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Estimating genetic parameters in commercial beef cattle populations

Dan T. Brown

To the Graduate Council:

I am submitting herewith a thesis written by Dan T. Brown entitled "Estimating genetic parameters in commercial beef cattle populations." I have examined the final electronic copy of this thesis for form and content and recommend that it be accepted in partial fulfillment of the requirements for the degree of Master of Science, with a major in Animal Science.

J.B. McLaren, Major Professor

We have read this thesis and recommend its acceptance:

Haley Jamison, Don Richardson

Accepted for the Council:
Carolyn R. Hodges

Vice Provost and Dean of the Graduate School

(Original signatures are on file with official student records.)

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Graduate Studies and Research

ESTIMATING GENETIC PARAMETERS IN COMMERCIAL BEEF CATTLE POPULATIONS

A Thesis
Presented for the
Master of Science
Degree
The University of Tennessee

Dan T. Brown

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ABSTRACT

The data used in this study were the Tennessee Beef Cattle Improvement Program weaning records of 18,393 Angus and Hereford calves accumulated over the nine year period, 1964 through 1972. The calves were classified according to weaning age (within the range of 120 to 300 days inclusive), sex (bulls, heifers, steers), age of dam (by years from two to 10 years inclusive and 11 years and over), month of birth, management (creep or non-creep fed), year and breed in preliminary analyses. The purpose of this study was to determine the effect of various methods of adjusting weaning weight for environmental variation and various methods of calculating genetic parameters on the magnitude of these estimates.

Nine combinations of four methods of adjusting weaning weight to an age-constant basis and four methods of adjusting age-constant weights fixed environmental effects were used to generate nine sets of adjusted weights. A nested analysis of variance procedure was used to analyze the nine sets of adjusted 205-day weights and weaning type score and to produce variance and covariance components to be used in estimating heritability parameters for the traits in question. It was determined by Barlett's Test for Homogeneity of Variances that the records of Angus and Hereford calves could be combined in a single analysis. However, the residual mean squares of creep and non-creep fed calves were heterogeneous and in all final analyses the two management groups were analyzed separately. Sire and herd were found to

significantly effect ($P < .01$) both weaning weight and weaning type score. The effect of herd had a tremendously pronounced effect upon both traits regardless of the management group (creep or non-creep fed).

Estimates of heritability and genetic correlations were calculated from components of variance by two different methods--inter-herd and intra-herd. The intra-herd estimates were calculated by the standard paternal half-sib methods. The inter-herd estimate was calculated by adding the component of variance of herd within year to the denominator of the standard paternal half-sib formulas for calculating heritability and genetic correlation.

Estimates of heritability calculated by the inter-herd method were similar to those reported in other studies when the estimates were calculated from commercial herds. The mean estimate of heritability for adjusted 205-day weight (average of nine methods of adjusting) was .424 and the estimate for weaning type score was .401 in non-creep calves. The estimates were .343 and .293 respectively, in creep-fed calves. Estimates in both management groups tended to be higher than those reported for experimental herds. The estimates calculated on an inter-herd basis tended to be closer to the estimates reported for these traits which were determined in experimental herds. The estimates for 205-day weight (average value) and weaning type score were .288 and .298, respectively, in non-creep calves and .177 and .180, respectively, in creep-fed calves.

Genetic correlations between weaning type score and adjusted 205-day weight were positive and fairly large in magnitude. The inter-herd method tended to increase the genetic correlations between different methods of correcting weaning weight in both the non-creep and the creep-fed calves. However, the intra-herd correlations between the traits (weaning type score and adjusted 205-day weight) were higher for non-creep-fed calves than were the inter-herd correlations.

Comparison of these results with estimates derived in experimental herds suggests that the component of variance for herd in a nested analysis of variance contains both genetic and environmental variation. The true estimates of the genetic parameters probably lie somewhere between the intra-herd and the inter-herd estimates calculated in this study.

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CHAPTER I

INTRODUCTION

Livestock numbers in the southeastern United States have increased at a rapid rate in recent years. This increase has been primarily in cow-calf operations where brood cows are maintained and calves are sold as feeders at weaning. The economic value of these feeder calves is determined primarily by two factors: (1) quality (weaning type or conformation score) and (2) weight (weaning). Therefore, the beef cattle producer strives to improve the genetic potential of his herd with respect to these traits by selection. His primary goal, to obtain maximum net returns from available resources, is dependent upon accurate estimates of the most probable producing ability and/or genetic merit of replacement animals.

Weaning weight in beef calves is a complex trait which reflects genetic potential of the calf, maternal influences, and environmental factors. The effects of certain influences such as sex of the calf and age of the dam are fairly constant and adjustments of this weight for variation with respect to this factor is standard in performance testing programs.

Genetic improvement in beef cattle by selection is dependent upon the heritability of traits in which progress is desired. Therefore, accurate estimates of genetic and phenotypic parameters are necessary to evaluate expected response. It would be desirable to base this selection on genetic merit alone. However, it is impossible to exclude all of the variation due to environmental effects.

Varying estimates of genetic parameters have been reported for most economic traits. Although some differences among published estimates may be due to sampling, the range of these estimates suggest that all differences are not adequately explained by the sampling variance. Two major reasons for these differences were proposed by Flock (1970): (1) variation in genetic composition of the sampled population and (2) biased estimates due to computational methods.

Recent increased interest in performance testing has resulted in the collection of large volumes of preweaning performance data on calves produced in breeders' herds. Estimates of heritability from these data tend to be higher than estimates from experimental herds (McLaren, 1970). Assumptions that standard statistical procedures adequately adjust for environmental variation may be invalid and this inefficiency may be responsible for some of the discrepancies between estimates of heritability calculated from performance test records collected in commercial herds. Therefore, the objectives of this study were to (1) evaluate the effects of various methods of adjusting weaning weights for age of dam, age and sex of calf on estimates of heritability, (2) to compare estimates of heritability calculated by different procedures, and (3) to study genetic correlations among these estimates of genetic parameters.

CHAPTER II

REVIEW OF LITERATURE

Many environmental and genetic factors affect weaning weight and weaning type score of beef calves. Numerous studies have been conducted under many different environments to estimate the effects of these factors. Therefore, reported variation with respect to their influence on various traits was not surprising.

Season of Birth

Month or season of birth is of major concern to the cow-calf producer due to the variation in conception rate among females in various seasons and variation in growth potential, feed availability, feed utilization, and market acceptability of calves dropped in different seasons. Results reported by Koch and Clark (1955a) involving 5,952 Hereford calves which were born during April and May suggested similar rate of gain. However, conformation score of early dropped calves were slightly higher than for those born later in the season. Calves born in January through March were heavier at weaning than those born in other months according to Rollins and Guilbert (1954), Clum, Kidder, and Koger (1956), Marlowe, Kincaid, and Litton (1958), Reynolds et al. (1958), and Dinkel, Minyard, and Ray (1963).

According to Sellers, Willham, and deBaca (1970), Angus and Hereford calves born in the winter (December, January, and February) and in the spring (March, April, and May) had similar weaning weights but were 7.7 and 4.5 kg heavier ($P < .05$) than calves born in the summer (June, July, and August) and fall (September, October, and November), respectively.

Most research reports suggest that weaning weights were generally highest for calves born in March and tended to decrease for calves born later in the year. Minimum weaning weight was observed for calves born in the fall (Barker, 1964; Warren, Thrift, and Cannon, 1965; McGuire, 1969; and McLaren, 1970).

Creep-fed and non-creep-fed calves born during March, April and May in Virginia gained faster than those born in other months, and calves born in August and September gained the slowest (Marlowe et al., 1965). Creep feeding tended to decrease the magnitude of these differences. Brown (1960) found a significant difference among weights of Hereford and Angus calves at 60, 120, 180, and 250 days of age and attributed these to differences in season of birth.

Neville, Warren, and Griffey (1974) studied two unrelated Hereford herds in Georgia and found that date of birth significantly affected milk production and 210-day weight in both. For each one day later in the calving period that birth occurred, daily milk production increased 0.014 ± 0.002 and 0.010 ± 0.002, and weaning weights increased 0.300 ± 0.044 and 0.176 ± 0.037 kg in the two herds, respectively. Variation in milk production accounted for approximately 60% of the variation in weaning weight of beef calves (Neville, 1962; Rutledge et al., 1971).

Marlowe and Vogt (1965) noted that calves born between June and September scored approximately one-third of a grade lower than calves born in other seasons. Nelms and Bogard (1965) suggested that season of birth effect on rate of calf gain was equal to if not greater than that of age of dam.

