinary way without transformation of the estimate except for low heritability level and for low incidence levels of the all-or-none trait (Olausson and Ronningen, 1978).

The estimation of the phenotypic correlation between an all-or-none trait and a normally distributed trait by the same method as described for the genetic correlation gives considerable and symmetrical bias in estimates (Olausson and Ronningen, 1978). However, the half-sib correlation method can be used to obtain an estimate of the phenotypic correlation from binomial data that when multiplied by the empirical quadratic regression equation of $f(p) = 2.28 - 5.58p + 7.22p^2$ will produce an estimate of the correlation corresponding to the underlying distribution of the all-or-none trait.

Selection using all-or-none traits. Lush et al. (1948) discussed different methods of breeding for greater resistance to death in chickens. If the birds which die leave no offspring then the average resistance of the survivors (on the probit scale) would be z/p times the heritability higher than the average resistance of the generation in which they were hatched. The effectiveness of such mass selection for an all-or-none characteristic, even under highly favorable conditions, falls off rapidly as the incidence of mortality falls under 30% and toward the point at which all mortality is from those accidents without genetic basis. Mass selection can operate only against the birds that die. Hence, it cannot be intense unless the average incidence of mortality is high. This limitation enables family selection for all-or-none characteristics to be many times more effective than mass selection when undesired individuals are rare.

The errors resulting from the use of heritability calculated on the binomial phenotypic scale would be of less importance in family selection than in individual selection (Dempster and Lerner, 1950). The larger the number of individuals per family, the less important would be the discrepancy between computed and attained gains. A reason for this is that environmental variance of different families does not cover as wide a range because the total genetic variance of family means is less than that of individuals.

In combined individual and family selection, extra weight should be assigned to the individual when selection is for a rare character or against one that is already frequent, since the actual gains from mass selection are greater than those calculated from p scale heritabilities. Conversely, extra weight should be given to family selection when selection is for a character with high frequency, since expected gains from mass selection are less than calculated (Dempster and Lerner, 1950).

Effect of selection on genetic parameters. Selection alters the theory of quantitative genetics and may have radical consequences not only for the estimation of genetic parameters but also for their use in the calculation of selection indexes (Robertson, 1977).

Truncation selection acts to reduce additive genetic variance. This reduction is due to negative linkage disequilibrium where for pairs of loci on excess of +- and -+ gametes are present above that expected from allele frequencies. In subsequent generations there is a further loss of additive genetic variance but some of the variance lost previously is regenerated by recombination of existing genes. This comes about from crossing over which releases further variation depending on the linkage relationship between loci. If the loci are independent then the gradual reduction in variance to a stabilized state will be achieved more quickly than if they are closely linked (Robertson, 1977; Fimland, 1979).

The magnitude of the effects of the genetic parameters are dependent not only on the selection intensity but also on the heritability of the selected character or index (Robertson, 1977). The regression of offspring on parent is not affected by selection of parents since the covariance between offspring and parent is reduced by the same amount corresponding to selection intensity as the parental variance. In half-sib analysis, the variance within groups will not be altered but the variance component between progeny groups is reduced significantly if heritability is high. The standard error for both estimates will be inflated. The overall conclusion derived from theory is that the individuals of one generation are the parents of the next. If they are accurately evaluated and selected in the first generation, the variance between families will be reduced in the next (Robertson, 1977).

The asymmetry in realized heritabilities and genetic correlations observed in two way selection for a single trait or selection for different traits may be explained by the observation that the distribution of a variable under selection tends to be skewed as selection advances, although the original distribution was normal (Yamada, 1977). When the distribution of the trait under consideration is not normal then selection differentials for both negative and positive directions will not be the same when one uses the same selection intensity. No mathematical solution is available as far as the problem related to deviation from normality is concerned.

Experimental Results

Fertility or breeding efficiency in its broadest sense refers to the ability of a cow to conceive, produce and wean a calf and then to rebreed quickly. The ability to wean a heavy calf each year is important because a cow that does not produce a calf eats almost as much feed as one which does, yielding nothing but her increased weight gain during the dry period. Within a herd, the cost per calf weaned is strongly dependent upon the percent calf crop weaned.

Overall fertility. There is automatic selection for fertility because animals of low fertility produce fewer offspring. As a result, little apparent genetic variation remains for the breeder to utilize. Milagres et al. (1979) reported that overall cow fertility of beef cows has a heritability of zero. This trait should be broken down into component parts to see if any yield higher heritabilities and repeatabilities.

The traits involved with reproductive performance can be divided into two groups, interval measures and measures of pregnancy rate. The interval measures, from general to more specific, include calving interval, the interval from calving to conception, the interval from calving to first service and the interval from first service to conception. The measures of pregnancy rate, also from general to more specific, include calving rate, number of services per conception and first service conception rate.

Interval Measures

Calving interval. This trait is defined as the interval from one calving to the next calving. The disadvantage of this trait is that the calving interval can be about a year or can be close to 2 yr if a cow did not conceive in the breeding season directly after calving and must wait a year for the next breeding season. This raises problems of measurement and interpretation. Calving interval in dairy herds has a mean of about 390 d (Dunbar and Henderson, 1953; Everett et al., 1966) with a standard deviation of 60 d (Everett et al., 1966). Heritability estimates from dairy data of 0, .08 ± .02 and .06 were found by Dunbar and Henderson (1953), Everett et al. (1966), and Hansen (1979), respectively, and Lindley et al. (1958) reported an estimate of .07 from data on beef cows. Repeatability estimates of .06 and -.12 ± .01 were determined by Lindley et al. (1958) from beef data and Everett et al. (1966) from dairy data, respectively. The negative repeatability should be assumed to be zero. The low heritabilities and repeatabilities reported could be due to the fact that calving interval is an extensive trait that is composed of the remaining intervals and also gestation length. The genetic variance of calving interval could be obscured by high environmental variance which would produce low heritabilities.

Interval from calving to conception. This interval takes into account all events from the parturition of one calf to the conception of another. The mean interval from calving to conception in both beef and dairy herds is about 108 d (Lindley et al., 1958; Everett et al., 1966) with a standard deviation of 60 d (Everett et al., 1966). Heritability estimates from dairy data of .07 ± .02 and .013 ± .005 were reported by Everett et al. (1966) and Janson (1980), respectively, and Lindley et al. (1958) found an estimate of .04 from data on beef cows. Repeatability estimates from data on dairy cows of .12 ± .01 and .07 were determined by Everett et al. (1966) and Janson (1980), respectively. The disadvantage of this trait is that a cow must conceive in order to be measured. This reduces the genetic variability because those that did not conceive are not included in the computations. Environmental influences also play an important role in reducing the proportion of genetic variance to total phenotypic variance.

Interval from calving to first service. This interval is the portion of the interval from calving to conception that is directly postpartum and is most often referred to as the postpartum interval. This interval indicates how quickly cows recover from calving to rebreed. Mean postpartum intervals range from 51.2 d for beef cows (Bellows and Short, 1978) to 77 d for dairy cows (Everett et al., 1966) with a standard deviation of about 30 d (Everett et al., 1966). The wide range in mean days postpartum indicates that this trait is also highly influenced by environmental factors such as feeding level, suckled vs nonsuckled cows and calving difficulty. Heritability estimates from dairy data of .04 ± .02 and .002 ± .055 were reported by Everett et al. (1966) and Janson (1980), respectively, and Lindley et al. (1958) reported an estimate of .02 from data on beef cows. Repeatability estimates from beef data of .06 and .03 were found by Warnick (1955) and Lindley et al. (1958), respectively, and Everett et al. (1966) reported an estimate of .07 ± .01 from data on dairy cows. The advantage of this trait is that all cows bred after the preceding calving can be measured regardless of whether they conceive or not. This increases the genetic variability of the population, but the expected increase in heritability due to this increase is still obscured by high environmental variation.

<u>Interval from first service to conception</u>. This interval is redundant if a cow conceives from the first service. This interval along with the interval from calving to first service make up the interval from calving to

conception. Selection for a shorter interval from first service to conception implies a high first service conception rate. The mean interval from first service to conception in both dairy and beef herds ranges from 31 d (Lindley et al., 1958; Everett et al., 1966) to 50 d (Pou et al., 1953) with a standard deviation of 55 d (Everett et al., 1966) Heritability estimates from dairy data of .07, .08 ± .02, and .017 ± .005 were reported by Pou et al. (1953), Everett et al. (1966) and Janson (1980), respectively, and Lindley et al. determined an estimate of .01 from data on beef cows. Repeatability estimates from dairy data of .11 and .10 ± .01 were determined by Pou et al. (1953), and Everett et al. (1966), respectively, and Lindley et al. (1958) found an estimate of .06 from data on beef cows. The low heritability and repeatability estimates for this trait stem from the fact that like the interval from calving to conception a cow must conceive in order to be measured. As with the previous interval, this leaves out those cows that did not conceive and lowers the genetic variability of the population.

A major disadvantage of all interval measures is that selection for any one of the intervals requires at least one calving. This may cause biases in the calculations of genetic parameters due to natural selection.

Measures of Pregnancy Rate

Calving rate. The percentage of cows that give birth to a live calf determines calving rate. This measure is very extensive and includes all of the interval traits as well as the other pregnancy rate traits. Mean calving percentage for beef herds is about 80% (Davenport et al., 1965; Dearborn et al., 1973; Bellows et al., 1974). Dearborn et al. (1973) reported a heritability estimate from beef data of .00 ± .13 for this trait. Heritability of calving rate for linecross beef cows was estimated to be .14 ± .12 and for inbred beef cows was .15 ± .09, and the average repeatability for both groups was determined to be .08 (Davenport et al., 1965). Milagres et al. (1979) found heritability estimates of .01 ± .02 for all beef cows and .21 ± .13 for nonbarren beef cows only. The higher estimate for nonbarren cows resulted from a small increase in genetic variation and a substantial decrease in environmental variance. Excluding nonfertile cows may have uncovered trends that were previously masked by physiological infertility.

Number of services per conception. This trait measures the number of inseminations required for conception. The advantage of this trait is that it is measurable early in life before any selection for fertility takes place. The disadvantage is that this only takes into account a small portion of fertility as defined. The average number of services per conception range from 1.7 for beef cows (Lindley et al., 1958) to 2.02 for dairy cows (Everett et al., 1966) with a standard deviation of 1.5 (Everett et al., 1966). Heritability estimates from dairy data of .07, .03 ± .02, and .015 ± .005 were reported by Pou et al. (1953), Everett et al. (1966), and Janson (1980), respectively, and Lindley et al. (1958) and Milagres et al. (1979) found estimates of -.24 and .64 ± .20, respectively, from beef data. The estimate obtained by Milagres et al. (1979) is much higher than those reported by the other authors. This estimate was obtained solely from data on heifers whose conception rate was only about 70%. The use of heifers and the low level of conception tended to magnify the genetic variability and thus heritability in relation to the other works. Repeatability estimates from dairy data of .12, and .11 ± .01 were determined by Pou et al. (1953), and Everett et al. (1966), respectively, and Lindley et. al. (1958) reported an estimate of .07 from beef data.

First service conception rate. The average percentage of cows and heifers that conceive from their first service in beef herds is about 67% (Bellows et al., 1974). Dearborn et al. (1973) subdivided the lowly heritable trait of "pregnant at the end of the breeding season" (h^2 = .09 ± .14) into a class recorded as first service conception rate

($h^2 = .22 \pm .17$). This subdivision tended to magnify genetic variability seen by an increase in heritability. The increased heritability estimate for first service conception rate resulted from partitioning first service conception from subsequent conceptions and failures to conceive.

The heritability of various fertility measures has been studied, but little attention has been paid to the relative size of the additive genetic variance per se, despite the fact that genetic trends that might be anticipated are directly proportional to the genetic standard deviation. A low heritability may not necessarily mean that the genetic variance is small, provided the phenotypic variance is large. For most measures of fertility the genetic variation, expressed as coefficients of variation in percentages of actual phenotypic means, is substantial and is almost as large as that for milk yield (Philipsson, 1981). Coefficients of variation were found for the interval from calving to conception of about 9% and for the interval from calving to first service of about 5%. However, the phenotypic distribution of the original values often deviates from normality and the standard deviations may be over-estimated.

MATERIAL AND METHODS

General Model Description

A mathematical, stochastic computer model was constructed to simulate cow reproductive performance. R. L. Willham's beef cattle genetic simulation program (Willham and Thomson, 1970) was modified to include reproductive traits, whereas yearling weight and gain performance were deleted from the program.

