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EVALUATION OF TECHNIQUES USED IN ESTIMATING PHENOTYPIC, GENETIC AND ENVIRONMENTAL TRENDS IN BEEF CATTLE

A Dissertation

Presented for the

Doctor of Philosophy

Degree

The University of Tennessee, Knoxville

A. Hayden Brown, Jr.

December 1976

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DEDICATION

In grateful appreciation for his personal interest and inspiration, this dissertation is affectionately dedicated to my grandfather, C. B. Flatt, the best cattleman I have ever known.

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ABSTRACT

Data collected between 1957 and 1975 in the University of Tennessee, Ames Plantation Angus herd was used to compare two methods of adjusting weaning weight for known sources of fixed environmental variation and four methods of estimating phenotypic, genetic and environmental trends. The method of adjusting age-constant (calculated 205-day weight) weaning weights using the coefficient of regression of weaning age on calculated 205-day weight, reported by Robertson (1974), was superior to standard procedures for calculating 205-day weight and in removing the effects of sex and age at weaning. The use of sex of calf and age of dam adjustment factors described by Robertson (1974) and readjustment of calculated 205-day weight removed 97 percent of the variation in weaning weight due to sex, age at weaning and age of dam compared to 89 percent for the Tennessee Beef Cattle Improvement Program method. Appropriate adjustment factors for non-genetic effects are important in subsequent estimates of genetic trends; therefore, only records adjusted for weaning age, sex of calf and age of dam were used in subsequent calculations. The techniques used in estimating phenotypic, genetic and environmental trends were (1) the sires-over-time technique, (2) the repeat-mating technique, (3) the dams-over-time technique and (4) the sires-and-dams-over-time technique. Three estimators involving the sires-over-time technique were described by Smith (1962) and evaluated in this study. The preferred sires-over-time estimator was minus twice the pooled within-sire regression of the deviation of performance on time. Each performance record was deviated from the annual population mean. The superiority of this estimator was probably due to the fact that converting performance records to deviations

from the annual population mean tended to minimize the effects of short term environmental fluctuations and more accurately express the genetic value of individuals. Estimates of the phenotypic, genetic and environmental trends from the sires-over-time technique, using deviations rather than records *per se*, were 2.89 ± .18, 2.58 ± .36 and .31 ± .40 lb, respectively. Estimates of phenotypic, genetic and environmental trends by the repeat-mating technique were 2.89 ± .18, 2.83 ± .61 and .06 ± .59 lb, respectively; 2.89 ± .18, 1.40 ± .39 and 1.49 ± .40 lb, respectively, for the dams-over-time technique; and 2.89 ± .18, 2.77 ± .36 and .12 ± .40 lb, respectively for the sires-and-dams-over-time technique. All phenotypic and genetic trends were positive but varied between techniques. Similar magnitude of standard errors was associated with estimates of genetic and environmental trends obtained by the sires-over-time technique, when deviations of performance from the population mean were regressed on time; those obtained by the repeat-mating technique and the sires-and-dams-over-time technique indicated that these methods were equal with respect to their accuracy in estimating genetic and environmental trends.

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CHAPTER I

INTRODUCTION

Although selection for higher production has been practiced in many herds in Tennessee, few attempts have been made to evaluate the various procedures for obtaining genetic and environmental trends in Tennessee beef cattle. One of the major tasks of the beef producer is to develop and institute procedures which result in heavier weaning weights in beef cattle populations. One may choose to achieve heavier weights either by improving the mean environment of the population, by improving the mean breeding value of the population or by a combination of both. The change in weight per unit of time due to change in mean environment is known as environmental trend and the change in weight per unit of time due to change in mean breeding value is the genetic trend. Positive genetic trends should occur as a result of intensified selection programs.

The objectives of this study were (1) to evaluate and compare the various techniques for obtaining estimates of genetic and environmental trends in Tennessee beef cattle from field data, (2) to apply these same techniques to data collected at Ames Plantation, (3) to apply two new techniques to the same data, and (4) to evaluate the results.

The five current techniques used in estimating genetic and environmental trends in beef cattle are (1) sires-over-time, (2) direct-selection, (3) repeat-mating, (4) repeat-record, and (5) generation-number. Few attempts have been made to evaluate and compare all of these methods simultaneously, using the same data. This is primarily due to the unbalanced nature of field data. Because each of the techniques approaches

estimation of genetic and environmental trends differently, seldom does a suitable data set exist for a collective comparison of the five methods. This study, however, based on weaning records collected at Ames Plantation, a field station of The University of Tennessee, concerns such a collective comparison; thus, permitting an evaluation of two of the five current techniques, use of two new techniques, a new estimator, and application of the same to the data of the Ames herd, and finally a discussion and evaluation of the results.

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CHAPTER II

REVIEW OF LITERATURE

Various techniques for estimating genetic and environmental trends in livestock breeding research have been reported. A review of the literature reveals that few attempts have been made to evaluate the efficiency of these varied techniques in one species using the same records. Therefore, this review of literature will include reported research in several species and/or classes of livestock.

I. METHODS OF ESTIMATING PHENOTYPIC, GENETIC AND ENVIRONMENTAL TRENDS

Sires-Over-Time Technique

The continued use of sire over several years (sires-over-time) is one technique used for estimating the magnitude of genetic change occurring in a population. This technique, proposed by Smith (1962) and applied by him in a swine population was used by Hillers and Freeman, 1966; Harville and Henderson, 1967; Branton, Evans, Steel and Farthing, 1967; Burnside and Legates, 1967; Everett, Meadows and Gill, 1967; Acharya and Lush, 1968; Hargrove and Legates, 1971; Verde, Wilcox, Martin and Reaves, 1972; Palmer, Wilcox, Martin, Verde and Barranges, 1972; and Powell and Freeman, 1974, to estimate genetic change in dairy cattle populations. Zabel (1973), Holbert (1975) and Anderson (1975) also used the sires-over-time technique to estimate genetic change in beef cattle populations.