Age of Calf at Weaning

The average weaning age of beef calves varies among the geographic areas of the United States. In the northern half of the United States, beef calves were weaned at a much younger age, approximately 180 days (Koch, 1951; Dawson et al., 1954; Koch and Clark, 1955b; Minyard and Dinkel, 1960; Brinks et al., 1961; Hohenboken and Brinks, 1969) than in the southern half where calves were mainly weaned at 240 days of age (Rollins and Wagnon, 1956; Brown, 1958; Neville, 1962; Marlowe, Mast, and Schalles, 1965; High, 1968; McGuire, 1969; McLaren, 1970).

In experimental herds, variation in weaning age does not usually exceed 90 to 120 days (Reynolds et al., 1963). They indicated that age difference among calves born in the same season was small. However, in commercial beef herds, weaning age varied as much as 290 days (Barker, 1964; Marlowe and Gaines, 1958).

Performance records of calves, in 111 Angus and 82 Hereford herds in Virginia, weaned at 90 to 299 days of age were divided into seven groups in which the range in weaning age was 30 days (Marlowe, Mast, and Schalles, 1965). Average daily gain was not significantly different between adjacent groups among non-creep-fed calves but age had a significant effect on average daily gain over the entire weaning age range. In general, as calves increased in age, their gains per day decreased. They found also that when seasonal influences were removed, growth was essentially linear from 120 days to weaning in non-creep-fed calves.

The effect of calf age on preweaning growth rate of Hereford calves was studied by Rollins, Guilbert, and Gregory (1952). When calves were weaned at less than four months of age, the coefficient of regression of weaning weight on weaning age was 1.90 lb per day. Whereas, the coefficient of this regression was only 1.81 lb per day for calves weaned between four and eight months of age. Several other reports have also shown that the relationship between rate of gain and age of calf was linear in calves weaned between 180 to 210 days of age (Koch, Schleicher, and Arthand, 1955; Marlowe and Gaines, 1958; Brinks et al., 1962, Swiger et al., 1962). Rollins and Guilbert (1954), Brown (1960), and Barker (1964) found that when average weaning age was 240 days or more, adjustments for weaning age was necessary in order to make valid comparisons of rate of gain between early and late calves.

Evans et al. (1955) reported a higher ($P < .05$) coefficient of regression of weaning weight on weaning age in grade herds (1.080) than in purebred herds (0.908). Mahmud and Cobb (1963) reported a coefficient of 0.71 lb per day for the regression of weaning weight on weaning age, but Koch and Clark (1955a) found the regression of average daily gain from birth to weaning on weaning age to be -.04 lb per day. They concluded further that the difference in growth rate between early and late calves was less important than previously indicated. In other studies, Koger and Knox (1945b), Sawyer, Bogard, and Oloufa (1949), Botkin and Whatley (1953), Burgess, Landblom, and Stonaker (1954), and Minyard and Dinkel (1965) found that weaning weight of calves increased with increasing weaning age at the rate of 1.20, 1.28, 1.43, 1.67, and 2.27 lb per day, respectively.

Records on 1,692 calves were collected by Vesely and Robison (1971) during the period from 1952 to 1968 in four North Carolina Hereford herds. They reported that age at weaning had a highly significant effect on weaning weight. The regression of weaning weight on weaning age was 0.44 kg. High (1970) noted also that age of calf had an appreciable effect on preweaning and weaning weights. Brown (1960) indicated a need for consideration of age of calf, in addition to sex, season of birth, and age of dam, when standardizing weaning weight.

Berg (1961) found a very high positive relationship between average daily gain and weight per day of age in calves approximately the same age and suggested that the two traits should be essentially equal in appraising preweaning gain. Similar results were reported by Cooper et al. (1965).

Inconsistent increases in weight for each increment of age were reported by Warren, Thrift, and Cannon (1965). A negative coefficient was obtained for the quadratic component of the weaning age polynomial indicating that rate of gain increased as age increased up to a point and then it declined as age increased beyond that point.

The validity of the assumption of linearity between growth rate and age has been evaluated in several studies. Cunningham and Henderson (1965b) plotted unadjusted mean weaning weight for each 10 day interval when calves were weaned from 120 to 250 days of age. This response appeared to be linear. When unadjusted weaning weights were regressed on weaning age, regression coefficients were 1.67 for Angus and 1.49 for Hereford calves. Deviations from linear regression were not significant and average daily gain from birth to weaning was considered to be an unbiased estimate of rate of growth.

Swiger et al. (1962) calculated coefficients of partial regression for rate of gain from birth to 130 days and from 130 to 200 days on weaning age in order to evaluate preweaning growth. They concluded that the curvilinear effect during the early growth period could be ignored. However, curvilinear correlation between age and gain during the later growth period was significant. From this, it was concluded that when calves were weaned between 130 and 200 days of age, the most accurate appraisal of weaning weight was obtained by adjusting gains for variation in age of calf.

Most cattlemen, under normal farm management, do not secure routine weights on each calf. To obtain actual average daily gains on an age basis, a few calves would have to be weighed each day over a period of time since birth dates vary. This is not generally practical and all calves in a herd are weighed at the same time regardless of age. When birth weight is not available and is taken as a constant, the standardized weaning weight may be considered the same trait as average daily gain, differing only because of a scaling factor. This assumption is supported by the genetic correlations of 0.98 and 0.93 between average daily gain and weaning weight reported by Koch and Clark (1955b) and Lehmann et al. (1961), respectively. McGuire (1969) reported similar correlations of 0.96 and 0.99 for 180- and 250-day weights with 180- and 250-day gain, respectively.

McLaren (1970) found that variation in weaning age accounted for 20 to 28% of the variation in weaning weight. Age of calf also had a pronounced effect on average daily gain according to Robertson (1974).

Average daily gain was highest during the early stages of growth, and gradually declines to 300 days of age.

With all of this in mind, several linear functions have been used to compute weaning weight (WW) at a standard age (SA) or a constant. One of the most frequently used methods is:

$$\text{Age-Constant Weight} = \frac{WW - BW}{WA} \times SA + BW$$

Where: WW = Weaning weight

BW = Birth weight

SA = Standard age

WA = Actual weaning age in days

However, birth weight is not always available. Anderson, Lowell, and Dinkel (1969) compared the use of a standard (70 lb) birth weight to the actual birth weight of the calves. This formula was used:

$$\text{Age-Constant Weight} = \frac{WW - 70}{WA} \times SA + 70$$

Lehmann et al. (1961), Cunningham and Henderson (1965a), Barker (1964), and McLaren (1970) suggested that a constant within each breed-sex group was a satisfactory estimate when birth weight is not available.

When rate of gain is evaluated as weight per day of age (WDA), it is expressed as:

$$WDA = \frac{WW}{WA}$$

Bywaters and Wilham (1935) and Whatley and Quaife (1937) in pigs and Minyard and Dinkel (1965) in calves used another method of adjusting weaning weight. This age adjustment employs multiplicative factors computed by linear regression. For each age, the appropriate factor was considered to be:

$$\frac{\text{Standard Age - Age Intercept}}{\text{Actual Age - Age Intercept}}$$

Age intercept being the intercept of the regression line on the age axis. Minyard and Dinkel (1965) compared interclass regression and age-intercept factors for adjusting weaning weights to a constant age. They found that the age intercept method resulted in a greater reduction of dependency between age and adjusted weight. It was suggested that the interclass regression method appeared to overadjust the extreme age groups. Adjusted weights of the youngest calves tended to exceed the weight of the calf when they were grown normally to the constant age, whereas, the adjusted weight of the oldest calves appeared to be smaller than would be expected of weights that were taken at 190 days of age. Johnson and Dinkel (1951) and McLaren (1970) also showed similar results in the extreme age groups. Adjustment of calculated 205-day weight by intra-class regression of that weight on weaning age made by McLaren (1970) removed the effect of the overadjustment.

Sex of Calf

In general, published results indicate that bull calves grow faster than steers and steers grow better than heifers. Weight and height increase was observed to be faster in bulls than in heifers by Morrison (1936). Knapp and Black (1941) also found that the heaviest calves at weaning were bulls.

Several workers (Brinks et al., 1961; Taylor et al., 1960; Barker, 1964; High, 1968; McGuire, 1969) reported that differences in average daily gain from birth to weaning between males and females generally ranging from 0.1 to 0.3 lb. However, Cunningham and Henderson

(1965a) observed that the difference between bulls and steers were, in part, attributable to the effects of selection.