Reproductive performance in its broadest sense refers to the ability of a cow to conceive, produce a calf and rebreed quickly and efficiently. In the modified program, single-service conception rate and the interval from calving to first estrus were used to simulate reproduction since together they seem to describe adequately overall reproductive performance. Also, the genetic variation (indicated by heritabilities) was apparently higher for these traits than for other reproductive traits.

The simulation program was based on a 63-d breeding season, such that cows received up to three chances to conceive. The actual maximum number of services possible for an individual cow depended upon the calving date and the interval from calving to first estrus. The calving season was also assumed to be 63-d; variation in gestation length was ignored. There was a 26-d lag period from the last day of the calving season to the first day of the breeding season. An idealized population structure was assumed such that no cows died.

The reproductive outputs simulated were chosen to try to describe completely the reproductive life of a cow. These included date of first service, number of services received in a breeding season, conception-calving date, first service conception rate and annual conception rate (reported as 0 or 1 binomial variables), and the interval from calving to first estrus in days (postpartum interval). Calf performance outputs were included in an attempt to describe the contribution of a cow to the herd in terms of pounds of calf produced. These included actual weaning weight and adjusted 205-d weaning weight.

Conception Rate Distribution

Single-service conception rate has an all-or-none binomial distribution which hinders its interpretation and analysis of data by traditional quantitative techniques due to biases from the binomial scale (See Review of Literature). To handle this, conception rate was assumed to have an underlying standard normal phenotypic distribution with mean of zero and standard deviation (σ_P) of one. Since a phenotype is the sum of genetic and environmental effects, the underlying genetic and environmental distributions were also assumed normal and independent. These assumptions made it possible to simulate single-service conception rate without biases due to the all-or-none nature of the trait.

The binomial parameters available from the literature (both genetic and environmental) were converted to the assumed normal basis using the formula

$$h_N^2 = \frac{h_B^2\, p(1-p)}{z^2},$$

where h_B^2 is the binomial heritability, p is the percentage incidence of conception and z is the height of the standard normal curve at the truncation point associated with p (Lush et al., 1948; Robertson and Lerner, 1949; Dempster and Lerner, 1950). Repeatability was also converted in this manner. This transformation reflects the underlying genetic and environmental variation and is not influenced by the fixed binomial scale.

The phenotype for conception rate on the assumed normal underlying scale was determined as the sum of genetic and environmental effects. Conception occurred when an individual's phenotypic value from the normal distribution of values fell above the truncation point on the underlying x-axis corresponding to a 70% single-service conception rate (Bellows et al., 1974). Even though the simulated phenotypic values were derived from the standard normal distribution, conception was scored binomially; either conception occurred (1) or it did not (0). The genetic and environmental distributions for single-service conception rate are shown in figure 1 and figure 2, respectively. The relationship between the phenotypic distribution and the point of truncation for conception rate are depicted in figure 3.

Postpartum Interval Distribution

Postpartum interval was defined and measured as the number of days from calving to first estrus. The phenotypic distribution of this trait was non-normal since 70 to 80% of individuals begin cycling during the first 21 d of the breeding season (Bellows and Short, 1978). One reason for this may lie in the theory that for physiological reasons, cows do not begin to cycle until about 25 to 30 d postpartum (Short et al., 1972). The majority of individuals apparently begin to cycle immediately following this period with a few taking longer to cycle. This pattern extends the right tail of the distribution.

Since phenotypes are the sum of genetic and environmental effects, the genetic and environmental distributions were defined so that in combination they would produce the desired skewed phenotypic distribution. The genetic distribution was assumed normal in order to minimize complications and biases in heritability determination that would arise from a non-normal genetic distribution. The

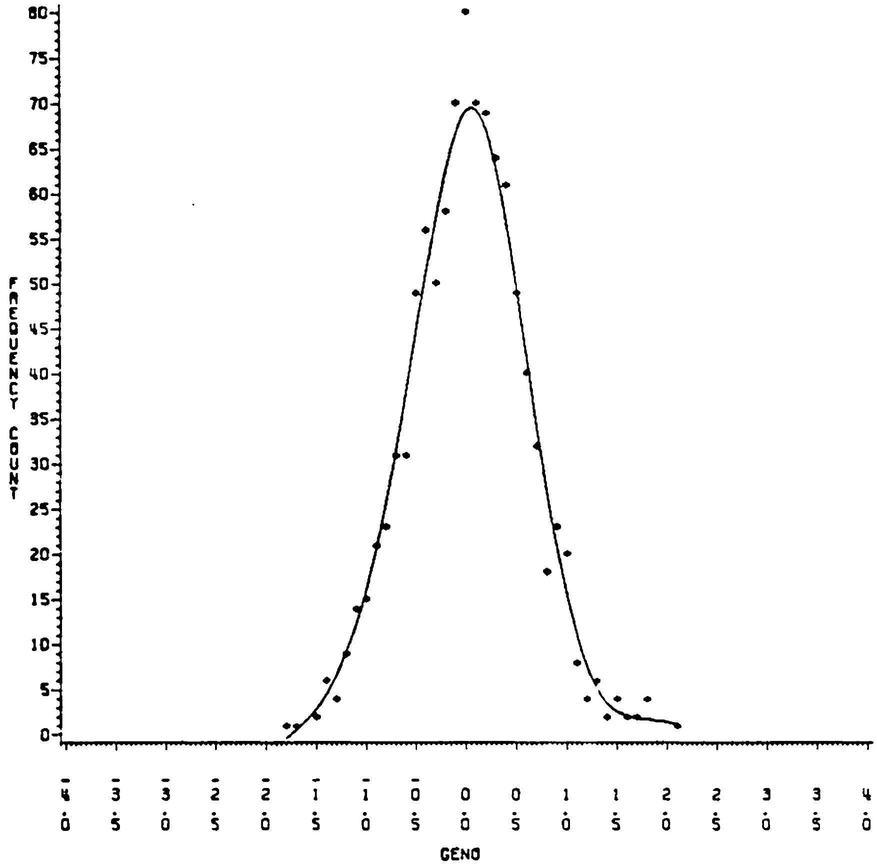

FIGURE 1. UNDERLYING NORMAL GENETIC DISTRIBUTION FOR SINGLE-SERVICE CONCEPTION RATE FROM 1000 SIMULATED DATA POINTS--FREQUENCY COUNT PLOTTED AGAINST GENOTYPE (GENO)

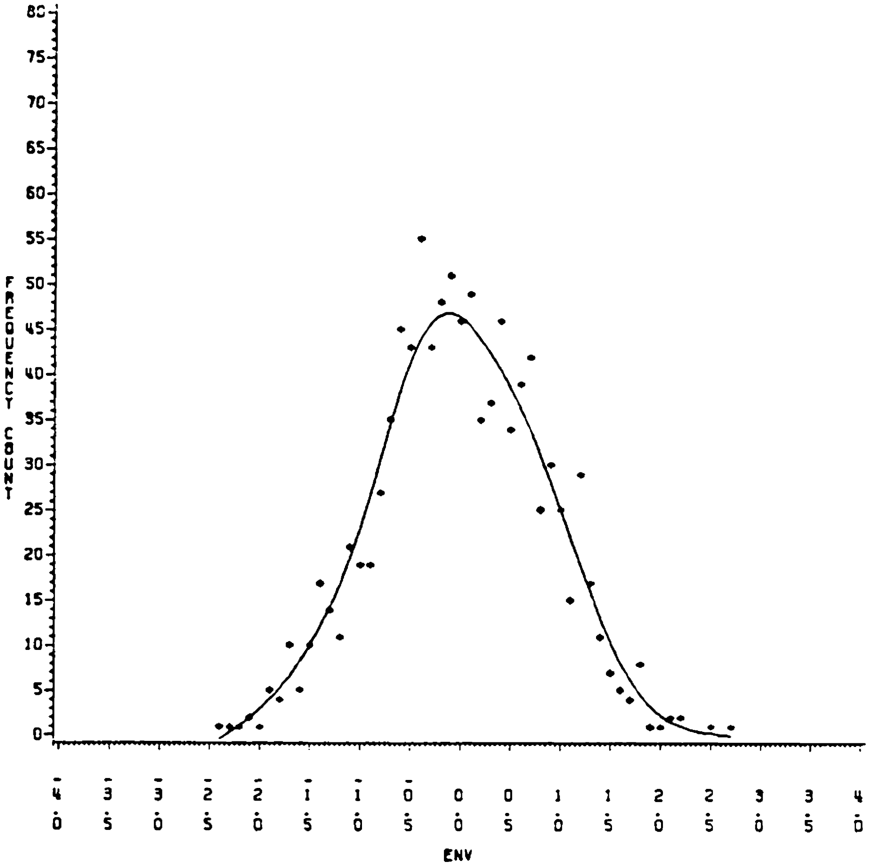

FIGURE 2. UNDERLYING NORMAL ENVIRONMENTAL DISTRIBUTION FOR SINGLE-SERVICE CONCEPTION RATE FROM 1000 SIMULATED DATA POINTS--FREQUENCY COUNT PLOTTED AGAINST ENVIRONMENTAL EFFECT (ENV)

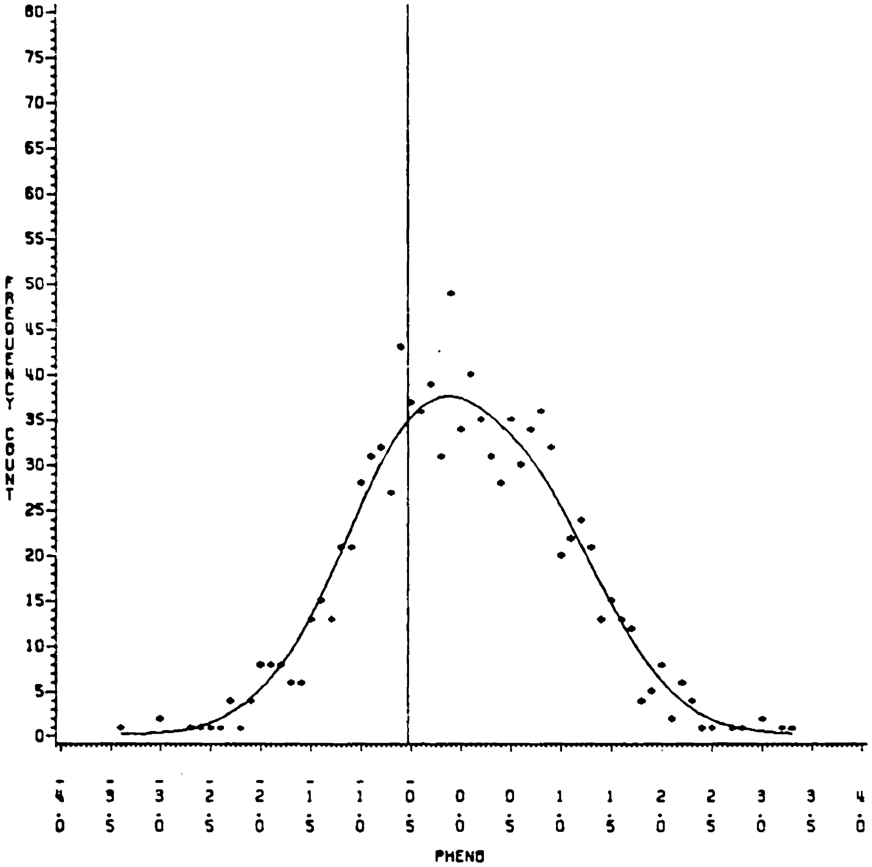

FIGURE 3. UNDERLYING NORMAL PHENOTYPIC DISTRIBUTION FOR SINGLE-SERVICE CONCEPTION RATE FROM 1000 SIMULATED DATA POINTS AND THE POINT OF TRUNCATION-FREQUENCY COUNT PLOTTED AGAINST PHENOTYPE (PHENO)

permanent environmental distribution was also assumed to be normal. The temporary environmental distribution was then assumed to be the skewed distribution that in conjunction with the assumed normal genetic distribution would produce the skewed phenotypic distribution.

The Pearson III gamma distribution was used to simulate the direct or temporary environmental effects for postpartum interval (Newman and Odell, 1971). Gamma distributions provide good descriptions of the distributions of biological waiting periods such as the interval from calving to first estrus. This particular gamma distribution was useful because a minimum could be set which would help in simulating the physiological "recovery time" of a cow after calving.