Smith (1962) hypothesized that sires used over a period of time provide some continuity of genetic material and allow measurement of

genetic change. Genetic trends can be visualized as a comparison of the change in performance of successive progeny groups, within sire, with change in the entire population. Genetic change (ΔG) occurs in both sexes at the same time. However, since the current dams are daughters of sires of the previous generation, it is unlikely that differential change could exist over an extended period of time in the two sexes. However, if there is a change in the rate of improvement in one sex, there will be a lag before that change is reflected in the other. Application of the sires-over-time technique involves the assessment of one-half the annual genetic change by the expression

$$.5g = (t + g) - (t + .5g),$$

where

$t + g$ = phenotypic change [environmental (t) plus genetic (g)],

$t + .5g$ = change in performance of successive groups of progenies of individual sires.

Genetic change (ΔG) in any sire was considered to be zero, thus the estimate includes only ΔG in the female population (Smith, 1962).

Three procedures that have been used to estimate ΔG by the sires-over-time technique were discussed by Smith (1962). Two of the procedures involve regression of performance on time, and the other involves differences in means-over-time. Regression of performance on time ($b_{P.T}$) represented the total change ($g + t$), while the regression of performance on time within sires ($b_{P.T/S}$) can be represented by $t + .5g$, which contains only the dams' contribution to genetic progress. Thus, Smith's (1962) first estimator of ΔG can be expressed as:

$$\Delta\hat{G} = 2(b_{P.T} - b_{P.T/S}),$$

Application of this estimator was discussed by Smith (1962), Harville and Henderson (1967), Burnside and Legates (1967), Everett, Meadows and Gill (1967), Acharya and Lush (1968), Verde, Wilcox, Martin and Reaves (1972), Palmer, Wilcox, Martin, Verde and Barrantes (1972), Powell and Freeman (1974), Holbert (1975) and Anderson (1975).

Smith (1962) suggested also that year-to-year fluctuation in environment could be avoided when ΔG was estimated as

$$\Delta\hat{G} = -2\, b_{(P-\overline{P}).T/S},$$

twice the pooled within-sire regression of the deviation of progeny performance on time. Each record was expressed as a deviation from the population mean and $b_{(P-\overline{P}).T/S}$ was equated to $(t + .5g) - (t + g)$. Hillers and Freeman (1966), Harville and Henderson (1967), Branton, Evans, Steele and Farthing (1967), Acharya and Lush (1968), Hargrove and Legates (1971), Zabel (1973) and Powell and Freeman (1974) used this estimator.

Using means rather than regressions, the third estimator involving differences in means can be written as

$$\Delta\hat{G} = \frac{\Sigma 2\,[(\overline{X}_{Ty} - \overline{X}_{To}) - (\overline{X}_{Sy} - \overline{X}_{So})]}{y},$$

where

$\overline{X}_{Ty}$ = population mean for the y^{th} year,

$\overline{X}_{To}$ = population mean for the o^{th} year,

$\overline{X}_{Sy}$ = the continued sire mean for the y^{th} year,

$\overline{X}_{So}$ = the continued sire mean for the o^{th} year,

y = number of years.

The expressions $(\overline{X}_{Ty} - \overline{X}_{To})$ and $(\overline{X}_{Sy} - \overline{X}_{So})$ were written as $(t + g)$ and $(t + .5g)$, respectively. Desired annual ΔG can be estimated, although the accuracy of individual yearly estimate will be lower. Genetic

change in a beef herd was estimated by Zabel (1973) using this technique.

Smith (1962) suggested that estimation of ΔG by regression procedures was more efficient than estimation by mean differences procedures. He suggested that the third procedure was accurate when the initial difference between $\bar{X}_{To}$ and $\bar{X}_{So}$ was zero, and can be calculated without error. Acharya and Lush (1968) reported that estimates made by $2(b_{P.T} - b_{P.T/S})$ were considerably larger than those by $-2b_{(P-\bar{P}).T/S}$. Powell and Freeman (1974) compared the two regression procedures above to estimate ΔG and stated that the preferred estimator was $-2b_{(P-\bar{P}).T/S}$. This estimator ($-2b_{(P-\bar{P}).T/S}$) was more efficient than the difference in means estimator according to Zabel (1973). Leech and Healy (1959) stated that an improved estimate could be obtained by combining ΔG's derived by the regression of sire on time and by the difference in means procedures.

Harville and Henderson (1967) proposed that

$$\Delta\hat{E} = b_{P.T} - \Delta\hat{G}$$

was an unbiased estimator of environmental change (ΔE), where the regression of performance on time ($t + g$) was represented by $b_{P.T}$ and the annual $\Delta G(g)$ was derived by the regression estimators discussed earlier. This estimator of ΔE was used by Harville and Henderson (1967), Everett, Meadows and Gill (1967) and Powell and Freeman (1974).

Phenotypic change (ΔP) can be estimated as $b_{P.T}$ which represents the total change $t + g$. The phenotypic change was estimated in this manner by numerous researchers including Smith (1962), Harville and Henderson (1967), Burnside and Legates (1967), Everett, Meadows and Gill (1967), Verde, Wilcox, Martin and Reaves (1972), Palmer, Wilcox, Martin, Verde and Barrantes (1972), Zabel (1973) and Powell and Freeman (1974).

Although this technique has advantages over the more conventional methods, there are certain disadvantages which prevent the general use of sires-over-time. Various non-additive effects may arise and a sire-year interaction is the most relevant because it frequently results in a within sire change over-time. In short term environmental fluctuations sire-year interactions can be regarded as additional error contributing to the within sire within time variance and with a large number of sires will not bias the estimates of genetic change. If there is a long term environmental change, the sire-year interaction will reflect real genetic change in the estimated breeding value of a sire and the within sire change will be appropriate for estimating ΔG (Smith, 1962).