The overall ratio of 1.082 between mean weight of bulls to that of heifers reported by Minyard and Dinkel (1965) was similar to 1.075 reported by Koch et al. (1959) and 1.064 found by Swiger et al. (1962). Marlowe (1962) reported that steer calves grow 7% faster than heifer calves, but 6% slower than bull calves. This agreed in part with McLaren (1970) who showed that 4 to 15% of the variation in weaning weight within various breed-management groups was attributable to the effect of sex of calf. Sex was a significant source of variance in the analyses of 205-day weights by Bair, Wilson, and Zieger (1972). The mean 205-day weight of males and females was 220.3 and 208.4 kg (5.7% difference), respectively. This 11.9 kg difference in 205-day weight between males and females was similar to the 13.6 kg difference reported by Marlowe and Gaines (1958).

Results reported by Thrift et al. (1970) supported earlier reports that steers gained faster and were heavier at weaning than heifers. High (1970) and Veseley and Robison (1971) found males calves to be 42.3 lbs and 18 kg heavier, respectively, at weaning than females. A study of Tennessee calves reported by Robertson (1974) showed that creep-fed bull calves were 52.8 lbs heavier than creep-fed steers and 65.6 lbs heavier than heifers. However, these differences were not as great among non-creep-fed calves (29.1 and 44.8 lbs, respectively).

In contrast, Knapp and Phillips (1942) and Gregory, Blunn, and Barker (1950) reported that there was no significant difference in weaning weight due to sex. However, variation in sex had a significant effect on weaning weight and type according to Francoise, Vogt, and Nolan (1973). Sellers, Willham, and deBaca (1970) also indicated that sex was an important source of variation. Their results suggested the use of multiplicative correction factors to adjust for differences in sex.

Most reports regarding the effect of sex on weaning conformation score indicate the effect to be small. Lehmann et al. (1961) found a sex difference of about 1/10 of a grade in favor of females, while Barker (1964) and High (1968) reported a difference of approximately 1/20 of a grade in favor of males. However, a later report by High (1970) suggested the sex difference for type score at weaning to be even less than 1/30 of a grade. Koch and Clark (1955a), Marlowe and Gaines (1958), Taylor et al. (1960), Marlowe (1962), and Cunningham and Henderson (1965b) concluded that sex influence on conformation score at weaning was negligible. However, Marlowe, Mast, and Schalles (1965) found bull and heifer calves significantly higher than steer calves (0.4 and 1.0 grade point, or about one-half standard deviation). Steers received slightly higher grades at weaning than heifers in Thrift et al. (1970) results.

In contrast, Francoise, Vogt, and Nolan (1973) found sex to be statistically significant using the weaning records of 1,108 bulls and 1,442 heifers from Angus and Hereford herds. Vesely and Robison (1971) reported differences due to sex in type scores at weaning ranked about the same as those for weaning weight. Bulls scored the highest (10.6), followed by steers (10.5) and heifers (10.1). As for grade, creep-fed calves graded significantly above the non-creep-fed calves for each sex, according to Robertson (1974). He found that bulls were .259 units above the average, steers .258 units below the average, and heifers intermediate between bulls and steers.

Age of Dam

Weaning weight is the most important factor affecting net income in a calf-raising and feeding operation when marketing calves, and the age of dam has been shown to have a tremendous effect upon the weaning weight of calves. Milk production accounts for approximately 60% of the variance in weaning weight of calves (Neville, 1962), and age of dam significantly influences milk production and weaning weight (Neville, Warren, and Griffey, 1974).

Studies by many workers (Botkin and Whatley, 1953; Lacy, 1957; Roubicek et al., 1957; Marlowe, Mast, and Sheehan, 1964; Christian et al., 1965; Marlowe, Mast, and Schalles, 1965; Cundiff, Willham, and Pratt, 1966; High, 1970; McLaren, 1970; Vesely and Robison, 1971; Bair, Wilson, and Zeigler, 1972; Wilson, 1973; Francoise, Vogt, and Nolan, 1973; Robertson, 1974) indicated that two- and three-year-old cows produced lighter calves than older cows. Most research workers report that the effects of age of dam on weaning weight tend to peak at five or six years of age (Cunningham and Henderson, 1965b; Mahmud and Cobb, 1963; Swiger, 1961; McLaren, 1970; High, 1970; Vesely and Robison, 1971; Wilson, 1973) and remained constant through nine or 10 years of age (Nelms and Bogart, 1956; Clark et al., 1958; Vernon, Harvey, and Warwick, 1964; Harricharan, Bratton, and Henderson, 1967; Robertson, 1974).

year. Type score at weaning averaged 1.1 grade points higher for calves of mature cows than from two-year-old cows (High, 1970).

Marlowe (1962) and Robertson (1974) reported a greater influence of age of dam in non-creep-fed calves than among calves that were creep-fed. His results indicated that creep-fed calves from two-year-old cows graded 0.5 units higher than those from six- to 10-year-old cows compared to a difference of 0.7 units in non-creep-fed calves.

Heritability

Selection is based on the phenotypic value of breeding animals and, sometimes, on those of their relatives. Therefore, the accuracy of phenotypic measurements as an indication of the genotype deserves careful attention. The relative agreement between phenotype and genotype is measured by the coefficient of heritability or simply heritability (h^2). The heritability of a trait was defined by Pirchner (1969) as the ratio of its genetic variance and total variance as shown by the following expression:

$$h^2 = \frac{V(G)}{V(P)}$$

Traits are often described as being "highly" heritable or "lowly" heritable depending upon how closely parents and offsprings, brothers and sisters, or other close relatives resemble each other phenotypically. Generally, speaking, heritability values below .2 are considered low, 0.2 to .4 are moderate, and those above 0.4 are considered high. An accurate estimate of heritability is important because it indicates the fraction of the phenotypic superiority of selected parents which is transmitted to the offspring. Thus, progress from intense mass selection may be relatively rapid for some traits and relatively slow for others, depending upon the magnitude of coefficient of the heritability for that trait. For this reason, knowledge of the respective heritabilities is an important factor in planning selection practices for several traits simultaneously.

The importance of heritability in a genetic study involving quantitative traits was pointed out by Lush (1945). He emphasized its predictive role in expressing the reliability of phenotypic value as an estimate of breeding value and suggested that the precision of the estimate was a function of the standard error of the estimate of heritability. He defined heritability of a trait in two ways, in the "Broad sense" and in the "Narrow sense." In the broad sense, heritability is the fraction of the phenotypic variation due to the effects of the genes singly and in combinations. Therefore, it includes the additive effects of the genes plus any variation within the population due to non-allelic gene interaction, dominance, and interaction between heredity and environment. In the narrow sense, heritability is the fraction of the phenotypic variation which is attributable to the additive effect of the genes; that is, attributable to the linear regression of phenotype on genotype.

Pirchner (1969) explained that "heritability in the broad sense" estimates the proportion of phenotypic variation caused by differences in the whole genotype. In terms of variance components, heritability in the broad sense is composed as follows:

$$h_B^2 = \frac{V(A) + V(D) + V(I)}{V(A) + V(D) + V(I) + V(E)}$$

"Heritability in the narrow sense" estimates the importance of differences in additive gene effects or in breeding values relative to the total phenotypic variation:

$$h^2_N = \frac{V(A)}{V(A) + V(D) + V(I) + V(E)} = \frac{V(A)}{V(A) + V(E')}$$

Where: V(A) = additive genetic variance

V(D) = variance due to dominance

V(I) = variance due to epistasis

V(E) = variance due to environmental factors

V(E') = denotes all variance not caused by additive gene effects

Since only additive genetic effects in a population contribute to the permanent gain from selection, an estimate of heritability in the narrow sense is more desirable for predicting the results of a selection procedure. Lush (1945) pointed out that this estimate contained some of the deviations due to dominance and usually a little of the epistatic variance, depending on the method by which is was obtained. Therefore, he concluded that most estimates of heritability fall somewhere between the broad and narrow definitions.

Different estimates of heritability for the same trait show a considerable range of variation according to Falconer (1960). He explained that this was partly due to statistical sampling, but some of the variation reflects real differences between the populations or the conditions under which they were studied.

The first estimates of heritability were reported in 1946 (Knapp and Nordskog, 1946). Many reports have been published since that time with respect to estimates of genetic parameters of economically important traits in beef cattle. Warwick (1958) made the first attempt to summarize heritabilities in beef cattle. Temple (1964), Petty and Cartwright (1966), and High (1968) also reported summaries. The summary made by High (1968) included estimates of heritability of various measures of preweaning growth rate and conformation score reported between 1958 and 1965. Average estimates from both Warwick's and High's summaries are given in Table 1 (McLaren, 1970). Almost all of the estimates in both summaries were made by the paternal half-sib method.