The frequency of various x values of a Pearson III distribution is given by

$$f(x) = [\frac{1}{\beta\Gamma(p)}] y^{p-1} e^{-y} ,$$

where

$$y = \frac{x-\alpha}{\beta}$$

and where α, β and p are parameters of the distribution. The minimum value is denoted by α, which may assume values from negative to positive infinity. The mean of the distribution is $\alpha + p\beta$ which was set equal to zero and the temporary environmental variance is $p\beta^2$. Both p and β must be greater than zero.

These Pearson III parameters (α, β, p) can be changed to produce curves of different shapes. The parameter p must be an integer, so p was initially set to 1, 2 and 3 and α and β were then determined from these given means and standard deviations from the literature. It was decided that for these simulation purposes the temporary environmental distribution should be strongly skewed so that when combined with the assumed normal genetic and permanent environmental distributions the desired skewed phenotypic distribution would still be produced. Evaluation of the three resulting distributions showed that the parameters when $p = 1$ best fit this criterion since the other two curves more closely approached a normal distribution. The Pearson III distributions where $p = 1$, $p = 2$ and $p = 3$ are shown in figure 4, figure 5 and figure 6, respectively.

The relationship between the genetic, environmental and phenotypic distributions for postpartum interval can be seen in figure 7, figure 8 and figure 9, respectively. A phenotypic distribution was produced with the desired minimum of 25 to 30 d and mean and standard deviation of 70 and 20 d, respectively (Everett et al., 1966).

Simulation of Reproduction

Parameter determination. Four data sets were simulated in which the heritability and repeatability (h^2, t) of both single-service conception rate (binomial) and postpartum

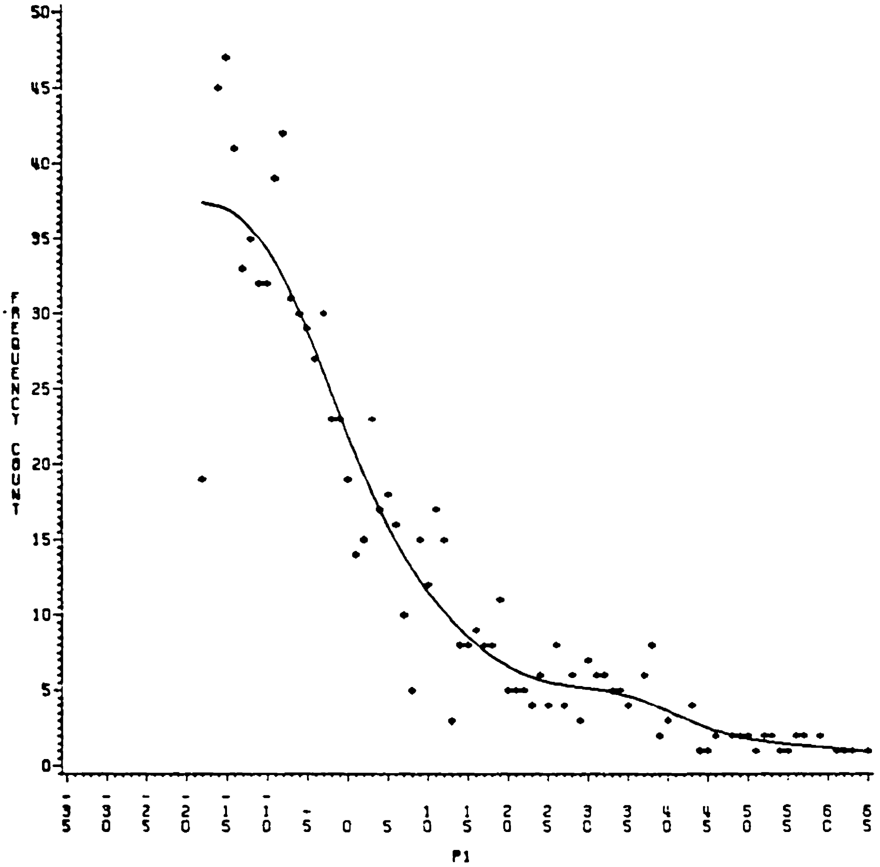

FIGURE 4. PEARSON III DISTRIBUTION WHEN P = 1 (P1) FROM 1000 SIMULATED DATA POINTS--FREQUENCY COUNT PLOTTED AGAINST P1

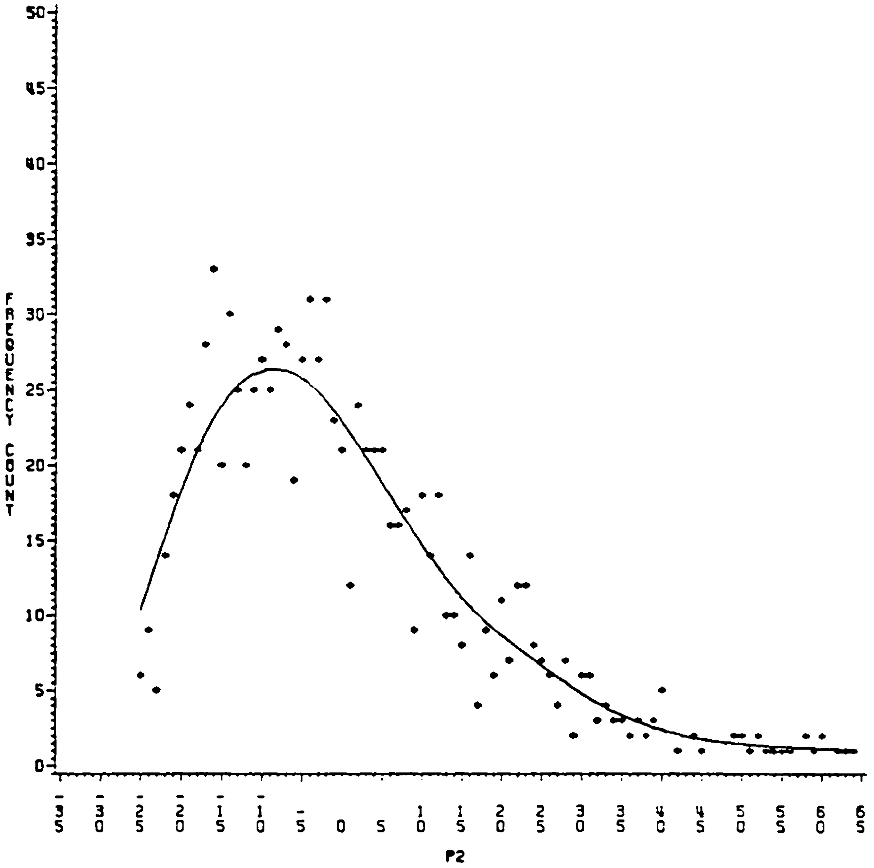

FIGURE 5. PEARSON III DISTRIBUTION WHEN P = 2 (P2) FROM 1000 SIMULATED DATA POINTS--FREQUENCY COUNT PLOTTED AGAINST P2

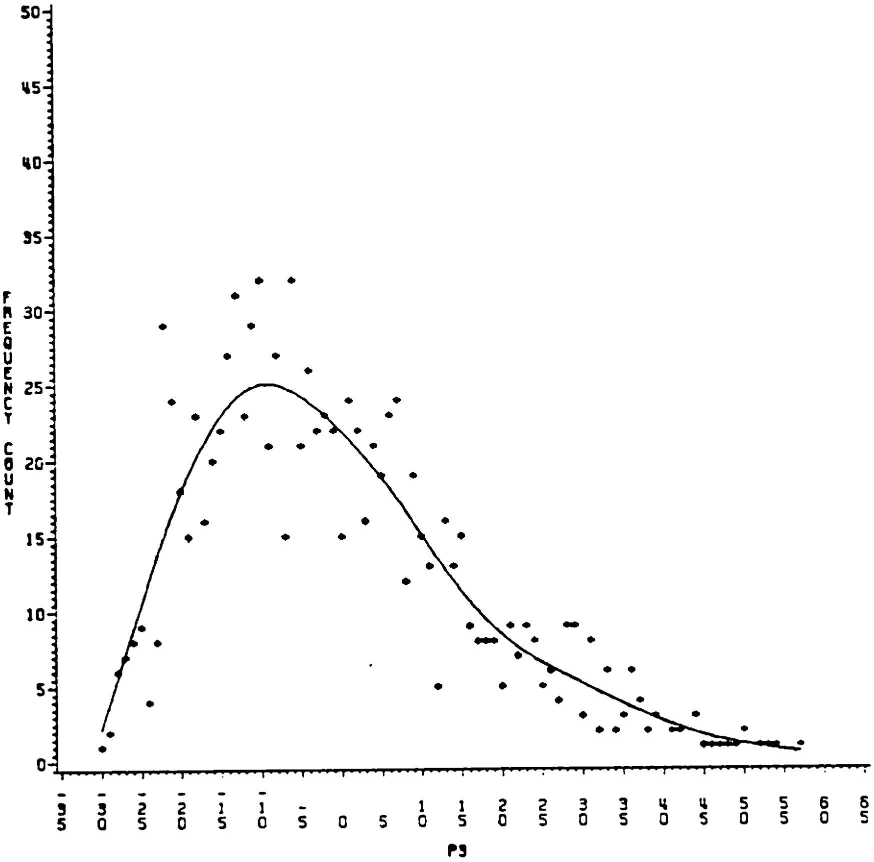

FIGURE 6. PEARSON III DISTRIBUTION WHEN P = 3 (P3) FROM 1000 SIMULATED DATA POINTS--FREQUENCY COUNT PLOTTED AGAINST P3

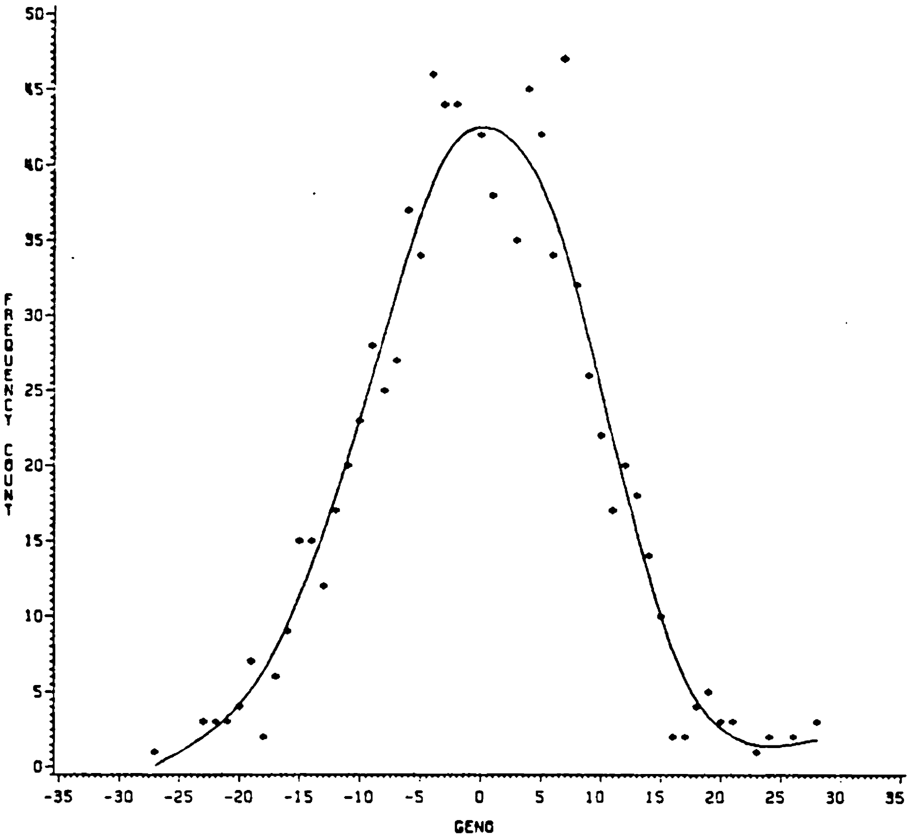

FIGURE 7. GENETIC DISTRIBUTION FOR POSTPARTUM INTERVAL FROM 1000 SIMULATED DATA POINTS--FREQUENCY COUNT PLOTTED AGAINST GENOTYPE (GENO)