Extended use of sires in a herd is often based on the performance of their early progeny. Regression to the mean performance of the subsequent progeny will effect a change in estimated progeny performance and bias the estimate of ΔG. Records of progeny born before or after selecting or culling of sires, on the basis of progeny performance, can each be used to give unbiased estimates of ΔG (Smith, 1962; Harville and Henderson, 1967). A progressive type of culling will result from initial selection of animals on progeny performance. Resulting bias will often be hard to eliminate because too few sires are used for a sufficient time to estimate the small rate of genetic change. In addition, it is likely that initial selection and progressive culling among sires will cause uncertain estimates of ΔG even when the number of sires is theoretically sufficient (Smith, 1962). Smith (1962) and Burnside and Legates (1967) suggested that biased $\Delta\hat{G}$ may occur when older sires are mated to older dams or when sires are mated to selected dams. Estimators involving performance records reduced to deviations from a population

mean substantially overestimate ΔG if the mean from which the records were deviated excluded the sires' progeny (Smith, 1962; Powell and Freeman, 1974). Powell and Freeman (1974) stated that sizeable biases may occur with improper definition of the population mean.

Various modifications of the procedures for estimating ΔG by the sires-over-time technique have been suggested in an attempt to improve their accuracy. Because older sires tend to be mated to older dams, Smith (1962) suggested the regression of age of dam on time within sire ($b_{DA.T/S}$) as an adjustment for selective mating with respect to age. This modification was expressed as $b_{P.T/S} = [t + g(1 - b_{DA.T/S})]/2$ where $b_{DA.T}$ is the regression of age of dam on time (Everett, Meadows and Gill, 1967). Powell and Freeman (1974) suggested that $b_{DA.T/S} - b_{DA.T}$ was a measure of non-random allotment of dams to older sires, with respect to age of dam (AD). This adjustment (AD) was also suggested as effective in alleviating bias in $b_{P.T/S}$ and g when older sires were mated to dams not of average genetic merit. After this additive adjustment, the expression $b_{P.T/S} = t + .5\ (1-b_{DA.T/S})\ g + \Delta D$ represented the genetic trend within sire with respect to additive genetic merit of dams relative to all available mates. One-half of this bias was passed on to the progeny and was removed by subtracting $\Delta D/2$ (Harville and Henderson, 1967; Powell and Freeman, 1974). Everett, Meadows and Gill (1967) and Powell and Freeman (1974) stated that accuracy was obtained in $\hat{\Delta G}$ by pooling the regression of performance on time within sire ($b_{P.T/S}$), weighted by the inverse of the variance of each regression.

Everett, Meadow and Gill (1967) estimated a term ΔC, defined as

the bias due to culling of dams over time. They calculated $\Delta\hat{C}$ as $b_{P.T} - b_{DP.T/S}$ and subtracted .5 $\Delta\hat{C}$ from $b_{P.T/S}$ in their estimator. Powell and Freeman (1974) stated that $\Delta\hat{C}$ represented a phenotypic trend and was not genetic as Everett, Meadows and Gill (1967) stated. They suggested that $\Delta\hat{C}$ should be regressed by heritability. Furthermore, Powell and Freeman (1974) stated that it should be added rather than subtracted.

Everett, Meadows and Gill (1967) stated that the estimator $\Delta\hat{E} = b_{P.T} - \Delta\hat{G}$, should be modified to $\Delta\hat{E} = b_{P.T} - \Delta\hat{G}(1-b_{DA.T/2})$ to obtain unbiased estimates of ΔE.

Additional accuracy may be associated with $\Delta\hat{G}$ if records are adjusted for fixed sources of environmental variation prior to imposing estimators. Smith (1962) used records adjusted for the effect of age of dam on progeny performance. Acharya and Lush (1968) used records corrected to average age at the beginning of each performance and expressed them on a first performance basis by using age correction factors. Hargrove and Legates (1971) removed variation between repeated cow performance with age correction factors. Zabel (1973) and Holbert (1975) used records adjusted for age, sex, season of birth and age of dam using least squares constants. Anderson (1975) used records adjusted for age, age of dam, sex and season of birth using coefficients described by Robertson (1974).

First records of individual dams are free from most of the complications of selection, repeatability and age adjustments. With no selection, the progeny represents a random sample of the additive genetic merit of their parents. The resulting estimates of ΔG from first performance records of the progeny is the same as that of the parents (Powell and Freeman, 1974). First records of dairy cows expressed on a mature equivalent basis

were used by Hillers and Freeman (1966), Harville and Henderson (1967), Branton, Evans, Steel and Farthing (1967), Burnside and Legates (1967), Verde, Wilcox, Martin and Reaves (1972), Palmer, Wilcox, Martin, Verde and Barrantes (1972), and Powell and Freeman (1974).

Hillers and Freeman (1966) included only sires with a relatively large number of progeny and those used over a rather extended period of time in order to increase the accuracy of estimation of within sire regression. The records used by Hargrove and Legates (1971); Verde, Wilcox, Martin and Reaves (1972); and Zabel (1973) were limited to sires that had 10 or more progeny in more than one year. Holbert (1975) and Anderson (1975) restricted sires to those with three offspring in at least two years.

Harville and Henderson (1967) and Powell and Freeman (1974) found that the accuracy of estimating ΔG in large populations was obtained initially by estimating on a within sub-population basis and then pooling these estimates for the overall change. Sub-population estimates were weighted by the inverse of their respective variances.

Reliability of $\Delta\hat{G}$ made by the sires-over-time technique is provided by appropriate standard errors (SE) of these estimates. Smith (1962) assumed that the maximum variance of $2(b_{P.T} - b_{P.T/S})$ was $4(Vb_{P.T} + Vb_{P.T/S})$ when the regressions were positively correlated. If $-2b_{(P-\overline{P})T/S}$ was the estimator used, Smith (1962) found the variance would simply be $4\ Vb_{(P-\overline{P})T/S}$. Theoretical variance of $2(b_{P.T} - b_{P.T/S})$ was approximately

$$4\sigma^2 \left(\frac{1}{NTy} + \frac{1}{\Sigma n_s Ty}\right),$$

where

σ = standard deviation of the trait being considered,

N = total number of records per year,

n_s = number of records per year for the s^{th} sire,

Y = total number of years,

y = number of years in which the s^{th} sire is present,

$Ty = y(y^2 - 1)12$.