Increased weaning weight is one of the primary goals of the cow-calf producer, and since this trait is moderately, if not highly heritable, it is an important part of any beef selection program either by itself or as a component of yearling weight. Estimates of heritability indicate that selection would be moderately effective in improving weaning weight (Dinkel and Busch, 1973). Vesely and Robison (1971) suggested that both weaning weight and weaning type were moderately heritable and that selection for either one should result in genetic improvement.

Weighted averages of the paternal half-sib estimates for weaning weight indicate that the heritability is about 0.30. The wide range of estimates reported by Warwick (1958) and High (1968) may have resulted from sampling error rather than true differences between parameters being estimated. Heritability of conformation score at weaning in the summary by High (1968) ranged from a low of 0.06 to a high of 0.60. The weighted average of the paternal half-sib estimates from both summaries was 0.31.

Estimates of heritability for weaning weight and weaning type

Table 1. Average Estimates of Genetic Parameters

Trait	Number of estimates	Range of estimates	Number of estimates	Weighted average	No. of animals in wtd. average
Weaning wt.	26	-0.13-1.00	0.30		
Weaning wt.	25	-0.01-0.69	0.29	0.29	20,638
Weaning type	16	0.00-0.50	0.26		
Weaning type	14	0.06-0.60	0.29	0.30	11,429

[1]The first estimate for each trait was taken from Warwick (1958) and the second estimate was taken from High (1968).

score and the phenotypic and genetic correlations from some recent published reports are shown in Tables 2 and 3. This compilation is an update of summary presented by McLaren (1970). These estimates were, for the most part, higher than those reported by Warwick (1958), Petty and Cartwright (1966), and High (1968). However, a larger percentage of the recent estimates was made by analysis of records collected in herds other than experimental breeding herds. It appears that estimates of these parameters are generally higher in commercial than in experimental herds. Data collected in 225 beef herds participating in the Alabama Beef Cattle Improvement Association (BCIA) performance testing program by McLaren (1970) tends to support this fact. He analyzed the weaning records of 23,139 calves using different methods of adjustment. These data were analyzed as three separate breed-management groups--creep-fed Angus and Hereford, non-creep-fed Angus and Hereford and Charolais calves. Estimates of heritability for weaning weight ranged from 0.318 to 0.446, 0.581 to 0.658, and 0.520 to 0.700 in the three groups, respectively. Conformation score was 0.293 for creep-fed, 0.486 for non-creep-fed, and 0.512 for the Charolais groups. The genetic and phenotypic correlations between these two traits were also quite high as shown in Table 3.

In order to evaluate the bias in estimates of genetic parameters derived from commercial herds, Cunningham and Henderson (1965a) computed variance components and estimated various genetic parameters on both an intra- and inter-herd basis. When heritability was calculated using the herd and within sire component of variance as the denominator of the heritability equation, the estimates were lower and agreed more

Table 2. Recent Estimates of Heritability for Weaning Weight and Weaning Type Score Traits

Source	Year	Animals	Breed[1]	Heritability WW	Heritability Wts
Cunningham and Henderson[2]	1965a	7,971	A, H, S	0.59	0.53
Marlowe and Vogt[2]	1965	20,424	A, H	0.38	0.36
Swiger et al.	1965	480	A, H, S	0.58	
Jamison	1966	3,503	A, H	0.39	0.34
Butts	1966	479	A	0.40	
Busch and Dinkel	1967	679	A	0.54	0.65
Harrickeran et al.[2]	1967	17,023	A	0.31	0.40
High	1968	2,747	A, H	0.50	0.51
McGuire	1969		A, H	0.26	0.38
Hokenbacken and Brinks[2]	1969	4,722	A	0.25	
McLaren[2,3]	1970	12,855	A, H[4]	0.37	0.29
			A, H[5]	0.60	0.49
			C[6]	0.59	0.51
Dunn et al.[2]	1970	737	A, H, S	0.42	0.28
Hokenboken and Brinks	1971	1,386	H	0.24	
Vesely and Robison[2]	1971	1,692	H	0.50	0.36
Dinkel and Busch[2]	1973	679	H	0.40	
Francoise, Vogt, and Nolan[2]	1973	2,550	A, H	0.81	0.53

[1]Angus, Hereford, Shorthorn, and Charolais.

[2]These estimates were made using records of calves in commercial herds.

[3]These estimates are an average of those found across adjustment methods used for weaning weight.

[4]Creep-fed.

[5]Non-creep-fed.

[6]Charolais calves by themselves.

Table 3. Recent Estimates of Phenotypic and Genetic Correlations for Weaning Weight and Weaning Type Score

				Correlation	
Source	Year	Animals	Breed	Phenotypic	Genetic
Cunningham and Henderson[2]	1965a	7,971	A, H, S	0.32	0.48
Marlowe and Vogt[2]	1965	20,424	A, H	0.23	0.23
Harricheran *et al.*[2]	1967	17,023	A		0.18
High	1968	2,747	A, H	0.40	0.54
McGuire	1969		A, H	0.32	0.24
McLaren[2,3]	1970	12,855	A, H[4]	0.427	0.315
			A, H[5]	0.475	0.603
			C[6]	0.378	0.706
Dunn *et al.*	1970	737	A, H, S	0.345	-0.31
Vesely and Robison	1971	1,692	H	0.54	0.11
Francoise, Vogt, and Nolan[2]	1973	2,550	A, H	0.34	0.34

[1]Angus, Hereford, Shorthorn, and Charolais.

[2]These estimates were made using records of calves in commercial herds.

[3]These estimates are an average of those found across adjustment methods used for weaning weight.

[4]Creep-fed.

[5]Non-creep-fed.

[6]Charolais calves by themselves.

closely with estimates of repeatability of these traits derived from the same data. Similar results were obtained by Nielsen and Willham (1974). However, their study involved classification data obtained from the American Angus Association. They likewise used different component of variance to calculate heritabilities of Angus classification scores which were moderate to high when type was evaluated subjectively.

Genetic and Phenotypic Correlations

The genetic correlation between two characters may be defined as the ratio of the genetic covariance to the product of their genic standard deviations (Falconer, 1967). A genetic correlation is thus a measure of the relationship between the genetically additive deviations of the two traits. When the genetic correlation between two traits is positive, simultaneous improvement of the two traits results. A negative genetic correlation, however, implies that selection for one trait will automatically cause some deterioration in the other.

The relationship between two traits which can be measured directly is the phenotypic correlation. In genetic studies, it is desirable to partition the correlation between traits according to the relative contributions of the two components of correlation, genetic and environmental. According to Falconer (1960), the genetic cause of correlation is chiefly pleiotropy, although linkage is a cause of transient correlation--especially in populations derived from recent crosses between divergent breeds. Environment is a cause of correlation insofar as two traits are influenced by the same differences in environmental conditions. Phenotypic correlations are useful indicators of the overall phenotypic relationships among traits, but offer little information on the magnitude of the genetic and environmental correlations even though they are direct functions of the genetic and environmental correlations (Kress and Burfening, 1972).

Estimates of genetic and phenotypic correlations among weanling traits in beef cattle have been reported from several studies. Koch and Clark (1955a) found genetic and phenotypic correlations to be 0.50 and 0.64, respectively, between preweaning rate of gain and type score at weaning. A genetic correlation of 0.49 between 182-day weight and type score was reported by Carter and Kincaid (1959), and the phenotypic correlation between the two traits was 0.37. In contract, Lehmann et al. (1961) reported a phenotypic correlation of 0.42 and a genetic correlation of 0.007 between daily gain and weaning type score.

Other estimates of phenotypic and genetic correlations between weaning weight and score of 0.53 and 0.74, 0.57 and 0.51, 0.37 and 0.25, and 0.61 and 0.36 were reported by Brinks et al. (1962), Shelby et al. (1963), Wilson et al. (1963), Marlowe and Vogt (1965), and Cunningham and Henderson (1965a), respectively.

More recent data also point out the positive relationship between weaning weight and type score. Dinkel and Busch (1973) reported that the genetic correlations indicated high positive relationship between weaning weight and daily gain in their study. Likewise, High (1970), using data from the experimental herds of the Tennessee Agricultural Experiment Stations, found positive phenotypic and genetic correlations among weaning traits and in each case the genetic correlation was equal to or larger than the phenotypic correlation.

Correlations between weaning weight and weaning type score was 0.40 (phenotypic) and 0.54 (genetic). Dunn et al. (1970) reported that high estimates of genotypic and phenotypic correlations were noted among the traits associated with weight (birth and 200-day weight).

Francoise, Vogt, and Nolan (1973) observed negative phenotypic correlations between the weaning weight per day of age and weaning conformation score. Positive genetic and phenotypic correlations were found between weaning weight and type score by Vesely and Robison (1971), but the genetic correlation of 0.11 was lower than those from other reports. The observed small positive genetic correlation suggests that only slight correlated response would be expected in either trait when selection pressure was applied for the other trait.