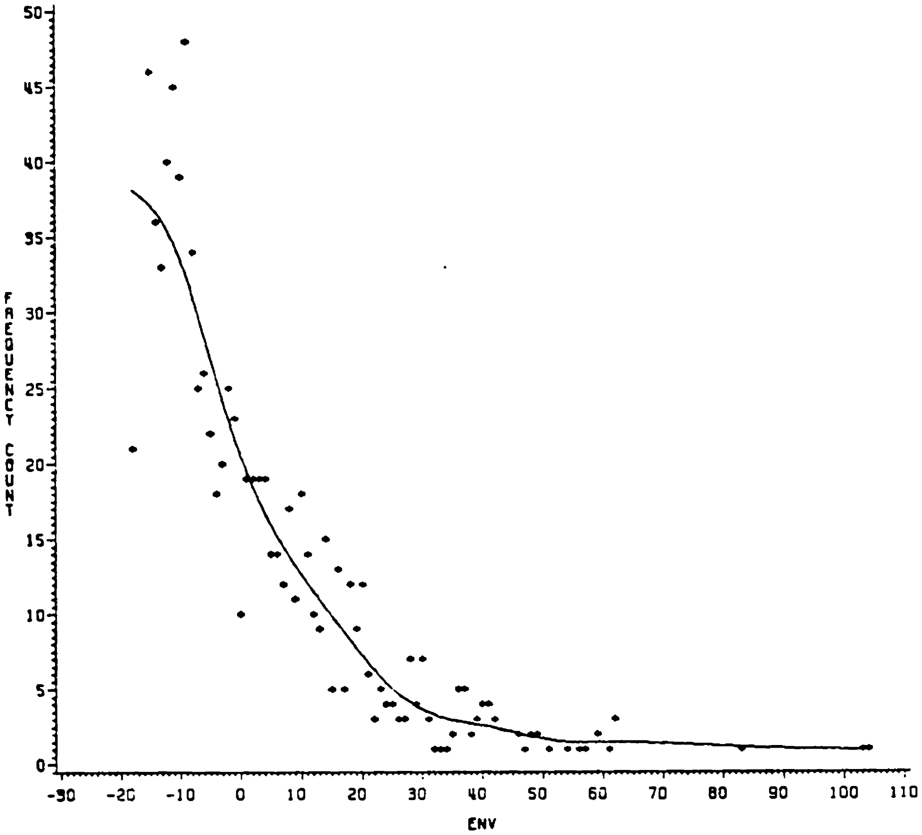

FIGURE 8. ENVIRONMENTAL DISTRIBUTION FOR POST-PARTUM INTERVAL FROM 1000 SIMULATED DATA POINTS--FREQUENCY COUNT PLOTTED AGAINST ENVIRONMENTAL EFFECT (ENV)

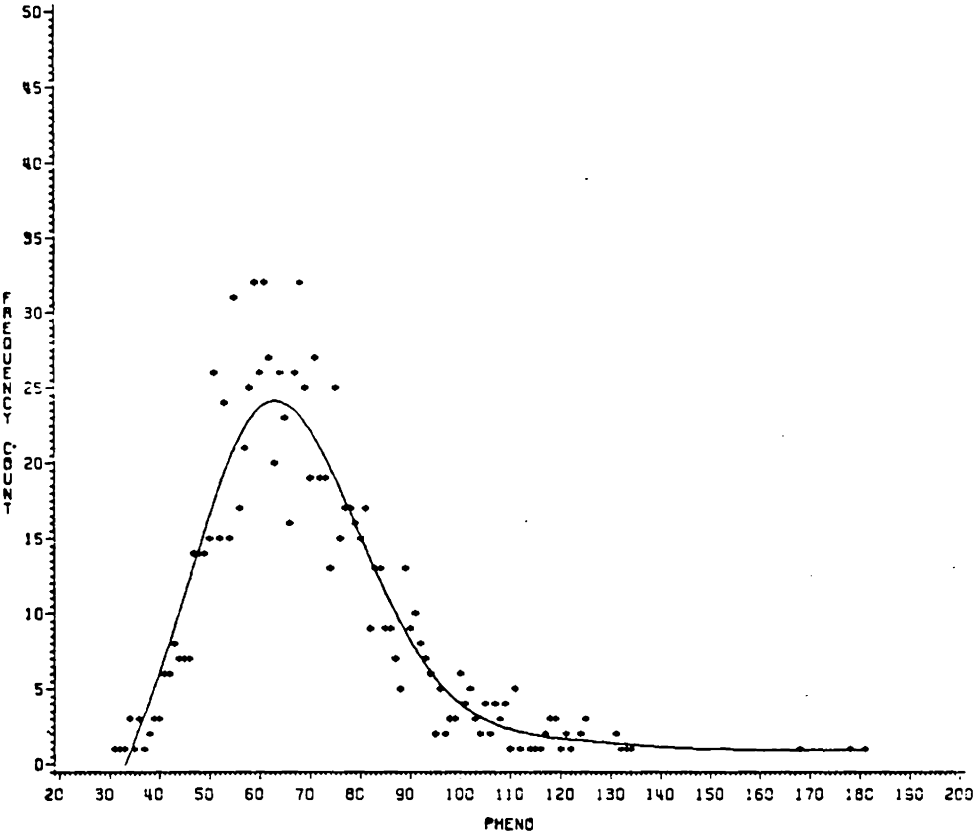

FIGURE 9. PHENOTYPIC DISTRIBUTION FOR POSTPARTUM INTERVAL FROM 1000 SIMULATED DATA POINTS--FREQUENCY COUNT PLOTTED AGAINST PHENOTYPE (PHENO)

interval (days) were (.20, .20), .15, .20), (.10, .10) or (.05, .10). These were chosen to represent the entire range of reported values. The genetic correlation between these two traits was assumed to be zero since none were available from the literature.

Genetic and environmental (temporary and permanent) parameters were derived from these four data sets in order to simulate phenotypic values for individuals. The direct genetic standard deviations for conception rate (DGSDCN) on the assumed underlying normal scale and for postpartum interval (DGSDPI) were calculated by $\sqrt{h^2\sigma_p^2}$. For normal conception rate $h^2 = h_N^2$ and since $\sigma_p^2 = 1$ (standard normal variance) this reduces to DGSDCN = $\sqrt{h_N^2}$.

The direct or temporary environmental standard deviations for conception rate on the normal scale (DESDCN) and for postpartum interval (DESDPI) were determined by $\sqrt{(1-t)\sigma_p^2}$. For normal conception rate $t = t_N$ so this reduces to DESDCN = $\sqrt{(1-t_N)}$.

When a permanent environmental factor was introduced the permanent environmental standard deviations for conception rate on the normal scale (PESDCN) and postpartum interval (PESDPI) were found by $\sqrt{(t-h^2)\sigma_p^2}$. Both t and h^2 equal their transformed counterparts on the underlying normal scale for conception rate so this reduces to PESDCN = $\sqrt{(t_N-h_N^2)}$. The conception rate and postpartum interval parameters used in each of the four data sets are shown in table 1 and table 2, respectively.

Genetic mechanism and phenotype simulation. The genetic and environmental parameters were used to simulate the genetic mechanism. This procedure involved not only simulation of the inheritance of genes and their effects but also of temporary and permanent environmental effects which influenced an individual's phenotype.

For the base generation, genetic standard deviations were multiplied by a random normal deviate to achieve breeding values for individuals from a normal distribution of values. Random normal deviates were generated in the same manner as in the original program by using a modification of the Box-Mueller method (Willham and Thomson, 1970). Breeding values remained constant throughout an individual's lifetime. Environmental standard deviations (temporary and permanent) were multiplied by a deviate from the chosen distribution to generate environmental effects from the particular distribution of effects. Random gamma variates from the Pearson III distribution were derived from the following formula:

$$W = -\beta \ln \prod_{i=1}^{K} U_i ,$$

where U_i are independent random uniform variables (Newman and Odell, 1971). The random variates were then coded to a specific distribution by adding them to the minimum

TABLE 1. NORMAL CONCEPTION RATE PARAMETERS

Item[a]	Run 1	Run 2	Run 3	Run 4
h^2_B	.20	.15	.10	.05
t_B	.20	.20	.10	.10
h^2_N	.35	.26	.17	.09
t_N	.35	.35	.17	.17
DGSDCN	.59	.51	.42	.29
DESDCN	.81	.81	.91	.91
PESDCN	.00	.29	.00	.29

[a] h^2_B = binomial heritability
t_B = binomial repeatability
h^2_N = normal heritability
t_N = normal repeatability
DGSDCN = genetic standard deviation
DESDCN = temporary environmental standard deviation
PESDCN = permanent environmental standard deviation.

TABLE 2. POSTPARTUM INTERVAL PARAMETERS

Item[a]	Run 1	Run 2	Run 3	Run 4
h^2	.20	.15	.10	.05
t	.20	.20	.10	.10
DGSDPI	8.94	7.75	6.32	4.47
DESDPI	17.89	17.89	18.97	18.97
PESDPI	.00	4.47	.00	4.47

[a] h^2 = heritability
t = repeatability
DGSDPI = genetic standard deviation
DESDPI = temporary environmental standard deviation
PESDPI = permanent environmental standard deviation

value (α). Permanent environmental effects were constant throughout an individual's life, whereas, temporary environmental effects were generated each time a phenotype for an individual was simulated and were not correlated within or between years.

In subsequent generations, a progeny individual's breeding value was determined by the sum of one-half of the breeding value of each parent and a component due to Mendelian segregation. This produced the desired resemblance for the basis of evaluation of traits. Environmental effects were generated as they were for the base generation.

Phenotypes for all generations were derived from the sum of the mean for the trait, the breeding value and environmental effects for an individual. Herd effects were assumed to be zero for this program.

The phenotype for adjusted 205-d weaning weight (205WW) was simulated in the same manner as in R. L. Willham's original program. Actual weaning weight was added to the current program. If a calf was born on day 30 of the calving season, then it was assumed weaned at exactly 205 d, therefore, no adjustment was needed to calculate actual weaning weight. If a calf was born on any day other than day 30, then an adjustment was made. Birth weight was assumed to be 70 lb (Bellows et al., 1974), so average daily gain (ADG) was calculated as

$$ADG = \frac{205WW - 70}{205} .$$

The weaning weight adjustment (WWADJ) needed to calculate actual weaning weight was calculated as

$$WWADJ = ADG(\text{Birth date} - 30).$$

Actual weaning weight (ACTWW) was then calculated as

$$ACTWW = 205WW - WWADJ.$$

The simulation of the underlying phenotype for single-service conception rate follows the same path as that for 205-d adjusted weaning weight since all distributions involved (genetic and environmental) were assumed normal. Reproductive phenotypes were only generated for females in the population. A phenotype was determined by the sum of the breeding value of a cow, the temporary environmental effect for a single service and any permanent environmental factor. The truncation point for the assumed 70% single-service conception occurred at .53 phenotypic standard deviations below the mean of zero. A binomial phenotype of 1 was achieved if the underlying normal phenotype for conception rate was greater than -.53, otherwise the binomial phenotype was zero, which indicated that conception had not occurred.

The phenotype for postpartum interval was simulated as the sum of the mean of 70 d, the breeding value and permanent environmental effects from the assumed normal distributions, and the temporary environmental effect from the Pearson III gamma distribution.

The combined phenotypes for single-service conception rate and days postpartum to first estrus of cows and for weaning weight of calves describe the reproductive as well as productive capacity and potential of beef cows.

First breeding simulation. All cows were assumed to be cycling at the beginning of the first breeding season, since no previous reproduction information was available. Date of first breeding was assumed randomly and uniformly distributed about a 21-d period. Single-service conception rate phenotypes were simulated and tested up to and including three times for each individual. The binomial phenotype for first service conception rate was treated as a value separate from annual conception rate (binomial). The date of first service was incremented by 21 d for each new service to simulate the date of breeding and possibly conception for the second and third services, if needed.

If conception was achieved at any time during the breeding season, then a value of 1 was assigned to binomial conception rate, and this value was stored along with the values simulated for date of first service, first service conception rate, the number of services received and date of conception. If conception did not occur during the breeding season, then binomial conception rate and date of conception were set to zero, the number of services received remained three and the same information was stored. These same reproductive outputs were stored every year for every cow regardless of conception status.

Cows were assigned to sires through the use of an algorithm that ensured that each year a cow was bred to a different service sire even though service sires had no effect on cow reproduction. This served to cross classify service sires with the sires of the cows so that there was no confounding. The resulting calf crop was produced from these sire-dam combinations and the stored reproduction information.