The first term in the theoretical variance was much smaller than the second term unless a large number of the sires were used over the entire period. The variance reduced to approximately $4\sigma^2/\bar{n}\Sigma_s Ty$, where $\bar{n}$ is the average number of records for each sire in any year. This expression also gave an approximate variance of the estimator $-2b_{(P-\bar{P}).T/S}$; however, it did not account for the degree of overlap of sires over time. The SE of the estimates of ΔG was found by the expression $2\sigma/\sqrt{\bar{n}\Sigma_s Ty}$ (Smith, 1962). Everett, Meadows and Gill (1967) suggested that the SE of ΔG found by $2(b_{P.T} - b_{P.T/S})$ should be

$$2\sqrt{[\sigma^2_P/\sigma^2_T - b^2_{P.T}]/(N-2) + 1/\Sigma_i[(N-2)/(\sigma^2_P/\sigma^2_T) - b^2_{P.T/S_i}]},$$

where

N = number of animals in the regression,

σ^2_P = variance of performance,

σ^2_T = variance of time,

$b_{P.T/S_i}$ = regression of performance of progeny of sire i on time.

Zabel (1973) indicated that no unbiased estimator of the variance components of the general means estimator has been devised.

Powell and Freeman (1974) stated that the SE of $\Delta\hat{E}$ estimated by $b_{P.T} - \Delta\hat{G}$ would be nearly the same as those associated with $\Delta\hat{G}$ because $b_{P.T}$ represented the total change. Everett, Meadows and Gill (1967)

stated that the SE for $\Delta\hat{E}$ was obtained as

$$\sqrt{\text{Var}(b_{P.T}) + V(\Delta G)}.$$

The SE of $\Delta\hat{P}$ was calculated by Everett, Meadows and Gill (1967) by the expression

$$\sqrt{[1/(N-2)][(\sigma^2_P/\sigma^2_T) - b^2_{P.T}]} \ ,$$

where

N = number of animals in the regression,

σ^2_P = variance of performance,

σ^2_T = variance of time,

$b^2_{P.T}$ = regression of performance on time.

If the same technique was used to calculate $\Delta\hat{G}$ on a within dam basis, variation in age of dam and culling could introduce bias according to Smith (1962).

In studies of ΔG Smith (1962), Harville and Henderson (1967), Burnside and Legates (1967) and Powell and Freeman (1974) applied both the sires-over-time technique and the repeat-mating technique and compared the results obtained. Smith (1962) stated that similar results were obtained when both techniques were used. Harville and Henderson (1967) found that the sires-over-time technique gave smaller $\Delta\hat{G}$ than obtained from the repeat-mating technique. Burnside and Legates (1967) stated that there was close agreement in the results obtained by the two techniques and that they appeared equal in detecting genetic change. Powell and Freeman (1974) stated that the sires-over-time technique gave the smaller $\Delta\hat{G}$ and was accompanied by the smaller SE.

Acharya and Lush (1968) used both the sires-over-time technique and

the direct-selection technique. The estimate obtained by the sires-over-time technique was smaller than the ΔG estimate directly from selection practiced.

Direct-Selection Technique

Rendel and Robertson (1950) provided a second technique for estimating ΔG in a population which was based on selection of males and females to become parents of the next generation. Their analysis and those by Stonaker (1953), Walton and Lush (1962), Acharya and Lush (1968) and Burnside, Rennie and Bowman (1968) applied this technique in estimating ΔG in dairy cattle populations. Rendel and Robertson (1950), Stonaker (1953), Walton and Lush (1962) and Acharya and Lush (1968) applied this technique to closed populations. Burnside, Rennie and Bowman (1968) used this technique in a study of a population where progeny tested AI sires originated outside the population.

The direct-selection technique involved assessment of ΔG based on four contributing sources of genetic material: sires of males, sires of females, dams of males and dams of females. Selection of progeny to become parents of the next generation was based on the performance of their parents, and the parental genes were transmitted to their progeny by the four sources (Rendel and Robertson, 1950).

For each progeny group Rendel and Robertson (1950) theorized that the superiority in breeding value (I) for a particular trait could be expressed as:

$$I = i\sigma_G r_{PG},$$

where

i = intensity of selection,

σ_G = genotypic standard deviation,

r_{PG} = correlation between phenotype and genotype.

Acharya and Lush (1968) calculated the genetic superiority in breeding value from the four sources individually. Genetic superiority of dams of males was calculated as

$$I_{DM} = \frac{nh^2}{1 + (n-1)\ r}\ (DR - RDA),$$

where

n = number of records,

h^2 = heritability of the trait,

r = repeatability (intraclass correlation),

DR = dam's record for a specified year,

RDA = average of all remaining dams in the population during the same year.

Each dam's genetic superiority was weighted by the number of daughters her son sired. The genetic superiority of dams of females (I_{DF}) was calculated by using the same formula used for estimating the average superiority of dams of males, but the value was weighted by the number of daughters of each dam retained in the population. The genetic superiority in the breeding value of the sires of males was calculated as

$$I_{SM} = \frac{2\ nh^2}{4 + (n-1)\ h^2}\ (DR - CA),$$

where

n = number of records,

h^2 = heritability of trait,

DR = average of the first records of all progeny of the sires,

CA = average of the first record of contemporaries (animal performing in the same year as the progeny of the sire).

In calculating the genetic superiority of sires of males, the superiority of each male was weighted by the number of granddaughters through his son. The genetic superiority of the sires of males was calculated in retrospect, because not all daughters required in the sire evaluation had progeny records at the time of evaluation. The genetic superiority of the sires of females (I_{SF}) was evaluated by the same formula as that of sires of males.