Analysis of performance test records (Alabama BCIA) by McLaren (1970) resulted in higher estimates of genetic correlation than had been previously reported. Genetic correlations between weaning type score and the various estimates of adjusted 205-day weight were similar within each of the three groups (creep-fed Hereford and Angus, non-creep-fed Hereford and Angus and Charolais calves). However, estimates of correlation among the same pair of traits differed widely across the three brred-management groups. The ranges of estimates of genetic correlation for the three groups were 0.26 and 0.35 for the creep-fed calves, 0.56 to 0.62 for the non-creep-fed calves, and 0.69 to 0.73 for the Charolais calves. The range in phenotypic correlations between weaning type score and various estimates of 205-day weight in the creep-fed Angus and Hereford, non-creep-fed Angus and Hereford and Charolais calves was 0.39 to 0.45, 0.39 to 0.45, and 0.36 to 0.39 respectively.

A summary of the more recent estimates of these parameters is presented in Table 3 (page 22).

CHAPTER III

EXPERIMENTAL PROCEDURE

Source of Data

Data used in this study were collected in 201 Angus, 138 Hereford, eight Shorthorn, 25 Charolais, one Red Polled, two Santa Gertrudis herds, and 28 herds with other breeds. Data were taken from weaning records of 36,521 calves collected in 395 herds during the nine-year period between 1964 and 1972 by the Tennessee Beef Cattle Improvement Program (TBCIP). The TBCIP began in 1956 as a joint project between the Tennessee Agricultural Experiment Station (Animal Science Department) and the University of Tennessee Extension Service. The extension service assumed the responsibility for administration of the program and collection of the data, and the experiment station was responsible for processing and analyzing the data.

These 395 farms were located throughout the state of Tennessee and the climatic conditions and management practices under which the calves were produced varied widely. Calves were born throughout the year; however, the smallest number were born in June, July, August, and September and the largest number were born in January, February, and March. Most Tennessee producers practiced a restricted calving season (90 to 120 days), but some producers practiced year-round calving.

Weaning records for each calf include parentage, breed, birth date, age of dam, weaning weight, and weaning age of calf. In addition to weaning weight, type or conformation score, condition grade of calf, and feed management practice were recorded for each calf. Birth weights were not required, but cows were required to be registered in the program before calving. Weaning weights were adjusted to an age-contant basis using birth-weight constants. The birth-weight constants used were average birth weights assumed for Angus and Hereford calves. These were 65 and 60 lbs for Angus and 70 and 65 lbs for Hereford male and female calves, respectively. The breed of the calf was designated from the breed of the sire and the dam. The TBCIP system for coding breed classified Horned and Polled Hereford separately. However, the calves of the two breeds were designated by a single breed code (Hereford) in this study. All breeds and breed crosses, except registered Hereford (Horned and Polled), registered Angus, grade Hereford, and grade Angus were eliminated from this study due to the small number of calves represented by these breeds or because these animals did not express specific breed characteristics.

Weaning weights of calves were generally taken when the calves were between 120 and 300 days of age. At the time weaning weights were taken, an official TBCIP grader or a member of Cooperative Extension Service assigned a conformation score to each calf. The scoring system used by the TBCIP conformed to the system recommended by S-10 Beef Cattle Breeding Committee. The scoring system for type scores used was for Prime = 17, Choice = 14, Good = 11, etc., with the average and low of each grade falling within these limits.

A total of 18,128 or 49.6% of the 36,521 weaning records was eliminated for failure to conform to one or more of the restrictions imposed on records to be included in this study. If weaning weight, birth date, sire number, breed of sire, age of dam, breed of dam, or conformation score of calf was missing, the record was deleted. If management practice code (creep or non-creep) was missing, the calf was likewise eliminated. All calves weaned at less than 120 days of age or over 300 days of age were omitted from this study. Any farm with less than two sires within one year and any sire with less than three calves were not included. On some farms, multiple-sire groups were used during a breeding season and the sire of individual calves could not be determined; records of these calves were also discarded.

Preweaning performance records of these 8,320 Angus and 10,073 Hereford calves weaned during the years 1964 through 1972 were used by Robertson (1974) to compute constants to adjust for environmental effects for various other factors necessary to adjust weaning weight to an age-constant basis. In the preliminary analyses, he divided the weaning records into four breed-feed-management groups. These groups included creep-fed Hereford, non-creep-fed Hereford, creep-fed Angus, and non-creep-fed Angus, as shown in Table 4.

In the previous study, preweaning growth was evaluated as weaning weight (WW), average daily gain (ADG), weight per day of age (WDA), and 205-day weight (WT_5). Coefficients of correlation between members of pairs of these various measures of growth rate were greater than 0.98 which indicated they were equally effective in expressing the trait. Weaning weight, adjusted for environmental factors and adjusted to 205-days of age, was the measure for preweaning growth rate used in the TBCIP for comparative reporting and was the measure of growth chosen in this study.

Table 4. Distribution of Calves Used in the Analysis by Breed, Management, and Year

	Breed			
	Hereford		Angus	
Year	Creep	Non-Creep	Creep	Non-Creep
1964	69	61	105	111
1965	240	616	156	407
1966	320	721	331	690
1967	435	784	158	688
1968	627	1,021	303	939
1969	524	999	571	733
1970	366	807	267	791
1971	385	939	307	862
1972	541	609	356	545
TOTAL	3,516	6,557	2,554	5,766

Method of Analysis

Data Background

Reports in the literature calculated from performance test program data with respect to estimates of heritability for weaning weight and weaning type score have reported high estimates compared to those calculated from data collected in experimental herds.

In order to study the effect of various methods of adjustment of data collected in non-experimental herds on estimates of heritability of adjusted 205-day weight, the adjustment procedures reported by Robertson (1974) were used to adjust weaning weights collected by the Tennessee Beef Cattle Improvement Program to an age-constant basis. Nine combinations of the four methods of adjusting weaning weight to an age-constant basis and the four methods of adjusting age-constant weights for fixed environmental effects were used to generate nine sets of adjusted 205-day weights. The combinations of these methods used to develop each set of adjusted 205-day weights are shown in Table 5 (Robertson, 1974). These nine sets of weaning weights and the weaning type score from the TBCIP data were the basis for this study.

Based on the earlier study by Robertson (1974), creep feeding appeared to influence growth rate and conformation score of calves. Therefore, records of creep and non-creep-fed calves were analyzed separately. In addition, unbiased comparisons of creep and non-creep feeding were not possible on an intra-herd basis because of the confounding of herd with that management practice.

Table 5. Methods of Adjusting for Age of Calf, Sex of Calf, Age of Dam, and Season of Birth

Dataset Number	Method of Adjusting for Age of Calf	Method of Adjusting for Sex, Age of Dam and Season of Birth
W1	Standard Method[a]	One Set of Factors[b]
W2	Standard Method[a]	By Management[c] (Creep and Non-creep)
W3	Standard Method[a]	TBCIP Factors[d]
W4	b_1 (One Value)[b,e]	One Set of Factors[b]
W5	b_1 (By Management)[c,e]	By Management[c] (Creep and Non-creep)
W6	Standard + b_2 (One Value)[a,b,f]	One Set of Factors[b]
W7	Standard + b_2 (By Management)[a,c,f]	By Management[c] (Creep and Non-creep)
W8	Age Intercept (One Value)[b]	One Set of Factors[b]
W9	Age Intercept (By Management)[c]	By Management[c] (Creep and Non-creep)

[a]Standard method = (Weaning Weight-Birth Weight)/(Weaning Age) x 205 + Birth Weight = Calculated 205-day weight.

[b]One b_1 value and one set of factors were calculated from the analysis of the combined records of creep- and non-creep-fed calves and used to adjust records of both management groups.

[c]Separate b_1 values and separate adjustment factors were calculated for creep- and non-creep-fed calves and used to adjust records of calves in the respective management groups.

[d]Adjustment factors currently used by The Tennessee Beef Cattle Improvement Association.

[e]b_1 = Coefficient of regression of weaning weight on weaning age.

[f]b_2 = Coefficient of regression of calculated 205-day weight on weaning age.

<u>Analysis</u>

Preliminary analyses were performed on each individual breed-management groups using a nested procedure.