Calving simulation. The birth date of the calves, or the calving date of the cows within the calving season, was assumed to be equal to the conception date of the cow within the breeding season, since no variation in gestation length was assumed. Gestation length was assumed to be 276 d.

The random death rate of calves was assumed to be 10% of those conceived (Wiltbank et al., 1961). Only calves that survived to weaning were assigned breeding values and environmental effects so that phenotypes could be derived.

The weaning weight of the calves was included to determine cow producing ability in terms of pounds of calf produced at weaning. No genetic correlation between weaning weight and reproduction was assumed. Adjusted 205-d weaning weight as well as actual weight was simulated. Both of these weights were stored in the cow's record as well as the calf's.

Rebreeding simulation. Cows that did not produce a calf because they did not conceive or because the calf died were bred for the next season just as they were for the first. All cows in this group were again assumed to be cycling at the beginning of the breeding season and they had three opportunities at which to conceive. After conception, or at the end of the breeding season, the same reproductive information was stored.

A postpartum interval phenotype was simulated for all cows that produced a calf. This interval was used to simulate breeding phenotypes for the upcoming breeding season.

The new first breeding date for those cows that calved was calculated as the date of calving plus the postpartum interval with the restriction that breeding date had to fall at least 89 d after the start of the calving season (63-d calving season plus 26 d to start of breeding) in order for the date to fall within the breeding season. If this was not the case then the breeding date was incremented by 21 d until the breeding date was finally within the breeding season.

Once this was attained, date of first service was calculated as the breeding date minus 88 d to retain the framework of the 63-d breeding season. If date of first service was greater than 63 d, then the cow had missed the breeding season and therefore her chance to be bred that season. In this case, date of first service was retained and number of services and date of conception were set to zero.

If the date of first service was within the breeding season, then simulation of reproduction was the same as for the first breeding season. Potentially, cows still had three opportunities at which to conceive as long as the date at any one service was less than 63 d. Whenever conception occurred or 63 d was exceeded, then the generated reproductive outputs were stored for use in the next calving season.

The principle difference between this breeding scheme and that for the first season is that not every cow was cycling at the beginning of the breeding season. In fact, some missed the breeding season entirely.

Statistical Analysis

As previously stated, four data sets were simulated with different heritabilities and repeatabilities that covered the range of reported values. Each data set consisted of records on 100 herds of 50 cows produced from 5 sires and serviced by 5 different sires. Records were simulated on the cows for 6 years. The first year of data was deleted since no previous calving information was available.

The model. Year effects were not significant in a preliminary analysis, therefore, year was not included in the model. This was expected since no year effects were included, but it was encouraging that the simulation program did not generate yearly trends.

A nested analysis was performed since sires of the cows occurred only within one herd and cows occurred only within one sire. The NESTED procedure of the Statistical Analysis System (Barr et al., 1979) was used to perform calculations. The model was

$$Y_{ijkl} = \mu + H_i + S_{j(i)} + C_{k(j(i))} + e_{ijkl}$$

where μ is the mean of the dependent variable, H_i is an effect due to the i-th herd, $S_{j(i)}$ is the effect of the j-th sire within the i-th herd, $C_{k(j(i))}$ is an effect due to the k-th cow within the j-th sire within the i-th herd, and e_{ijkl} is random error associated with the individual observation. All effects were assumed to be random. The sources of variation and expected mean squares associated with this model are shown in table 3.

The NESTED procedure was used since it is efficient, especially for designs involving large numbers of observations. Mean squares, estimates of variance components and

TABLE 3. NESTED ANALYSIS OF VARIANCE OF REPRODUCTIVE PERFORMANCE FOR BEEF COWS - SOURCES OF VARIATION AND EXPECTED MEAN SQUARES

Source of variation	E(MS)[a]
Herd	$\sigma_e^2 + K\sigma_{C/S/H}^2 + K'\sigma_{S/H}^2 + K''\sigma_H^2$
Sire/herd	$\sigma_e^2 + K\sigma_{C/S/H}^2 + K'\sigma_{S/H}^2$
Cow/sire/herd	$\sigma_e^2 + K\sigma_{C/S/H}^2$
Error	σ_e^2

[a] K, K' and K" are the coefficients associated with the variance components for random effects.

coefficients of the variance components necessary for the estimation of genetic parameters and their standard errors were calculated. Variance component correlations were also calculated for use in estimation of genetic and environmental correlations.

The analysis. Two analyses were performed on each data set. The first analysis was conducted on the entire set of data while the second assumed that cows that failed to calve in a given year were culled. Thus, if a cow did not conceive in one year, then that year's record was kept, but her subsequent records were deleted.

For both analyses, the evaluation of the reproductive traits fell into four groups. Binomial conception rate, actual weaning weight and the percentage of cows that mated were analyzed for all cows that were exposed. Date of first service, number of services and first service conception rate were evaluated for all cows that were bred during the breeding season. Date of first service, number of services, calving date and actual weaning weight were also analyzed for all cows that conceived or calved. Actual weaning weight, adjusted 205-d weaning weight and postpartum interval were evaluated for all cows that weaned a live calf.

Estimates of genetic parameters. A pedigreed cow herd was simulated as the base generation cow herd so that analyses for genetic parameters could be conducted on halfsister groups. The heritabilities (h^2) and repeatabilities (t) of cow reproductive traits were estimated from variance components derived from the nested analysis using the following formulas:

$$h^2 = \frac{4\sigma^2_{S/H}}{\sigma^2_{S/H} + \sigma^2_{C/S/H} + \sigma^2_e} = \frac{\text{variance between families}}{\text{total variance}}$$

and

$$t = \frac{\sigma^2_{S/H} + \sigma^2_{C/S/H}}{\sigma^2_{S/H} + \sigma^2_{C/S/H} + \sigma^2_e} = \frac{\text{cow variance}}{\text{total variance}} ,$$

where $\sigma^2_{S/H}$, $\sigma^2_{C/S/H}$ and σ^2_e are the sire within herd, cow within sire within herd and residual error variances, respectively. The underlying assumption is that only genetic effects make progeny resemble one another; no environmental correlations between the half-sib cows was assumed.

The heritability and repeatability estimates obtained from the first analysis on the entire data set should reflect the genetic and permanent environmental variance present in the population. The estimates obtained from the analysis on the culled data set could be biased downward by the effect from selection.

Standard errors of estimates. Standard errors of heritability (h^2) and repeatability (t) estimates were calculated as (Dickerson, 1969):

$$\sigma_{h^2} = \frac{4}{\sigma^2_{S/H} + \sigma^2_{C/S/H} + \sigma^2_e}\sqrt{V(\,{}^{2}_{S/H})}$$

and

$$\sigma_t = \frac{\sqrt{V(\sigma^2_{S/H} + \sigma^2_{C/S/H})}}{\sigma^2_{S/H} + \sigma^2_{C/S/H} + \sigma^2_e}$$

where

$$V(\sigma^2_{S/H}) = \frac{2}{K^2_{SS}}\left(\frac{MS(S/H)^2}{df_{S/H}} + \frac{MS(C/S/H)^2}{df_{C/S/H}}\right)$$

and

$$V(\sigma^2_{S/H} + \sigma^2_{C/S/H}) = \left[\frac{2}{K^2_{SS}}\left(\frac{MS(S/H)^2}{df_{S/H}} + \frac{MS(C/S/H)^2}{df_{C/S/H}}\right)\right] +$$

$$\left[\frac{2}{K^2_{CC}}\left(\frac{MS(C/S/H)^2}{df_{C/S/H}} + \frac{MS(E)^2}{df_E}\right)\right] +$$

$$2\left[\frac{-2}{K_{SS}K_{CC}}\left(\frac{MS(C/S/H)}{df_{C/S/H}}\right)\right]$$

These theoretical standard errors were compared with empirical standard errors of both heritabilities and repeatabilities. To do this, separate h^2 and t estimates were calculated from 50 sets of data each consisting of 10 herds with 50 cows each from 5 sires using the parameters from the data set where heritability was .15 and repeatability was .20. The empirical standard error of these estimates was calculated and compared with the theoretical standard error. The mean square and k values for estimation of the theoretical standard errors were obtained from a single analysis on all 500 herds and were considered to be population parameters. The degrees of freedom used for the theoretical computation were obtained from the individual analyses of 10 herds so that comparisons could be made between theoretical and empirical estimates.

Correlation of reproduction with actual weaning weight. The NESTED procedure also calculated the variance component correlations between traits from an analysis of covariance. The sire variance component correlation was the relationship between the additive genetic variance of two traits (the genetic correlation). The error variance component correlation was the correlation of environmental deviations (the environmental correlation). Estimates of genetic and environmental correlations were calculated for all traits output with actual weaning weight to determine the relationship between reproduction and production.

The response of a correlated character can be predicted if the genetic correlation and the heritabilities of the two characters are known. The correlated response of actual weaning weight per cow exposed (CR_{WW}) was calculated as

$$CR_{WW} = h_X h_{WW} r_G ,$$

where h_X is the square root of the heritability of the directly selected trait, h_{WW} is the square root of the heritability of actual weaning weight per cow exposed and r_G is the genetic correlation between the two traits. The intensity of selection for reproduction was assumed to be the same for all traits. The response of actual weaning weight per cow exposed, when directly selected, was determined by h^2_{WW}. The correlated response of weaning weight was compared to the response from direct selection of weaning weight to determine the impact that selection for reproduction would have on actual weaning weight per cow exposed.

RESULTS AND DISCUSSION

General Simulation Results

The general simulation results in terms of frequencies, means and standard deviations served to build confidence in the modified simulation model. These results were very close to values found in the literature and, thus, tended to support the subsequent heritability and repeatability estimation.

Table 4 contains pooled frequency values for the simulated reproductive traits. When all data were analyzed, it was found that all cows were bred at least once in the 5 yr of the study. However, an average of .2% of the cows never conceived and .3% never weaned a calf during this time span. These results translated into an average of 10 and 15 "barren" cows per 5000 cows, respectively.

In any given year an average of 2.2% of the cows missed the breeding season because they never cycled and therefore were never bred. Wiltbank et al. (1961) reported that 1.5% of heifers and cows did not cycle during a breeding season. Dearborn et al. (1973) determined that 99% of unselected heifers and all cows cycled during the breeding season over a 4 and 6 yr period, respectively.

An average of 88% of the cows calved and 76.8% weaned

TABLE 4. POOLED FREQUENCY VALUES OF THE PERCENTAGE OF COWS WITH AT LEAST ONE RECORD FOR ALL YEARS (% COWS) AND THE PERCENTAGE OF COWS WITH RECORDS IN ANY ONE YEAR (% RECORDS) FOR SIMULATED REPRODUCTIVE TRAITS FROM DIFFERENT TYPES OF RECORDS

Type of records	All data % cows	 % records	Culled data % cows	 % records	Traits[a]
All cows	100	100	100	80.1 (100)[b]	BCR, ACTWW, MATE
Cows that were bred	100	97.8	98.4	78.5 (98.0)	FS,NS,FSCR,ACTWW
Cows that conceived	99.8	88.0	89.9	73.9 (92.2)	FS,NS,CD,ACTWW
Cows that weaned a calf	99.7	76.8	89.3	64.4 (80.4)	ADJWW,ACTWW,PPI

[a] BCR = binomial conception rate
ACTWW = actual weaning weight
MATE = percent mated
FS = date of first service
NS = number of services
FSCR = first service conception rate
CD = calving date
ADJWW = adjusted weaning weight
PPI = postpartum interval.

[b] Numbers in parentheses indicate the percentage of cows in the culled data base with records in any one year.

a calf in any given year. Wiltbank et al. (1961), Dearborn et al. (1973) and Bellows et al. (1974) reported values of 86%, 85% and 81%, respectively, for cows that calved and 70% 78% and 75%, respectively, for cows that weaned a calf.

An average of 20% of the cows were culled from the complete data set for failure to conceive in any given year. A somewhat lower value of 15% was reported by Greer et al. (1979). Of this culled base, an average of 98% of the cows were bred, 92.2% conceived or calved and 80.4% weaned a calf in any given year. All of these values are higher than those for the complete data set. This result was expected because cows were culled on the basis of conception.