Rendel and Robertson (1950) stated that the ΔG per generation (y) could be computed by the estimator

$$\Delta\hat{G}_y = \frac{\Sigma I}{\Sigma A},$$

where

I = superiority of breeding value from each of the four sources,

A = generation interval (average age of parents at birth of progeny) from each of the four sources.

This estimator, or modifications thereof, have been used by several researchers. Rendel and Robertson (1950) used information on dams of males and dams of females and assumed that the other two I's contributed nothing to the progeny generation. Burnside, Rennie and Bowman (1968) used the superiority in breeding value of dams of females and sires of females and made the same assumption as Rendel and Robertson (1950) in regard to the other two sources of genetic material. The use of progeny group means negated the effects of environmental variation (Stonaker, 1953; Acharya and Lush, 1968; Burnside, Rennie and Bowman, 1968); however, routine use of progeny testing may not always increase

annual ΔG (Acharya and Lush, 1968). Walton and Lush (1962) stated that overcorrection of first records and inclusion of low terminal records could introduce positive genetic biases but tended to cancel when computing selection intensities. Acharya and Lush (1968) stated that inaccuracies in the estimates of heritability and repeatability used in the calculation of genetic trends were a more serious source of bias than inaccurate age correction factors.

In genetic studies, various adjustments have been made to remove nongenetic variations. In studies of ΔG in applied selection, Rendel and Robertson (1950), Stonaker (1953) and Walton and Lush (1962) used age adjustment factors to remove the effect of age of dam. Acharya and Lush (1968) adjusted to a first performance basis and Burnside, Rennie and Bowman (1968) adjusted for the effects of age by expressing performance as a percentage of the appropriate breed age-class mean.

Acharya and Lush (1968) compared the direct-selection technique and the sires-over-time technique. The estimate obtained by the direct-selection technique was larger than the estimate by the sires-over-time technique. Acharya and Lush (1968) stated that the estimate of genetic change from the direct-selection technique was probably biased upward due to the estimates of heritability and repeatability being calculated from limited data.

Walton and Lush (1962) and Burnside, Rennie and Bowman (1968) compared both the direct-selection technique and the repeat-record technique in studies of ΔG. They reported that the estimates obtained by selection agreed reasonably well with ΔG estimated by the repeat-record technique. Burnside, Rennie and Bowman (1968) found that the

direct-selection technique gave smaller estimates of ΔG than the repeat-record technique. Inability to accurately estimate breeding value of many of the sires used in the direct-selection technique was the explanation given. In one breed studied where information was available on all parents, the estimates agreed closely (Burnside, Rennie and Bowman, 1968).

Repeat-Mating Technique

The repeat-mating technique was proposed by Goodwin, Dickerson and Lamoreaux (1960) to estimate ΔG in an experimental poultry population. This technique was adapted to non-experimental populations of swine by Smith (1962); and Harville and Henderson (1967), Burnside and Legates (1967) and Powell and Freeman (1974) used it to study ΔG in dairy cattle populations. Other workers, studying ΔG beef cattle populations, have used the repeat-mating technique (Flower, Brinks, Urick and Wilson, 1964; Scarsi, 1971; and Fahmy and Lalande, 1973).

By this technique ΔE was estimated and ΔG was the difference between $\Delta\hat{E}$ and $\Delta\hat{P}$. Smith (1962) suggested that the genic material of full sibs was alike and any difference in their performance reflected ΔE between years. Genetic change (g) in one year was estimated as the differential change in the performance of the population $(t + g)$, and t; thus $g = (t + g) - t$.

The repeat-mating technique assumes equal change in both sexes even when selection is limited to one but does not imply that both sexes are equal as sources of improvement (Powell and Freeman, 1974). Since dams are daughters of selected sires of the previous generation, ΔG in females would be expressed later than that in males (Smith, 1962).

The three estimators of ΔG using the repeat-mating technique involve regression of performance on time. The first estimator proposed by Smith (1962) and used by Harville and Henderson (1967), Burnside and Legates (1967) and Powell and Freeman (1974) was calculated on a within sire and dam ($b_{P.T/SD}$) basis and contained only $\Delta E(t)$. Regression of performance on time ($b_{P.T}$) represented the total change (g + t). Genetic change was estimated as

$$\Delta\hat{G} = b_{P.T} - b_{P.T/SD}.$$

The second estimator suggested by Flower, Brinks, Urick and Wilson (1964) and used by Scarsi (1971) and Fahmy and Lalande (1973) was calculated as the regression of performance on time $b_{P.T} = (t + g)$, minus $b_{(P_2-P_1).T} = t$, the regression of the difference in the performance of full sibs born in consecutive years on time, and symbolized as

$$\Delta\hat{G} = b_{P.T} - b_{(P_2- P_1).T}.$$

Powell and Freeman (1974) proposed the third estimator:

$$\Delta\hat{G} = -b_{(P-\bar{P}).T/SD}.$$

This estimator assumed that ΔG was equal to the negative of the regression on deviation of performance from the population mean on time within full-sib families. Powell and Freeman (1974) stated that $b_{(P-\bar{P}).T/SD}$ may be written as $t - (t + g)$.

The estimate of ΔG will be biased if the parents have been selected or if the dam's age affects her progeny's performance (Smith, 1962). Biases may also result if the number of progeny in the sire-dam subclass have been partially determined by the performance of previous progeny (Harville and Henderson, 1967). Scarsi (1971) stated that the comparison of full-sibs is only a part of the estimate of environmental variation

because genotypic difference exists through segregation and independent assortment of genes and can cause serious bias in year-to-year estimates of ΔE. The validity of the repeat-mating technique in determining $\Delta\hat{G}$ depends on the adjustment of records to a common basis. Smith (1962) adjusted performance for the effects of age of dam, and Flower, Brinks, Urick and Wilson (1964) and Scarsi (1971) adjusted records to a constant length, sex, age of dam and season of birth basis.