Homogeneity was tested using Barlett's Test for Homogeneity of Variances as described by Ostle (1954) to determine the feasibility of combining sub groups in subsequent analyses. In these analyses, each effect in the model was assumed to be a random effect. The residual mean square of the breed groups (Angus and Hereford) were homogenous and were pooled in subsequent analyses. However, those of creep and non-creep calves were heterogenous and the management groups were considered as separate entities. A final nested analysis of variance was conducted to access the effects of year, breed within year, herd within year-breed, and sire within year-breed-herd. The final model is shown below:

$$Y_{ijklm} = \mu + Y_i + B_{ij} + H_{ijk} + S_{ijkl} + E_{ijklm}$$

Where: Y_{ijklm} = the observation value of a given trait of the ijklm-th individual record

μ = a constant (μ) common to all observations

Y_i = effect of i-th year

B_{ij} = effect of j-th breed within the i-th year

H_{ijk} = effect of k-th herd within the j-th breed and i-th year

S_{ijkl} = effect of l-th sire within the k-th herd, the j-th breed, and i-th year

E_{ijklm} = random variation

Heritability Estimates

Estimates of heritability were calculated from the nine sets of adjusted weights and for weaning type score. The resulting heritability estimates from the nine sets of 205-day weights were compared to evaluate the affect of method of adjustment on the estimates. Estimates of heritability (intra-herd) were obtained by quadrupling the standard paternal half-sib correlations. Sire variance components derived from the among-sire mean squares on a within herd basis were assumed to be estimates of 25% of the additively genetic variance. The variance components computed from the within-sire mean squares were assumed to contain all environmental variance plus 75% of the additively genetic variance. This was amply shown by Kazzal (1973) (Table 6). Cunningham and Henderson (1965a) reported that overestimation of genetic parameters was reduced when the estimates were calculated on an inter-herd basis. They also reported that the estimates calculated by the inter-herd method were closer to the estimate of repeatibility calculated from the same data. Therefore, a second set of estimates were calculated by the inter-herd method. This was accomplished by the addition of the herd component of variance to the denominator of the standard intra-herd paternal half-sib formula. This procedure allowed for comparison of the estimates of heritability calculated on an intra-herd basis with those calculated on an inter-herd basis.

Heritability estimates were calculated by the following formulas:

(Intra-herd)

$$h^2 = \frac{4\,s^2_S}{s^2_s + s^2_W}$$

(Inter-herd)

$$h^2 = \frac{4\,s^2_S}{s^2_S + s^2_W + s^2_H}$$

Table 6. Form of the Analysis of Variance for Estimating Heritability from Paternal Half-sib Correlation

Source of Variation	Degrees of Freedom	Composition of Mean Square[1]
Between Sires	(S-1)	$s_W^2 + k_o\ s_S^2$
Within Sires	(k.-S)	s_W^2

[1]Explanation of symbols are as follows:

S = number of sires

k. = total number of offspring

s_W^2 = variance due to differences between offspring of same sire

s_S^2 = variance due to sire differences

k_o = average numbers of progeny per sire group

Where: s^2_S = component of variance due to differences between sires

s^2_W = component of variance due to differences among paternal half-sibs

s^2_H = component of variance due to difference between herds

Estimates of standard errors of the heritability estimates were calculated according to the method discussed by Osborne and Paterson (1952). An adequate visual presentation of this concept was proposed by Kazzal (1973) as follows:

(Intra-herd)

$$\text{Standard Error} = \sqrt{\frac{2(s^2_W)^2 \left[s^2_W + K_o\, s^2_S\right]^2}{(s^2_W + s^2_S)^4\; K_o\; (K. - S)}}$$

The general form of these calculations are shown in Table 6.

The average number of progeny (K_o) per sire was computed according to the following formula outlined by Becker (1968):

$$K_o = \frac{1}{S - 1}\left[K. - \frac{\sum k^2_i}{k.}\right]$$

Where: $k. = k_i$

k_i = number of offspring of the i-th sire

In order to determine inter-herd estimates of standard errors for the heritability parameters, it was necessary to rearrange the above formula into the following form to include the herd component of variance:

$$\text{Standard Error} = \sqrt{\frac{2(s^2_W + s^2_H)^2 \left[(s^2_W + s^2_H) + K_o\, s^2_S\right]^2}{(s^2_W + s^2_H + s^2_S)^4\; K_o\; (k. - S)}}$$

Genetic Correlations

In general, any method of estimating heritability also may be adapted to estimate genetic correlations among different traits. It is necessary to isolate the covariances corresponding to each component of variance to estimate genetic correlations between traits (Dickerson, 1969). Estimates of genetic correlations were calculated using the following formulas:

(Intra-herd)

$$\gamma_G = \frac{Cov_S\ (XY)}{\sqrt{\left(s^2_S\ (X)\right)\left(s^2_S\ (Y)\right)}}$$

(Inter-herd)

$$\gamma_G = \frac{Cov_S\ (XY) + Cov_H\ (XY)}{\sqrt{\left[s^2_S\ (X) + s^2_H\ (X)\right] \times \left[s^2_S\ (Y) + s^2_H\ (Y)\right]}}$$

Where:

r_G = estimate of genetic correlations

$Cov_S\ (XY)$ = sire component of covariance of trait X and trait Y

$Cov_H\ (XY)$ = herd component of covariance of trait X and trait Y

$s^2_S\ (X)$ = sire component of variance of trait X

$s^2_S\ (Y)$ = sire component of variance of trait Y

$s^2_H\ (X)$ = herd component of variance of trait X

$s^2_H\ (Y)$ = herd component of variance of trait Y

In this analysis the genetic correlations were computed as the ratio of the sire component of covariance and/or the sire plus herd components of covariance between the two traits to the product of the square roots of the respective components of variance.

CHAPTER IV

RESULTS AND DISCUSSION

Residual mean squares from preliminary analyses of individual breed-management sub-groups were compared by Bartlett's Test for Homogeneity of Variances to determine the effects of combining various groups in subsequent analyses. Results of these comparisons showed that variation with respect to weaning weight and type score was similar for Angus and Hereford calves and data on these breeds were combined. However, when the test for homogeneity was applied to the residual mean square from analyses of the different management groups (non-creep-fed and creep-fed), it was found that the variances were heterogeneous and not conducive to pooling. Thus, in all final analyses the data were considered as two separate entities--records of non-creep-fed calves and records of those that were creep-fed.

Effect of Environmental Factors

Results of the final analyses are incorporated into analysis of variance tables (Tables 7 and 8) with respect to the influence of year, breed within year, herd within breed-year, and sire within herd-breed-year on the variation in the various estimates of adjusted weaning weights and on weaning type scores.

The analyses indicate the important influence of year, breed, herd, and sire on weaning type score, and the importance of herd and sire on weaning weight. Year significantly affected type score.

Table 7. Analysis of Variance of Various Estimates of 205-day Weight and Weaning Type Score of Creep-fed Calves[a]

		Mean Squares									
		Weaning	Estimates of 205-day adjusted weight[b]								
Source of Variation	df	Type Score	W1	W2	W3	W4	W5	W6	W7	W8	W9
Year	8	130.2*	35537.5	35124.3*	55522.7	39735.1	38372.6	36808.7	36927.3	38197.6	37017.5
Breed	9	20.9	48598.8	49829.3	60600.5	61571.9	58416.1	52461.6	51037.8	53984.1	51217.1
Herd	198	22.6*	79058.1*	78861.1*	98230.5*	92410.4*	91704.9*	79563.8*	79808.6*	82450.7*	81526.6*
Sire	402	1.8*	4700.4*	4612.3*	6026.9*	5423.5*	5464.8*	4571.1*	4652.0*	4726.5*	4738.3*
Error	5452	1.1	2639.6	2624.5	3314.0	3091.2	3028.7	2615.3	2631.9	2688.5	2666.1
Total	6069	2.0	5380.8	5356.3	6744.1	6294.7	6211.8	5374.3	5400.6	5548.6	5493.4

*P < .01

[a]Nested analysis with each component nested within that component immediately proceeding it.

[b]Various methods of computing weaning weights are shown in Table 5, page 32.

Table 8. Analysis of Variance of Various Estimates of 205-day Weight and Weaning Type Score of Non-Creep-fed Calves[a]

		Mean Squares									
		Weaning Type Score	Estimates of 205-day adjusted weight[b]								
Source of Variation	df		W1	W2	W3	W4	W5	W6	W7	W8	W9
Year	8	428.2*	97119.0	95529.1	119012.8	104053.6	102255.7	86174.3	87795.4	91720.2	93028.9
Breed	9	58.8*	36380.6	33945.4	51329.3	36328.0	37582.4	31272.2	33324.9	32250.3	34239.2
Herd	311	22.8*	46098.4*	46188.6*	56801.0*	50440.1*	49305.1*	43802.0*	43589.0*	45238.0*	44878.4*
Sire	732	3.0*	4617.1*	4630.4*	6085.1*	5154.2*	5158.1*	4529.9*	4499.4*	4628.9*	4640.3*
Error	11262	1.4	2096.2	2101.1	2562.4	2295.3	2276.5	2026.4	2019.4	2051.0	2046.5
Total	12322	2.3	3443.2	3448.2	4251.8	3771.2	3725.4	3305.6	3294.4	3374.5	3364.2

*P < .01

[a]Nested analysis with each component nested within that component immediately proceeding it.