The means and standard deviations of all reproductive outputs are listed in table 5. An average of 98% of all cows mated each year, as indicated in the previous findings of the frequency analysis. First service conception rate averaged 70% and 74% for the complete and culled data sets, respectively. Wiltbank et al. (1961) determined a first service conception rate of 65% for heifers and cows. Bellows et al. (1974) reported than an average of 61.5% of heifers and 74.5% of lactating cows conceived at their first service. Annual conception rate was 90% for all data and 92% for culled data. Wiltbank et al. (1961) and Dearborn et al. (1973) found values of 88% and 89%,

TABLE 5. POOLED ESTIMATES OF MEANS AND STANDARD DEVIATIONS (SD) FOR SIMULATED REPRODUCTIVE TRAITS FROM DIFFERENT TYPES OF RECORDS

Type of records	Trait[a]	All data		Culled data	
		Mean	SD	Mean	SD
All cows	BCR	.90	.28	.92	.23
	ACTWW	380.49	183.53	387.52	174.73
	MATE	.98	.13	.98	.12
Cows that were bred	FS	14.78	10.50	15.04	10.19
	NS	1.39	.61	1.34	.56
	FSCR	.70	.42	.74	.41
	ACTWW	387.37	177.27	395.02	168.77
Cows that conceived	FS	14.22	9.74	14.45	9.69
	NS	1.30	.54	1.27	.51
	CD	20.50	13.79	20.20	13.31
	ACTWW	420.92	150.14	421.64	151.01
Cows that weaned a calf	ADJWW	449.98	45.15	450.05	45.19
	ACTWW	467.60	53.93	468.25	53.69
	PPI	69.55	18.44	69.35	17.70

[a] See table 4 for definition of traits.

respectively, for cows diagnosed pregnant at the end of the breeding season.

Date of first service was evaluated for all cows that were bred and also for those that conceived. The means of both were very close, but the cows that conceived had a slightly earlier date of first service. Cows that are bred earliest in the breeding season have a better chance to ultimately conceive due to an increased number of opportunities for conception.

The number of services received by a cow in a breeding season were also evaluated for all cows that were bred and for those that conceived. The average number of services received for the complete and culled data sets were 1.39 and 1.34, respectively, for cows that were bred and 1.30 and 1.27, respectively, for cows that conceived. Lindley et al. (1958), Everett et al. (1966) and Short et al. (1972) reported values of 1.7, 1.95 and 1.93, respectively. Wiltbank et al. (1961) determined values for services per conception of 1.49 for all cows and 1.34 for cows that conceived.

The initial mean of adjusted 205-d weaning weight in the simulation program was 450 lb (Willham and Thomson, 1970). The means that were output for the complete and culled data sets were 449.98 lb and 450.05 lb, respectively. The simulation of weaning weight phenotypes was not affected by the simulation of reproduction when weaning weight was evaluated for cows that weaned a calf. This was expected since the genetic correlation between reproduction and weaning weight was assumed to be zero.

Actual weaning weight was evaluated for all four types of records: cows exposed (all cows), cows that were bred, cows that conceived, and cows that weaned a calf. The means of the first three categories were lower than the last because of the inclusion of dead calves and reproductive failures. The mean of actual weaning weight per cow that weaned a calf was higher than that for adjusted 205-d weaning weight since the mean calving date of the cows (birth date of the calves) was day 20 which was less than the day 30 calving date associated with adjusted 205-d weaning weight.

For the complete and culled data sets, the means of postpartum interval were 69.55 d and 69.35 d, respectively, and the pooled standard deviations were 18.44 d and 17.70 d, respectively. The initial mean and standard deviation of the simulation program were 70 d and 20 d, respectively (Everett et al., 1966).

Heritabilities and Repeatabilities

Heritability and repeatability estimates were calculated from sire, cow and error variance components obtained from a nested analysis performed on data collected on half-sisters. The sire component is an estimate of the variance between the records of daughter groups of a sire and represents one-quarter of the additive genetic variance for reproductive traits. The cow component (nested within sires) is an estimate of the variance between cow records and represents three-quarters of the additive genetic variance and the permanent environmental variance. The error component is an estimate of the variance among records of a cow and represents true random error associated with the temporary environmental variance.

The variance components that were used to calculate heritability and repeatability estimates for percentage of cows that mated, annual conception rate (binomial) and first service conception rate are found in table 6. Table 7 contains the heritability and repeatability estimates for these traits.

Heritabilities and repeatabilities for the trait "percent mated" estimated from all of the data were negative in all except one case. The sire and cow variance components were very close to zero. On the average, 98% of the cows mated every year which implied that there was little or no variance between the mating rate of daughter groups or of cows. The positive and moderate repeatability estimates from the culled data indicated that cows selected on the basis of conception tended to mate each year and were

TABLE 6. ESTIMATES OF SIRE ($\sigma^2_{S/H}$), COW ($\sigma^2_{C/S/H}$) AND ERROR (σ^2_E) VARIANCE COMPONENTS FOR PERCENT MATED (MATE), ANNUAL CONCEPTION RATE (BCR) AND FIRST SERVICE CONCEPTION RATE (FSCR) FROM DIFFERENT TYPES OF RECORDS

Type of records	Trait	Data set (h^2,t)	All data			Culled data		
			$\sigma^2_{S/H}$	$\sigma^2_{C/S/H}$	σ^2_E	$\sigma^2_{S/H}$	$\sigma^2_{C/S/H}$	σ^2_E
All cows	MATE	Run1 (.20,.20)	-.00001	-.00009	.01698	-.00043	.00513	.01310
		Run2 (.15,.20)	.00004	-.00022	.01662	-.00036	.00502	.01281
		Run3 (.10,.10)	-.00002	-.00022	.01888	-.00050	.00568	.01520
		Run4 (.05,.10)	-	-	-[a]	-.00053	.00635	.01306
All cows	BCR	Run1 (.20,.20)	.0039	.0131	.0787	-.0001	.0251	.0515
		Run2 (.15,.20)	.0023	.0135	.0791	-.0010	.0260	.0510
		Run3 (.10,.10)	.0009	.0024	.0727	-.0009	.0219	.0505
		Run4 (.05,.10)	.0006	.0042	.0753	-.0015	.0243	.0509
Cows bred	FSCR	Run1 (.20,.20)	.010	.035	.166	.005	.025	.156
		Run2 (.15,.20)	.007	.038	.164	.003	.030	.152
		Run3 (.10,.10)	.004	.015	.191	.003	.016	.179
		Run4 (.05,.10)	.003	.020	.190	.001	.019	.179

[a] Data not available due to tape malfunction.

TABLE 7. ESTIMATES OF HERITABILITY (h^2) AND REPEATABILITY (t) FOR PERCENT MATED (MATE), ANNUAL CONCEPTION RATE (BCR) AND FIRST SERVICE CONCEPTION RATE (FSCR) FROM DIFFERENT TYPES OF RECORDS

Type of records	Trait	Data set (h^2,t)	All data		Culled data	
			h^2	t	h^2	t
All cows	MATE	Run1 (.20,.20)	-.002 ± .006	-.006 ± .004	-.097 ± .008	.264 ± .009
		Run2 (.15,.20)	.010 ± .006	-.011 ± .005	-.082 ± .009	.267 ± .009
		Run3 (.10,.10)	-.004 ± .005	-.013 ± .004	-.098 ± .008	.254 ± .009
		Run4 (.05,.10)	-	- [a]	-.112 ± .008	.308 ± .010
All cows	BCR	Run1 (.20,.20)	.165 ± .020	.178 ± .008	-.007 ± .020	.326 ± .015
		Run2 (.15,.20)	.096 ± .016	.166 ± .007	-.054 ± .012	.329 ± .010
		Run3 (.10,.10)	.046 ± .010	.043 ± .004	-.049 ± .011	.294 ± .009
		Run4 (.05,.10)	.028 ± .009	.059 ± .005	-.081 ± .010	.309 ± .010
Cows bred	FSCR	Run1 (.20,.20)	.187 ± .023	.212 ± .008	.105 ± .018	.162 ± .008
		Run2 (.15,.20)	.131 ± .019	.216 ± .008	.072 ± .016	.181 ± .008
		Run3 (.10,.10)	.079 ± .013	.093 ± .006	.051 ± .012	.092 ± .007
		Run4 (.05,.10)	.055 ± .012	.108 ± .006	-.024 ± .011	.100 ± .007

[a] Data not available due to tape malfunction.

not allowed to miss the breeding season more than once due to reproductive failure.

The heritability and repeatability estimates for annual conception rate were somewhat lower than the initial program parameters, but were significantly different from zero. This decrease could be due to the three-time truncation of the assumed normal underlying phenotypic distribution for single-service conception rate that determined annual conception rate. The mean annual conception was 90%, and it is highly unlikely that genes would have the same effects near the limits of a distribution as in the middle of the range. Dearborn et al. (1973) reported a heritability estimate of .09 ± .14 for the trait "pregnant at the end of the breeding season" which is comparable to annual conception rate. The moderate repeatability estimated from the culled data was generated from the binomial scoring system. Culling on the basis of conception produced an automatic and predictable variance between cow records.

First service conception rate was the portion of annual conception rate that was indicative of the first truncation of the normal underlying phenotypic distribution of conception rate. The estimated heritabilities and repeatabilities were markedly close to those that were input. When Dearborn et al. (1973) subdivided the lowly heritable trait of "pregnant at the end of the breeding season" (h^2 = .09 ± .14) into a class recorded as first service conception rate, an increase in genetic variation as seen through the reported heritability of .22 ± .17 was noted. The increased heritability estimate for first service conception rate resulted from partitioning first service conception from subsequent conceptions and failures to conceive.

Date of first service and the number of services that a cow received per breeding season were evaluated for cows that were bred and also for cows that conceived. The variance components are contained in table 8 and the heritability and repeatability estimates are in table 9.

The heritabilities of date of first service per cow bred and date of first service per cow conceiving, estimated from all of the data, were essentially zero and followed no trend for the four runs. Over the 5 yr of the study, an average of 64% of the cows were cycling before the beginning of each breeding season. The date of first service then largely became a random event, and this fact caused a reduction in the expression of genetic variation as indicated by the low heritabilities. The repeatabilities were much higher than the heritabilities and were possibly generated by effects due to the length of intervals in the reproductive cycle which could produce a lower limit to the time that must elapse between successive first services.

TABLE 8. ESTIMATES OF SIRE ($\sigma^2_{S/H}$), COW ($\sigma^2_{C/S/H}$) AND ERROR (σ^2_E) VARIANCE COMPONENTS FOR DATE OF FIRST SERVICE (FS) AND NUMBER OF SERVICES RECEIVED (NS) FROM DIFFERENT TYPES OF RECORDS

Type of records	Trait	Data set (h^2,t)	All data			Culled data		
			$\sigma^2_{S/H}$	$\sigma^2_{C/S/H}$	σ^2_E	$\sigma^2_{S/H}$	$\sigma^2_{C/S/H}$	σ^2_E
Cows bred	FS	Run1 (.20,.20)	.42	13.77	108.23	.02	25.57	102.42
		Run2 (.15,.20)	.15	14.68	108.09	-.30	26.05	101.84
		Run3 (.10,.10)	.54	10.05	113.20	.13	20.99	106.34
		Run4 (.05,.10)	.33	11.06	111.24	.05	21.88	104.83
Cows conceiving	FS	Run1 (.20,.20)	.63	12.81	94.77	.38	18.91	93.54
		Run2 (.15,.20)	.35	14.38	93.18	.19	20.11	91.80
		Run3 (.10,.10)	.43	10.26	96.88	.36	13.82	96.20
		Run4 (.05,.10)	.27	10.43	94.78	.22	14.92	94.07
Cows bred	NS	Run1 (.20,.20)	.027	.088	.353	.009	.079	.297
		Run2 (.15,.20)	.017	.100	.357	.005	.092	.295
		Run3 (.10,.10)	.009	.034	.377	.004	.053	.330
		Run4 (.05,.10)	.008	.044	.384	.002	.060	.338
Cows conceiving	NS	Run1 (.20,.20)	.007	.034	.275	.004	.032	.245
		Run2 (.15,.20)	.004	.041	.276	.002	.043	.243
		Run3 (.10,.10)	.003	.014	.309	.002	.022	.284
		Run4 (.05,.10)	.003	.021	.308	.001	.026	.287

TABLE 9. ESTIMATES OF HERITABILITY (h^2) AND REPEATABILITY (t) FOR DATE OF FIRST SERVICE (FS) AND NUMBER OF SERVICES RECEIVED (NS) FROM DIFFERENT TYPES OF RECORDS