Burnside and Legates (1967) equated the variance of the estimator

$$\Delta\hat{G} = b_{P.T} - b_{P.T/SD} \text{ to } {}^{Var}b_{P.T} + {}^{Var}b_{P.T/SD}.$$

The standard error of $\Delta\hat{G}$ by the repeated-mating technique was obtained by Goodwin, Dickerson and Lamoreaux (1960) as:

$$S_{\overline{\Delta G}} = \sqrt{{}^{V}b_{P.T} + {}^{V}\overline{\Delta E} - 2 \text{ cov}} \quad ,$$

where

${}^{V}b_{P.T}$ = variance of the regression of performance on time, including all progeny,

${}^{V}\overline{\Delta E}$ = variance of the environmental change, including full-sib progeny.

Smith (1962), Harville and Henderson (1967), Burnside and Legates (1967) and Powell and Freeman (1974) compared the repeat-mating technique and sires-over-time technique. Smith (1962) and Burnside and Legates (1967) reported similar estimates of ΔG but Harville and Henderson (1967) and Powell and Freeman (1974) calculated higher estimates by the repeat-mating technique than by the sires-over-time technique.

Repeat-Record Technique

The repeat-record technique was introduced by Nelson (1943) in a study of ΔG in a dairy cattle population. This technique was used to estimate ΔG in dairy cattle populations by Henderson (1949), Walton and Lush (1962), Arave and Laben (1963), Arave, Laben and Mead (1964) and Burnside, Rennie and Bowman (1968) and in a beef cattle population by Bailey, Harvey, Hunter and Torell (1971). Environmental change was estimated from the difference in records of consecutive years and ΔG was estimated as the difference between the environmental change (t) and the overall change in performance of the population (t + g). The repeat-record technique is based on calculation of $\Delta\hat{E}$ and subtracting $\Delta\hat{E}$ from $\Delta\hat{P}$ to give $\Delta\hat{G}$. Four methods of determining ΔE have been proposed: (1) The algebraic sum of mean difference for all individuals which had records in consecutive years was used by Nelson (1943); (2) Least-squares procedures were used to minimize errors in computing differences between non-consecutive years and resulted in more conservative estimates of ΔE (Nelson, 1943); (3) Maximum likelihood (ML) procedures were used for measuring yearly environmental differences (Henderson, 1949) and (4) The best linear unbiased predictor (BLUP) allows analysis of records which are not a random sample of a population (Henderson, 1973).

Maximum likelihood automatically takes into account incomplete repeatability and annual culling levels and utilizes all of the records in such a way as to obtain the most precise estimates of yearly environmental effects (Henderson, 1949).

Adapting the ML technique to the estimation of ΔE required defining the material involved and its behavior. Validity of estimation rested

on the accuracy with which the model described the actual situation. Henderson, Kempthorne, Searle and von Krosigk (1959) let a 305-day-2X-M.E. lactation record in the kth year produced by the jth cow in the ith group of cows be designated as y_{ijkl} and

$$y_{ijkl} = b_i + c_{ij} + a_k + e_{ijkl} .$$

b_i was the mean true producing ability of the ith group of cows.

c_{ij} was the deviation of the jth cow's true producing ability from the mean true ability of the ith group, of which she was a member.

a_k was the deviation, in pounds of milk, which was added to the ijth cow's true ability because she produced the record in the condition of the kth year.

e_{ijkl} was the chance deviation of the record from its expected value, $b_i + c_{ij} + a_k$.

Additional asusmptions required for use of maximum likelihood procedure were (1) b_i's and a_k's were fixed quantities, (2) c_{ij}'s in each b_i were normally and independently distributed with variance, σ_c^2, and (3) e_{ijkl}'s were normally and independently distributed with variance, σ_e^2, and (4) the classifications were independent of each other.

Required for the solution of the problem was the joint frequency function, $f(e_{ijkl}, c_{ij})$. Since the e_{ijkl} and c_{ij} were independent, the joint frequency distribution function was the product of the two constituent frequency functions or

$$f(e_{ijkl}, c_{ij}) = \frac{1}{2\Pi\sigma_e\sigma_c} e^{-\frac{1}{2}\left[\frac{e_{ijkl}^2}{\sigma_e^2} + \frac{c_{ij}^2}{\sigma_c^2}\right]} .$$

Likelihood of the sample of records was equated to the product of the frequency functions of individual records. Estimates of parameters maximizing the likelihood of the sample were obtained by partial differentiation of the logarithm of the likelihood equations with respect to each of the parameters, equating the partial differentials to zero and solving the resulting equations simultaneously. The equations obtained were similar to those obtained by least squares, except that a constant $\frac{\hat{\sigma}_e^2}{\hat{\sigma}_c^2}$ was added to the coefficient (number of records) of $\hat{c}_{ij}$ in the c_{ij} equation, and two additional equations, one for $\hat{\sigma}_e^2$ and one for $\hat{\sigma}_c^2$ were obtained as a part of the set of ML equations:

$$\hat{\sigma}_c^2 = \frac{\Sigma\Sigma_{ij} \hat{c}_{ij}^2}{\Sigma\Sigma_{ij} n_{ij}} \text{ and } \hat{\sigma}_e^2 = \frac{\Sigma\Sigma\Sigma_{ijkl} (y_{ijkl} - \hat{b}_i - \hat{c}_{ij} - \hat{a}_k)^2}{\Sigma\Sigma\Sigma_{ijkl} n_{ijkl}} .$$

The simultaneous solution of these equations was not apparent but unbiased estimates of σ_c^2 and σ_e^2 were available from other sources and were substituted for $\hat{\sigma}_c^2$ and $\hat{\sigma}_e^2$ in the maximum likelihood equations to allow valid estimates of the remaining parameters (Henderson, Kempthorne, Searle and von Krosigk, 1959). Due to the invariant property of ML, approximate ML estimates could be calculated from the individual least-squares parameters to provide estimates of the true producing abilities of individuals, average producing ability of the progeny of one sire, and the average producing ability of a population at any particular time.