[b]Various methods of computing weaning weights are shown in Table 5, page 32.

However, since type score was a subjective measure and graders varied from year to year, part of the effect of year could be attributed to this confounding. There was no significant variation among years with respect to adjusted weaning weight. Variation in year accounted for a larger fraction of the variation in type score (Table 9) in non-creep-fed calves than in creep-fed calves (11.38% to 8.37%). Year did not significantly affect adjusted 205-day weight and accounted for less than 1% of the variation in both creep and non-creep calves. Herd within breed-year accounted for a larger amount of variation in both weaning type score (36.03% in creep-fed and 24.60% in non-creep-fed calves) and adjusted 205-day weight (48.17% in creep calves and 33.64% in non-creep calves) than any source of variation included in the model. About 5 to 7% of the total variation with respect to both 205-day weight and type in the total population of performance tested calves was attributable to sire. This represents the fraction of variation which can be utilized in selection programs and the portion upon which genetic progress is dependent.

The within sire mean squares for both traits were relatively large. It appears that the sire component of variance could be distorted either upward or downward from the expected component by the use of the nested procedure in comparison to the use of Henderson's Method I or Method II to calculate the components. However, regardless of type of analysis, the mean square for within sire should be the same. The magnitude of the influences of herd and sire on 205-day weight and weaning type score and the high F values for these sources of variation ($P < .01$) indicate that both must be considered as important components

Table 9. Precent Variation Explained by the Various Components in the Nested Analyses

Source of Variation	Creep-fed Calves: Type Score	Creep-fed Calves: 205-day Weight[a]	Non-creep-fed Calves: Type Score	Non-creep-fed Calves: 205-day Weight[a]
Year	8.37	0.89	11.88	1.78
Breed	1.51	1.40	1.84	0.74
Herd	36.03	48.17	24.60	33.64
Sire	5.88	5.73	7.87	8.16
Within	48.20	48.86	53.90	55.67

[a]Mean of nine estimates of 205-day weight explained in Table 3, page 22.

in the calculations of estimates of genetic parameters.

Variation in the contribution of each environmental factor to variation regardlesss of type of adjustment in weaning weight and score among management groups is shown in Table 9.

Effect of Method of Adjustment

Different methods of adjusting weaning weight for environmental factors (W1-W9) were compared by Robertson (1974). He suggested that 205-day adjusted weights calculated using regression of weaning weight on weaning age, regression of calculated 205-day weight on weaning age or age-intercept methods for adjusting for age of calf (W5, W6, W7, W8, and W9) were similar in creep-fed calves. However, methods W5, W7, and W9, which included adjustment factor calculated from weaning records of non-creep calves, were more effective than the other methods in adjusting weaning weights of non-creep-fed calves. On the other hand, W6 and W8 (Table 3, page 22) were more effective in adjusting weaning weights when creep-fed and non-creep-fed calves were combined and management was disregarded. Removal of the effect of age of calf was least effective when using the standard method of adjustment (W1, W2, W3). Robertson (1974) also noted the inefficiency of the TBCIP method (W3) to adjust for environmental variation due to sex of calf, age of dam and season of birth in both creep-fed and non-creep-fed calves. The method of adjusting for environmental factors could possible explain some of the variation between estimates of parameters calculated from data collected in commercial and experimental herds that were noted in the review of literature.

The relative effectiveness of the different sets of adjustment procedures to remove environmental variation was measured by using each set to calculate an array of adjusted 205-day weights and estimates of heritability and genetic correlations were calculated from each data set. Comparison of the estimates of heritability (h^2) resulting from analysis of the data sets by the standard paternal half-sib method indicated that the adjustment factors currently used by the Tennessee Beef Cattle Improvement Association (W3) produced the highest h^2 values for both non-creep-fed and creep-fed calves (.460 and .361, respectively). The average h^2 of the other eight methods was .361 for non-creep-fed and .341 for creep-fed calves (Table 10). A similar trend was observed when the herd component of variance was added to the calculation to determine heritability estimates (inter-herd method). These results support those of Robertson (1974) who suggested that adjustment methods W5, W6, W7, W8, and W9 were similar.

Methods of Calculating Heritability

Estimates of heritability of each trait were computed from herd, sire, and within sire variance components on both an intra-herd and inter-herd basis and are presented in Tables 11, 12, 13, and 14. Both formulas (intra- and inter-herd) required the following assumptions:

(1) that identifiable environmental variation has been corrected for;

(2) that epistatic gene action may be neglected;

(3) that mating was random with respect to the genes involved in the respective trait;

Table 10. Heritability Estimates and Their Standard Errors of Angus and Hereford Calves

	Non-creep-fed				Creep-fed			
	Intra-herd[1]		Inter-herd[2]		Intra-herd[1]		Inter-herd[2]	
Trait[1]	h^2	SE	h^2	SE	h^2	SE	h^2	SE
WTS	.401 ±	.012	.298 ±	.008	.293 ±	.018	.180 ±	.009
W1	.409 ±	.215	.277 ±	.292	.346 ±	.226	.180 ±	.311
W2	.409 ±	.217	.277 ±	.292	.336 ±	.226	.174 ±	.311
W3	.460 ±	.219	.313 ±	.277	.361 ±	.226	.189 ±	.310
W4	.422 ±	.217	.286 ±	.292	.335 ±	.226	.174 ±	.310
W5	.428 ±	.217	.292 ±	.291	.355 ±	.226	.184 ±	.310
W6	.419 ±	.217	.286 ±	.292	.332 ±	.226	.171 ±	.311
W7	.416 ±	.217	.284 ±	.292	.340 ±	.226	.175 ±	.311
W8	.425 ±	.217	.288 ±	.292	.337 ±	.226	.172 ±	.311
W9	.428 ±	.217	.291 ±	.289	.344 ±	.226	.177 ±	.311

[1]Heritabilities were calculated by the standard paternal half-sib method ($h^2 = \sigma_s^2/\sigma_s^2 + \sigma_w^2$).

[2]Heritabilities were calculated by adding the Herd variance component to the denominator of the standard paternal half-sib method ($h^2 = \sigma_s^2/\sigma_s^2 + \sigma_h^2 + \sigma_w^2$),

Table 11. Intra-herd Heritabilities and Genetic Correlations in Non-creep-fed Angus and Hereford Calves[1,2]

	Weaning Type Score	Estimates of 205-day adjusted weight[3]								
		W1	W2	W3	W4	W5	W6	W7	W8	W9
WTS	.401	.362	.368	.419	.420	.452	.453	.449	.452	.461
W1		.409	.998	.968	.958	.936	.965	.970	.963	.954
W2			.409	.969	.963	.939	.970	.971	.969	.957
W3				.460	.931	.905	.935	.936	.933	.921
W4					.422	1.000	.972	.970	.984	.980
W5						.428	.974	.975	.986	.989
W6							.419	.998	.998	.995
W7								.416	.995	.996
W8									.425	.998
W9										.428

[1]Heritabilities and genetic correlations were calculated by the standard paternal half-sib method.

[2]Heritabilities appear on the diagonal; genetic correlations to the right of the diagonal.

[3]Methods used to estimate 205-day weight (W1 through 9) are explained in Table 5, page 32.

Table 12. Intra-herd Heritabilities and Genetic Correlations in Creep-fed Angus and Hereford Calves[1,2]

	Weaning Type Score	Estimates of 205-day adjusted weight[3]								
		W1	W2	W3	W4	W5	W6	W7	W8	W9
WTS	.293	.381	.346	.387	.368	.361	.392	.427	.388	.408
W1		.346	.996	.970	.944	.980	.964	.972	.958	.987
W2			.336	.964	.949	.974	.971	.970	.965	.983
W3				.361	.899	.940	.929	.938	.921	.952
W4					.335	.971	.979	.977	.991	.980
W5						.355	.950	.960	.960	.983
W6							.332	.996	.997	.988
W7								.340	.993	.994
W8									.337	.989
W9										.344

[1]Heritabilities and genetic correlations were calculated by the standard paternal half-sib method.

[2]Heritabilities appear on the diagonal; genetic correlations to the right of the diagonal.

[3]Methods used to estimate 205-day weight (W1 through 9) are explained in Table 5, page 32.