Type of records	Trait	Data set (h^2,t)	All data		Culled data	
			h^2	t	h^2	t
Cows bred	FS	Run1 (.20,.20)	.014 ± .010	.116 ± .006	.001 ± .012	.200 ± .008
		Run2 (.15,.20)	.005 ± .009	.121 ± .006	-.009 ± .012	.202 ± .008
		Run3 (.10,.10)	.017 ± .009	.085 ± .006	.004 ± .012	.166 ± .008
		Run4 (.05,.10)	.011 ± .009	.093 ± .006	.002 ± .012	.173 ± .008
Cows conceiving	FS	Run1 (.20,.20)	.023 ± .011	.125 ± .007	.013 ± .013	.171 ± .008
		Run2 (.15,.20)	.013 ± .011	.136 ± .007	.007 ± .013	.181 ± .008
		Run3 (.10,.10)	.016 ± .010	.099 ± .006	.013 ± .012	.128 ± .008
		Run4 (.05,.10)	.010 ± .009	.101 ± .006	.008 ± .012	.139 ± .008
Cows bred	NS	Run1 (.20,.20)	.227 ± .026	.244 ± .009	.094 ± .019	.229 ± .009
		Run2 (.15,.20)	.142 ± .021	.246 ± .009	.051 ± .017	.248 ± .009
		Run3 (.10,.10)	.082 ± .014	.102 ± .006	.041 ± .013	.147 ± .008
		Run4 (.05,.10)	.071 ± .013	.118 ± .006	.020 ± .012	.155 ± .008
Cows conceiving	NS	Run1 (.20,.20)	.088 ± .015	.128 ± .007	.050 ± .014	.238 ± .008
		Run2 (.15,.20)	.052 ± .013	.141 ± .007	.027 ± .014	.155 ± .008
		Run3 (.10,.10)	.042 ± .010	.053 ± .006	.026 ± .011	.078 ± .007
		Run4 (.05,.10)	.034 ± .010	.073 ± .006	.014 ± .011	.085 ± .007

The heritabilities and repeatabilities for the number of services received per cow bred estimated from all data closely followed the input reproductive parameters in magnitude. There was considerable genetic variation between daughter groups when compared to other reproductive measures and the problem of generated repeatabilities was not perceived for this trait. However, when estimates were calculated on only those cows that conceived, the genetic variation was greatly reduced. Heritability estimates of .07, .03 ± .02 and .015 ± .005 were reported by Pou et al. (1953), Everett et al. (1966) and Janson (1980), respectively, where some sort of selection on the basis of reproductive performance was carried out on each of these data bases. Repeatability estimates of .12 and .11 ± .01 were determined by Pou et al. (1953) and Everett et al. (1966), respectively. These values agree closely with values for number of services per cow bred from the culled data set and number of services per cow conceiving estimated from all of the data.

The variance components used in the calculation of heritability and repeatability estimates for conception-calving date and the interval from calving to first estrus (postpartum interval) are contained in table 10. The heritability and repeatability estimates are shown in table 11.

TABLE 10. ESTIMATES OF SIRE ($\sigma^2_{S/H}$), COW ($\sigma^2_{C/S/H}$) AND ERROR (σ^2_E) VARIANCE COMPONENTS FOR CONCEPTION-CALVING DATE (CD) AND POSTPARTUM INTERVAL (PPI) FROM DIFFERENT TYPES OF RECORDS

Type of records	Trait	Data set (h^2,t)	All data $\sigma^2_{S/H}$	All data $\sigma^2_{C/S/H}$	All data σ^2_E	Culled data $\sigma^2_{S/H}$	Culled data $\sigma^2_{C/S/H}$	Culled data σ^2_E
Cows conceiving	CD	Run1 (.20,.20)	4.05	38.47	184.50	2.72	45.75	170.83
		Run2 (.15,.20)	1.70	45.25	182.13	.55	53.18	166.92
		Run3 (.10,.10)	2.63	27.62	199.32	1.99	35.64	187.22
		Run4 (.05,.10)	1.85	33.82	195.06	.86	42.29	184.20
Cows weaning a calf	PPI	Run1 (.20,.20)	16.00	67.98	322.23	12.54	101.66	294.07
		Run2 (.15,.20)	11.31	71.06	312.58	9.44	91.02	291.89
		Run3 (.10,.10)	6.88	33.73	372.61	3.19	78.12	342.04
		Run4 (.05,.10)	2.21	44.30	354.53	1.85	78.92	326.14

TABLE 11. ESTIMATES OF HERITABILITY (h^2) AND REPEATABILITY (t) FOR CONCEPTION-CALVING DATE (CD) AND POSTPARTUM INTERVAL (PPI) FROM DIFFERENT TYPES OF RECORDS

Type of records	Trait	Data set (h^2,t)	All data h^2	All data t	Culled data h^2	Culled data t
Cows conceiving	CD	Run1 (.20,.20)	.071 ± .015	.187 ± .008	.050 ± .017	.221 ± .008
		Run2 (.15,.20)	.030 ± .013	.205 ± .008	.010 ± .015	.244 ± .009
		Run3 (.10,.10)	.046 ± .012	.132 ± .007	.035 ± .014	.167 ± .008
		Run4 (.05,.10)	.032 ± .012	.155 ± .007	.015 ± .014	.190 ± .008
Cows weaning a calf	PPI	Run1 (.20,.20)	.158 ± .022	.207 ± .009	.123 ± .024	.280 ± .011
		Run2 (.15,.20)	.115 ± .019	.208 ± .009	.096 ± .022	.256 ± .010
		Run3 (.10,.10)	.067 ± .014	.098 ± .007	.030 ± .015	.192 ± .009
		Run4 (.05,.10)	.022 ± .011	.116 ± .007	-.018 ± .013	.191 ± .009

The heritability estimates of conception-calving date were low and did not follow the same trend as the input reproduction heritabilities. The repeatability estimates were much higher relative to the input parameters than were the heritabilities and, like the date of first service estimates, appear to have been generated by effects possibly due to prior events in the simulation such as first calving date. Burris and Priode (1958) reported a significant positive correlation (r = .367) between calving dates in successive years. Cows which calved late one year also tended to calve late in the next year. This phenomenon was apparently due almost entirely to environmental effects since the genetic variation associated with calving date was so low.

The heritabilities of postpartum interval estimated from all of the cows that weaned a calf were close to but consistently lower than the input heritabilities. Cows with extremely long intervals were less likely to conceive and wean a calf and, therefore, were less frequently included in the calculations. This fact could cause a reduction in genetic variation. The heritabilities calculated from the culled data were not biased downward by a great amount. Culling on the basis of conception did not greatly affect the genetic variation of postpartum interval in those cows that weaned a calf.

The variance components that were used to calculate heritability and repeatability estimates for actual weaning weight from all types of records and adjusted 205-d weaning weight from records on cows that weaned a calf are in table 12. Table 13 contains the heritability and repeatability estimates.

The input heritability for adjusted weaning weight as a trait of the dam was .18 which was derived from the sum of one-quarter of heritability as a trait of the calf, the heritability of maternal effects and any correlation between direct and maternal effects. The initial repeatability was .29 which was the sum of the input heritability and peranent environmental effects associated with the maternal ability of cows. The heritability and repeatability estimates of adjusted 205-d weaning weight were markedly close to those input; any deviations were due to random error.

The estimates of heritability and repeatability for actual weaning weight per cow exposed and actual weaning weight per cow bred were almost identical. Since an average of 98% of the cows were bred each year, the groups of records that each estimate was calculated from were essentially the same. The heritability estimates for both traits decreased with each corresponding decrease in initial reproduction heritabilities. The close association indicated that weaning weight was a composite or index of

TABLE 12. ESTIMATES OF SIRE ($\sigma^2_{S/H}$), COW ($\sigma^2_{C/S/H}$) AND ERROR (σ^2_E) VARIANCE COMPONENTS FOR ACTUAL WEANING WEIGHT (ACTWW) AND ADJUSTED 205-D WEANING WEIGHT (ADJWW) FROM DIFFERENT TYPES OF RECORDS

			All data			Culled data		
Type of records	Trait	Data set (h^2,t)	$\sigma^2_{S/H}$	$\sigma^2_{C/S/H}$	σ^2_E	$\sigma^2_{S/H}$	$\sigma^2_{C/S/H}$	σ^2_E
All cows	ACTWW	Run1 (.20,.20)	1045.3	3115.1	33894.4	278.4	4185.3	30642.7
		Run2 (.15,.20)	618.0	3077.6	34055.4	66.7	4228.4	30635.6
		Run3 (.10,.10)	296.2	1090.7	32922.8	47.3	3659.1	29994.9
		Run4 (.05,.10)	263.4	1098.1	33865.8	39.0	3601.2	30844.2
Cows bred	ACTWW	Run1 (.20,.20)	1073.3	3365.0	31716.0	284.3	3993.7	28611.8
		Run2 (.15,.20)	603.7	3268.0	32063.2	65.2	3976.5	28749.5
		Run3 (.10,.10)	285.2	1387.3	30382.6	33.8	3402.2	27719.5
		Run4 (.05,.10)	260.0	1302.9	31543.5	86.2	3230.4	28855.3
Cows conceiving	ACTWW	Run1 (.20,.20)	86.3	637.6	22614.0	57.9	395.7	22773.1
		Run2 (.15,.20)	84.4	456.0	22942.6	107.1	216.5	23016.6
		Run3 (.10,.10)	50.0	727.6	22033.9	54.1	463.7	22321.7
		Run4 (.05,.10)	123.5	406.5	22584.7	178.6	13.4	23121.8
Cows weaning a calf	ACTWW	Run1 (.20,.20)	146.5	906.2	2900.2	132.8	947.2	2858.9
		Run2 (.15,.20)	134.7	917.6	2873.2	138.0	927.1	2840.7
		Run3 (.10,.10)	161.4	811.2	2975.2	171.7	826.9	2942.3
		Run4 (.05,.10)	171.8	856.0	2887.1	181.3	856.4	2888.1
Cows weaning a calf	ADJWW	Run1 (.20,.20)	110.9	687.2	2052.0	100.2	693.1	2053.4
		Run2 (.15,.20)	111.4	696.9	2001.0	116.5	687.3	2006.7
		Run3 (.10,.10)	141.6	674.9	2074.4	150.5	670.2	2065.5
		Run4 (.05,.10)	144.0	669.0	2026.0	155.3	644.6	2043.3

TABLE 13. ESTIMATES OF HERITABILITY (h^2) AND REPEATABILITY (t) FOR ACTUAL WEANING WEIGHT (ACTWW) AND ADJUSTED 205-D WEANING WEIGHT (ADJWW) FROM DIFFERENT TYPES OF RECORDS

Type of records	Trait	Data set (h^2,t)	All data		Culled data	
			$\bar{h}^2$	t	$\bar{h}^2$	t
All cows	ACTWW	Run1 (.20,.20)	.110 ± .015	.109 ± .006	.032 ± .012	.127 ± .007
		Run2 (.15,.20)	.065 ± .012	.098 ± .006	.008 ± .011	.123 ± .007
		Run3 (.10,.10)	.035 ± .009	.040 ± .005	.006 ± .010	.110 ± .007
		Run4 (.05,.10)	.030 ± .009	.039 ± .005	.004 ± .010	.106 ± .003
Cows bred	ACTWW	Run1 (.20,.20)	.119 ± .016	.123 ± .007	.034 ± .013	.130 ± .007
		Run2 (.15,.20)	.067 ± .013	.108 ± .006	.008 ± .011	.123 ± .007
		Run3 (.10,.10)	.036 ± .009	.052 ± .005	.004 ± .010	.110 ± .007
		Run4 (.05,.10)	.031 ± .009	.047 ± .005	.011 ± .010	.103 ± .007
Cows conceiving	ACTWW	Run1 (.20,.20)	.015 ± .008	.031 ± .005	.010 ± .009	.020 ± .006
		Run2 (.15,.20)	.014 ± .008	.023 ± .005	.018 ± .009	.014 ± .006
		Run3 (.10,.10)	.009 ± .008	.034 ± .005	.009 ± .009	.023 ± .006
		Run4 (.05,.10)	.021 ± .008	.023 ± .005	.031 ± .010	.008 ± .006
Cows weaning a calf	ACTWW	Run1 (.20,.20)	.148 ± .023	.266 ± .010	.135 ± .024	.274 ± .011
		Run2 (.15,.20)	.137 ± .022	.268 ± .010	.141 ± .025	.273 ± .011
		Run3 (.10,.10)	.164 ± .023	.246 ± .009	.174 ± .026	.253 ± .010
		Run4 (.05,.10)	.176 ± .025	.263 ± .010	.185 ± .027	.264 ± .011
Cows weaning a calf	ADJWW	Run1 (.20,.20)	.156 ± .024	.280 ± .010	.141 ± .025	.279 ± .011
		Run2 (.15,.20)	.159 ± .024	.288 ± .010	.166 ± .026	.286 ± .011
		Run3 (.10,.10)	.196 ± .026	.282 ± .010	.208 ± .029	.284 ± .011
		Run4 (.05,.10)	.203 ± .026	.286 ± .010	.218 ± .029	.281 ± .011

multiple factors and that the more lowly heritable reproductive traits strongly affected the genetic variation for this composite trait. The true genetic potential of weaning weight was masked by factors associated with reproduction.