The exact mechanism of separating time trends by this method was not immediately apparent. An element, b_i, which presumably took into account the changing composition of the population with time was present in the ratio of two variances,

$\frac{\hat{\sigma}_e^2}{\hat{\sigma}_c^2}$, to allow for the incomplete repeatability of production records of the same individual. Cows with only one record of performance were not eliminated but entered into the computations (Henderson, Kempthorne, Searle and von Krosigk, 1959).

Removal of differences between years was demonstrated in a set of simulated records with known parameters. When the simulated data contained no yearly differences, ML estimates of year differences were similar to sampling variation with no apparent consistent trend from the effects of selection. When yearly differences were added to the simulated records and estimation of yearly deviations by ML procedures was repeated, the differences between the new and the old estimate of year effects were identical to the yearly differences in the simulated records. Bias from selection was not apparent even though individuals were selected more intensely on their own records than usually occurs in dairy cattle (Henderson, Kempthorne, Searle and von Krosigk, 1959).

Practical application of the ML method involves classification of records and cows. Choice of the groups in the analysis of time trends seemed mainly a problem of forming large enough groups to make the sampling variance of the mean small and to make the groups correspond to the changing herd composition.

The second problem was classification of records in such a way as to measure differences in temporary environment from year to year. Another system would be to use only the amounts of milk produced by cows in a specified time period much in the manner in which DHIA herd averages are computed and converted to a discrete classification. However,

differences in the number of days in milk and in the stages of lactation from year to year complicated the interpretation (Henderson, Kempthorne, Searle and von Krosigk, 1959).

The best linear unbiased predictor (BLUP) (Henderson, 1973) is basically that of ML but has more utility because it allows analysis of records which are not random samples from a single population where sires are non-randomly distributed across the population (Henderson, 1973).

Two estimators of ΔG have been presented with the repeat-record technique. The first was used by Arave and Laben (1963), Arave, Laben and Mead (1964) and Bailey, Harvey, Hunter and Torell (1971) to estimate average annual ΔG by linear regression of performance on year of records and adjusting for yearly environmental effects by the ML method. Burnside, Rennie and Bowman (1968) suggested the second estimator as

$$\Delta\hat{G} = b_{P.T} - b_{YC.T},$$

where

$b_{P.T}$ represented the regression of the population performance on time $(t + g)$ and

$b_{YC.T}$ the regression of year constants obtained by the maximum likelihood procedure on time which represents the environmental change t.

Burnside, Rennie and Bowman (1968) stated that ΔE was obtained by

$$\Delta\hat{E} = b_{YC.T},$$

the regression of year constants obtained by the ML procedure on time.

Least squares or modified-least-squares methods for obtaining such measures give biased estimates when records of cows culled from the herd are either above or below the herd average (Henderson, 1949). This

bias results from erroneous estimates of repeatability of records (Bailey, Harvey, Hunter and Torell, 1971). Henderson (1949) showed that estimates of environmental changes can be biased by the use of age-correction factors and repeatability values that were not appropriate to the population under investigation.

Standard errors for the yearly environmental effects were obtained from the following relationship:

$$\sigma^2(d_K - d_K) = (A_{KK} + A_{ff} - 2A_{Kf})\sigma_e^2 ,$$

where

$\hat{d}_K$ = environmental effect of the K^{th} year,

d_f = environmental effects of the final year,

A = square symmetric matrix of inverse elements,

σ_e^2 = within cow and herd mean square for production.

To solve the normal equations for year effects, the restriction that the final year effect was equal to zero was imposed. Therefore, the last row and column of the A matrix corresponding to $\hat{d}_f$ were deleted and the $A_{ff} - 2A_{Kf}$ terms became zero (Arave, Laben and Mead, 1964). Arave, Laben and Mead (1964) calculated the standard error of an estimate of yearly environmental effect as

$$S_{J_K} = A_{KK}\sigma_e^2.$$

Walton and Lush (1962) and Burnside, Rennie and Bowman (1968) used the repeat-record technique and the direct-selection technique in studies of ΔG. Walton and Lush (1962) reported that the estimate obtained by the repeat-record technique agreed with $\Delta\hat{G}$ by the direct-selection technique. Burnside, Rennie and Bowman (1968) found that the

repeat-record technique gave a larger $\Delta\hat{G}$ than the direct-selection technique. Inability to estimate breeding value of many of the sires used in the direct-selection technique was given as a possible explanation for this difference. In a study where information was available on all parents, estimates of the two methods agreed closely (Burnside, Rennie and Bowman, 1968). Arave, Laben and Mead (1964) compared the repeat-record technique and the generation-number technique and found that the two techniques gave similar estimates of ΔG.

Generation-Number Technique

The fifth technique for estimating genetic change in a population (generation number) was presented by Brinks, Clark and Rice (1961) in a study of a beef cattle population and applied by Arave, Laben and Mead (1964) in a dairy cattle population.

Generation number was obtained for each individual using the formula

$$G_o = \frac{G_s + G_d + 2}{2},$$

where

G_o = generation of the offspring,

G_s = generation of the sire,

G_d = generation of the dam.

Generations were grouped by one-half generations from zero to six with foundation animals considered generation zero (Brinks, Clark and Rice, 1961; Arave, Laben and Mead, 1964). In the generation-number technique ΔG (g) was represented by the change in performance of successive generations. The total change (t + g) was represented by the change in performance from one year to the next (Brinks, Clark and Rice, 1961). Brinks,

Clark and Rice (1961) also used a least-squares procedure to obtain an estimate of generation effect. A second estimator based on the within sire regression of progeny performance on generation number was used by Arave, Laben and Mead (1964) as follows:

$$\Delta\hat{G} = 2(b_{P.GN/S}).$$

Estimates derived in this manner may be biased downward due to inaccuracies in classifying animals according to generation number (Arave, Laben and Mead, 1964). The validity of the generation-number technique in measuring ΔG depends on the degree of accuracy in adjusting for fixed environmental effects. Brinks, Clark and Rice (1961) used means conventionally adjusted for sex, age of calf, inbreeding of calf and age of dam and Arave, Laben and Mead (1964) expressed performance of a sire's progeny as her most probable producing ability.