Table 13. Inter-herd Heritabilities and Genetic Correlations for Non-creep-fed Angus and Hereford Calves[1,2]

	Weaning Type Score	Estimates of 205-day adjusted weight[3]								
		W1	W2	W3	W4	W5	W6	W7	W8	W9
WTS	.298	.374	.358	.420	.362	.379	.365	.382	.363	.380
W1		.277	.998	.983	.982	.973	.984	.987	.984	.981
W2			.277	.978	.986	.974	.987	.987	.987	.982
W3				.313	.962	.955	.962	.969	.961	.962
W4					.286	.996	.991	.989	.996	.993
W5						.292	.991	.991	.993	.997
W6							.286	.998	.999	.997
W7								.284	.997	.998
W8									.288	.998
W9										.291

[1]Heritabilities and genetic correlations were calculted by the paternal half-sib inter-herd method described on page 34.

[2]Heritabilities appear on the diagonal; genetic correlations to the right of the diagonal.

[3]Methods used to estimate 205-day weight (W1 through 9) are explained in Table 5, page 32, and inter-herd methods of calculating h^2 and r_{G1G2} are explained on page 37.

Table 14. Inter-herd Heritabilities and Genetic Correlations for Creep-fed Angus and Hereford Calves[1,2]

	Weaning Type Score	Estimates of 205-day adjusted weight[3]								
		W1	W2	W3	W4	W5	W6	W7	W8	W9
WTS	.180	.680	.671	.676	.670	.682	.670	.680	.673	.683
W1		.180	.999	.993	.989	.995	.994	.995	.993	.998
W2			.174	.991	.990	.994	.995	.994	.995	.997
W3				.189	.979	.990	.986	.957	.986	.991
W4					.174	.995	.995	.994	.998	.995
W5						.184	.991	.992	.993	.996
W6							.171	.999	1.000	.998
W7								.175	.998	.999
W8									.172	.998
W9										.177

[1]Heritabilities and genetic correlations were calculated by the paternal half-sib inter-herd method described on page 34.

[2]Heritabilities appear on the diagonal; genetic correlations to the right of the diagonal.

[3]Methods used to estimate 205-day weight (W1 through 9) are explained in Table 5, page 32, and the inter-herd methods of calculating h^2 and r_{G1G2} are explained on page 37.

(4) that the frequencies of these genes are stable; and

(5) that the effects of these genes, as deviations from the mean, do not change from one generation to the next.

The formula for inter-herd heritability requires, in addition, the assumption that all herd-to-herd variation is non-genetic.

The results of these methods of estimating heritabilities on both an intra- and inter-herd basis are shown in Table 10 (page 45). Basically, the estimates for both non-creep-fed and creep-fed data followed the same pattern. The inter-herd estimates of heritability were smaller than those estimated by the intra-herd method in both management groups. The nine methods of estimating heritability of adjusted 205-day weight were averaged to produce one value. The mean estimate by the intra-herd method was .424 compared to .288 for the inter-herd method in non-creep-fed calves. The values were .343 and .177, respectively, in creep-fed calves. Heritability estimates of weaning type score were .401 and .298 for non-creep-fed and .293 and .180 for creep-fed calves by the intra- and inter-herd method, respectively.

Estimates of heritability obtained in this study by the inter-sire method were similar to those reported in the review of literature which were calculated from data collected in experimental herds (Table 2, page 21). It seems probable that the more recent values calculated from performance test data are overestimates resulting from biases in the variance components.

Several factors may have contributed to the inflation of these recent intra-herd estimates of heritability. The denominator may be reduced due to underestimation of the within sire component of variance.

This could be due to the fact that many observations were results of repeated records on the same dam, or records on closely related dams would reduce the estimate. The denominator could also be reduced, and the estimate of sire variance simultaneously increased, by any differential or assortative mating; for example, mating the better cows with respect to a specific trait with one sire, and the poorer with another. Although the records were corrected for age of dam, differential mating with respect to age of dam might have a similar effect when correction efforts were less effective. Also, the fact that sires were confounded with years, due to the necessity of coding each year-sire group as a separate sire in such data, would have an inflationary effect on the sire variance if an interaction of sires with years existed and was ignored in the analysis. All of these factors tend to bias the intra-herd paternal half-sib ratio upward. This ratio is multiplied by four to give heritability, and hence even a moderate bias in the estimation of variance components would result in a larger bias in heritability.

An alternative interpretation of the high heritability estimates is that there exists considerably more additive genetic variation for these traits in commercial beef herds. This would tend to support the inter-herd method of determining heritability parameters from data collected in commercial herds in order to help account for some of the variation and to reinforce the hypothesis that the intra-herd estimates recently calculated from such data are too high.

Methods of Calculating Genetic Correlations

Genetic correlations were computed separately for non-creep and creep-fed data. There appears to be a positive and fairly large genetic relationship between these two traits (weaning type score and adjusted 205-day weight). A comparison of the estimate of genetic correlation obtained from the standard paternal half-sib method (intra-herd) to that in which the herd variance component was added (inter-herd) are presented in Tables 11, 12, 13, and 14 (pages 46 through 49). The inter-herd method produced a higher genetic relationship between the different methods of adjusted 205-day weight within both management groups. However, this did not hold true for the correlations between traits (weaning type score and 205-day weight) across management groups. In non-creep-fed calves, the intra-herd method showed the greater amount of genetic relationship (Tables 11 and 13), whereas, for the creep-fed, the reversal was true (Tables 12 and 14).

These results suggest the inter-herd method is more realistic in obtaining estimates of heritability as far as commercial herd data is concerned for such traits as 205-day weight and weaning type score. This was especially true when the correction factors currently used by The TBCIP for calculating the standard 205-day weaning weight was used. Inflated heritability estimates could concievably explain why progress from selection for specific traits actually made is lower than expected.

CHAPTER V

SUMMARY

The data used in this study were the Tennessee Beef Cattle Improvement Program weaning records of 18,393 Angus and Hereford calves accumulated over the nine year period, 1964 through 1972. The calves were classified according to weaning age (within the range of 120 to 300 days inclusive), sex (bulls, heifers, steers), age of dam (by years from two to 10 years inclusive and 11 years and over), month of birth, management (creep or non-creep fed), year and breed in preliminary analyses. The purpose of this study was to determine the effect of various methods of adjusting weaning weight for environmental variation and various methods of calculating genetic parameters on the magnitude of these estimates.

Nine combinations of four methods of adjusting weaning weight to an age-constant basis and four methods of adjusting age-constant weights fixed environmental effects were used to generate nine sets of adjusted weights. A nested analysis of variance procedure was used to analyze the nine sets of adjusted 205-day weights and weaning type score and to produce variance and covariance components to be used in estimating heritability parameters for the traits in question. It was determined by Bartlett's Test for Homogeneity of Variances that the records of Angus and Hereford calves could be combined in a single analysis. However, the residual mean squares of creep and non-creep fed calves were heterogeneous and in all final analyses the two

management groups were analyzed separately. Sire and herd were found to significantly affect ($P < .01$) both weaning weight and weaning type score. The effect of herd had a tremendously pronounced effect upon both traits regardless of the management group (creep or non-creep fed).

Estimates of heritability and genetic correlations were calculated from components of variance by two different methods--inter-herd and intra-herd. The intra-herd estimates were calculated by the standard paternal half-sib methods. The inter-herd estimate was calculated by adding the component of variance of herd within year to the denominator of the standard paternal half-sib formulas for calculating heritability and genetic correlation.

Estimates of heritability calculated by the inter-herd method were similar to those reported in other studies when the estimates were calculated from commercial herds. The mean estimate of heritability for adjusted 205-day weight (average of nine methods of adjusting) was .424 and the estimate for weaning type score was .401 in non-creep calves. The estimates were .343 and .293, respectively, in creep-fed calves. Estimates in both management groups tended to be higher than those reported for experimental herds. The estimates calculated on an inter-herd basis tended to be closer to the estimates reported for these traits which were determined in experimental herds. The estimates for 205-day weight (average value) and weaning type score were .288 and .298, respectively, in non-creep-fed calves and .177 and .180, respectively, in creep-fed calves.

Genetic correlations between weaning type score and adjusted

205-day weight were positive and fairly large in magnitude. The inter-herd method tended to increase the genetic correlations between different methods of correcting weaning weight in both the non-creep and the creep-fed calves. However, the intra-herd correlations between the traits (weaning type score and adjusted 205-day weight) were higher for non-creep-fed calves than was the inter-herd correlations.

Comparison of these results with estimates derived in experimental herds suggests that the component of variance for herd in a nested analysis of variance contains both genetic and environmental variation. The true estimates of the genetic parameters probably lie somewhere between the intra-herd and the inter-herd estimates calculated in this study.

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