Actual weaning weight per cow conceiving was affected by random calf deaths which reduced the expression of genetic and permanent environmental effects so that the resulting heritability and repeatability estimates were essentially zero. This measure was influenced almost entirely by the alive or dead status of the calves which was associated with temporary environmental effects.

The estimates for actual weaning weight per cow that weaned a calf were very close to, but consistently lower than, those input due to effects associated with the birth date of the calves. The genetic variation of actual weaning weight was increased, but there was also a greater increase in the error variance.

The heritability and repeatability estimates obtained for each trait analyzed from all of the data should be unbiased since no selection took place. Selection acts to reduce additive genetic variance through the absence of individuals of low quality and through a negative linkage disequilibrium between loci (Robertson, 1977; Fimland, 1979). This phenomenon was evident in the heritabilities estimated from the culled data for most traits analyzed. Repeatability estimates from the culled data tended to be inflated due to an increased correlation between cow records and a weaker temporary environmental influence.

Standard Errors

The method used for the computation of standard errors of heritability and repeatability was derived by Dickerson (1969). Empirical standard errors were calculated from 50 sets of data each consisting of 10 herds with 50 cows and 5 sires each. These were compared with the theoretical standard errors to determine if there was any significant over- or under-estimation of the standard errors by the theoretical method.

An F-test of the equality of two variances was performed on the empirical and theoretical variances. A two tailed test was performed since there was no prior reason to anticipate inequality of variance (Snedecor and Cochran, 1967). Table 14 lists the variances and test statistics corresponding to the larger variance divided by the smaller. Analyses were performed on annual conception rate; actual weaning weight per cow exposed, first service conception rate, conception-calving date, postpartum interval and adjusted 205-d weaning weight.

The approximate theoretical method of estimating standard errors almost always yielded higher variances

TABLE 14. ANALYSIS OF THE EQUALITY OF EMPIRICAL AND THEORETICAL VARIANCES OF HERITABILITY ($\sigma^2_{h^2}$) AND REPEATABILITY (σ^2_t)

Type of records	Trait[a]	Empirical		Theoretical		F statistic	
		σ^2_h	σ^2_t	$\sigma^2_{h^2}$	σ^2_t	F_{h^2}	F_t
All cows	BCR	.00490	.00116	.00296	.00055	1.655*	2.102**
All cows	ACTWW	.00194	.00063	.00209	.00092	1.077	1.476
Cows bred	FSCR	.00336	.00058	.00409	.00068	1.216	1.180
Cows conceiving	CD	.00185	.00058	.00195	.00063	1.057	1.091
Cows weaning a calf	PPI	.00410	.00063	.00447	.00083	1.091	1.330
Cows weaning a calf	ADJWW	.00757	.00102	.00672	.00108	1.130	1.050

[a] See table 4 for definition of traits.
*$P < .05$.
**$P < .01$.

than the empirical method but these differences were not significant. Funkhouser and Grossman (1982) also found an upwards bias in the approximate sampling variances of heritability. An exception to this finding was determined in the test of the variances for annual conception rate. In this case, the theoretical variances were significantly smaller than the empirical estimates. The approximate standard errors, like the heritability estimates themselves, were apparently biased due to the high incidence of annual conception (binomial). The incidence does seem to affect the accuracy of the estimates since first service conception rate, which had a moderate incidence, was not seriously biased and there were no significant differences found between the empirical and theoretical variances. The large sample size minimized the bias associated with the approximate standard errors of the remaining traits (Funkhouser and Grossman, 1982).

Correlations

All traits derived from the simulation program were correlated with actual weaning weight to determine the relationship between reproduction and production and to evaluate if direct selection for reproduction would indirectly improve actual weaning weight per cow exposed. The genetic (r_G) and environmental (r_E) correlations are shown in table 15.

TABLE 15. ESTIMATES OF GENETIC (r_G) AND ENVIRONMENTAL (r_E) CORRELATIONS BETWEEN ALL TREATMENTS AND ACTUAL WEANING WEIGHT (ACTWW) FROM ALL DATA

		Data set (h^2,t)							
		Run1 (.20,.20)		Run2 (.15,.20)		Run3 (.10,.10)		Run4 (.05,.10)	
Type of records	Trait[a]	r_G	r_E	r_G	r_E	r_G	r_E	r_G	r_E
All cows	BCR	.980	.635	.958	.631	.953	.621	.812	.626
	MATE	-[b]	.282	.370	.270	-[b]	.308	-[c]	-[c]
Cows bred	FS	-.456	-.208	-.311	-.207	-.720	-.212	-.612	-.208
	NS	-.930	-.297	-.934	-.291	-.842	-.268	-.730	-.289
	FSCR	.914	.285	.924	.285	.869	.272	.745	.290
Cows conceiving	FS	-.719	-.129	-.493	-.115	-.571	-.116	-.180	-.116
	NS	-.455	-.105	-.357	-.100	-.289	-.110	-.202	-.121
	CD	-.681	-.178	-.596	-.164	-.449	-.172	-.235	-.182
Cows weaning a calf	ADJWW	.955	.882	.979	.883	.973	.877	.982	.876
	PPI	-.167	-.228	-.474	-.218	-.721	-.250	.123	-.239

[a] See table 4 for definition of traits.
[b] Unavailable due to negative variance components.
[c] Unavailable due to tape malfunction.

As the input heritability of the reproductive traits decreased, so did the genetic correlations between most of the measures with actual weaning weight. When the genetic influence of reproduction is low, the relationship between reproduction and production is not as strong and is influenced more by environmental effects.

The reproductive traits of annual conception rate, first service conception rate and number of services received per cow bred had a strong relationship ($r_G > .9$) with actual weaning weight per cow exposed. The strong relationship between annual conception rate with actual weaning weight per cow exposed was expected, but the relationship between first service conception rate and number of services with actual weaning weight was more surprising. Cows that conceived at their first service and therefore received only one service tended to produce heavier calves at weaning apparently because these cows calved earlier in the calving season. Also, some cows that did not conceive at their first service never did conceive. An early date of first service and calving date and a shortened postpartum interval might also cause a cow to calve earlier in the calving season but these traits were only moderately or lowly correlated with actual weaning weight.

Correlated responses of actual weaning weight per cow exposed were determined by using annual conception rate, number of services received per cow bred and first service conception rate as the directly selected reproductive traits. The comparison between the correlated responses and direct responses to selection are shown in table 16. The correlated response in actual weaning weight per cow exposed when direct selection was for number of services received per cow bred was higher in all runs than the direct response of actual weaning weight alone. Direct selection for annual conception rate and first service conception rate also produced higher correlated responses in relation to direct responses except when the genetic variation of either conception rate was lowest. Actual weaning weight per cow exposed, as a composite trait, was highly influenced by reproductive factors except when the genetic variation of those factors was close to zero.

TABLE 16. COMPARISON OF CORRELATED RESPONSES WITH DIRECT RESPONSES TO SELECTION FOR ACTUAL WEANING WEIGHT PER COW EXPOSED

Reproductive trait[a]	Data set (h^2,t)	Correlated response[b]	Direct response[c]
BCR	Run1 (.20,.20)	.132	.110
	Run2 (.15,.20)	.076	.065
	Run3 (.10,.10)	.038	.035
	Run4 (.05,.10)	.024	.030
NS	Run1 (.20,.20)	.153	.119
	Run2 (.15,.20)	.091	.067
	Run3 (.10,.10)	.046	.036
	Run4 (.05,.10)	.034	.031
FSCR	Run1 (.20,.20)	.136	.119
	Run2 (.15,.20)	.087	.067
	Run3 (.10,.10)	.046	.036
	Run4 (.05,.10)	.031	.031

[a] See table 4 for definition of traits.

[b] $CR_{WW} = h_1 h_2 r_{G_1 G_2}$.

[c] $DR_{WW} = h_1^2$.

SUMMARY AND CONCLUSIONS

A simulation study was conducted where parameters for single-service conception rate, the interval from calving to first service (postpartum interval) and adjusted 205-d weaning weight were input to describe the reproductive and productive ability of beef cows. Heritabilities and repeatabilities for reproduction and production outputs were estimated from data on 500 sire daughter groups consisting of 10 half-sisters each for 5 yr. Genetic and environmental correlations with actual weaning weight were also estimated for all traits output.

The reproductive ability of females is of importance and deserves attention since it is usually the limiting factor in beef cattle production. In order to improve overall reproductive and possibly the productive ability of cow, the measures of reproduction should be as comprehensive, heritable and repeatable as possible.

From the traits analyzed, first service conception rate, number of services received per cow bred and postpartum interval appeared to best fit these criteria. All of the above had moderate heritabilities and repeatabilities and all except postpartum interval were highly correlated ($r > .9$) with actual weaning weight. First service conception rate was more heritable and repeatable as a measure of pregnancy rate than annual conception rate since conception at first service was partitioned from subsequent conceptions and failures to conceive. Number of services received per cow bred is measurable early in life before any selection for fertility takes place and is indicative of early conception and therefore early calving. Although date of first service and calving date would be better indicators of early calving, they had low heritabilities and were not as highly correlated with actual weaning weight. Postpartum interval was important to overall cow reproductive ability because it indicated how quickly cows recovered from calving to efficiently rebreed.

The results of this study seemed to indicate that the use of reproductive measures in an index that covers all aspects of reproduction (conception, calving and rebreeding) might improve overall cow fertility and would not be detrimental to the producing capacity of beef cows if the herd is experiencing reproductive problems. The genetic variation (in terms of heritability) of some of the reproductive traits considered was moderate when the input genetic variation was moderate. Genetic progress in reproductive performance could be made in these circumstances. However, when cows were culled on the basis of failure to conceive the genetic variation was markedly reduced and in some instances went to zero. All reproductive traits were favorably correlated with actual weaning weight; positive selection for reproduction would result in an increase in herd weaning weight. Further study into actual selection methods and programs is needed to properly quantify the amount of progress that could be attained from the selection of reproductive traits.

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SIMULATION OF GENETIC CONTROL OF REPRODUCTION IN BEEF COWS

by

Maribeth Hepp

(ABSTRACT)

A stochastic computer model was constructed to simulate cow reproductive performance. Parameters for single-service conception rate and days from calving to first service (postpartum interval) were developed from the literature. Estimates of the heritability and repeatability (h^2, t) of each of these traits in four simulated data sets were RUN1 (.20, .20), RUN2 (.15, .20), RUN3 (.10, .10), RUN4 (.05, .10). Binomial conception rate parameters were normalized to simulate assumed normal underlying genetic and environmental distributions. Postpartum interval has a non-normal phenotypic distribution that was produced by combining an assumed normal genetic distribution with a Pearson III gamma distribution of environmental effects. The breeding season was 63 d. Simulation outputs included annual conception rate (BCR), first service conception rate (FSCR), date of first service (FS), number of services (NS), conception-calving date (CD), postpartum interval (PPI), actual weaning weight (ACTWW) and adjusted 205-d weaning weight (ADJWW).

Realized heritabilities and repeatabilities for these outputs were estimated from half-sib intraclass correlations based on 5 yr of records on 100 herds of 50 cows each. Realized heritabilities (RUN1-RUN4) for BCR, FSCR, FS, NS, CD, PPI, ACTWW and ADJWW ranged from .165-.028, .187-.055, .023-.010, .227-.071, .071-.032, .158-.022, .148-.176 and .156-.203, respectively. Repeatability estimates (RUN1-RUN4) for BCR, FSCR, FS, NS, CD, PPI, ACTWW and ADJWW ranged from .178-.059, .212-.108, .125-.101, .244-.118, .187-.155, .207-.116, .266-.263 and .280-.286, respectively.