II. ESTIMATES OF PHENOTYPIC, GENETIC AND ENVIRONMENTAL TRENDS IN ANIMAL POPULATIONS

Sires-Over-Time Technique

Smith (1962) calculated annual $\Delta\hat{G}$ in a swine herd using the sires-over-time technique to be: age at slaughter in days, -.11 ± .81; carcass weight (lb), -.74 ± .21; dressing percentage, -.25 ± .08; carcass length (mm), 5.26 ± .79; fat depth shoulder (mm), -.89 ± .18; and fat depth mid-back (mm), -.63 ± .14. Hillers and Freeman (1966) expressed the annual genetic improvement in a dairy population as a percent of the average production (.26 percent for milk and .24 percent for milk fat).

Harville and Henderson (1967) investigated DHIA records initiated between December 1956 and November 1962 to determine the magnitude of

intraherd environmental and genetic trend in milk and milk fat production of New York State sire evaluation procedures. Using the sires-over-time technique, $\Delta\hat{G}$ and $\Delta\hat{E}$, found by comparing the change within sire with the change in the entire population, were -12 ± 38 and 188 ± 39 kg for milk, and -0.1 ± 1.4 and 6.4 ± 1.4 kg for milk fat, respectively; while the within sire regression of the deviation of the records of the sire progeny on time provided estimates of genetic and environmental trends of 58 ± 23 and 118 ± 24 kg for milk, and 1.6 ± .8 and 4.8 ± .9 kg for milk fat, respectively.

Accurate estimates of actual genetic and environmental trends were obtained by Everett, Meadows and Gill (1967) in simulated data by pooling the regression of production on time within sires and adjusting by the inverse of the variance of each regression. When trends were estimated by pooling the regression within sires by the inverse of the variance of each regression, the estimated genetic and environmental trends were 67.7 and -8.4 kg of production per year, respectively.

Acharya and Lush (1968) analyzed data from a closed Hariana herd to assess the genetic gains in milk production through selection over twenty years and also to evaluate the ΔG made in age at first calving and in first calving interval, toward which no attention had been directed. Genetic progress in milk production, estimated as twice the pooled intra-sire regression of sire progeny on time, the records being deviated from contemporary average, was 10 kg, or 1.5 percent of the average first lactation yield per year. The annual ΔG in age at first calving and in first calving interval was estimated by the same procedure as -1.48 and -.29 months, respectively. The ΔG also was estimated for these three

traits by comparing the within sire change with the change in the entire population. The estimates obtained were -2.90 months in age at first calving, 30.7 kg for milk and -.66 months in age at first calving interval.

Genetic trends in milk production of dairy cattle populations were estimated to be 55 ± 26 kg milk and 0.016 ± 0.005 percent fat by Burnside and Legates (1967) and genetic trends were estimated as 53 and 25 kg for Holsteins and Jerseys, respectively, by Hargrove and Legates (1971). Verde, Wilcox, Martin and Reaves (1972) reported results of a study of first-lactation records of 4,779 Holstein, Jersey, and Guernsey paternal half-sisters, representing 155 sires and 181 herds for 1958 to 1967. They reported annual genetic trends of 33 kg milk in Holsteins, 22 kg in Jerseys and 92 kg in Guernseys.

Zabel (1973) attempted to measure phenotypic time trends with respect to 205-day weight and weaning grade in Virginia Angus herds and to separate them into genetic and environmental components. Two modifications of Smith's (1962) procedure, designated as Dickerson's Regression Method and General Means Method, were used. Pooled estimates of ΔP for 205-day weight show a significant positive trend (0.6 lb per year) by the regression method, but a negative trend (-1.2 lb per year) by the general means method. Pooled estimates of 205-day weight for ΔG were negative (-.34 and -.20 lb per year), but non-significant by both methods. Estimates of ΔE were 1.1 and -1.0 lb per year by the two methods, respectively. All pooled estimates of ΔP, ΔG and ΔE for weaning grades were positive for both methods (.07, .008, .06 and .07, .06 and .01 for ΔP, ΔG and ΔE by the two methods, respectively).

Powell and Freeman (1974) compared two regression estimators of intraherd genetic trend on 13,615 Holstein first lactations from 220

progeny test herds. Estimates of annual intra-herd ΔG from the comparison of the within sire change and the change in the entire population were 84.8 ± 29.9 kg of milk and 1.94 ± 1 kg of fat. While the within sire regression of the deviation of the records of the sire progeny on time provided estimates of genetic trends of 81.9 ± 28.5 kg of milk and 1.54 ± .97 kg of fat.

The performance records of 3,144 non-creep fed Angus calves born in the Ames Plantation herd over a 19 year period (1957-74) were divided into two groups (1957-66 and 1967-74) by Holbert (1975). Estimates of genetic progress were .0078 and .0343 lb increase in average daily gain per year for groups I and II, respectively. The estimation, in terms of progress per generation, was .036 and .172 lb increase in average daily gain. Anderson (1975) analyzed 10,501 weaning records collected from calves on the Tennessee Beef Cattle Improvement Program over the nine year period from 1964-73, and estimated annual ΔG in non-creep fed Hereford and Angus and creep-fed Hereford and Angus herds to be -.30, 3.49, 5.42 and 17.67 lb, respectively.

Direct-Selection Technique

Rendel and Robertson (1950) estimated ΔG of milk yield in an English dairy herd from records collected between 1903 and 1950. Most of the animals born from 1903 to 1933 were produced by home-bred bulls and it was possible to calculate a selection differential for females. The theoretical change was 1.0 percent per year and actual change was 0.7 percent. Stonaker (1953) found that the annual $\Delta\hat{G}$ in the closed Allahabad Agricultural Institute Red Sindhi herd, in which the inbreeding was 7 percent, was .5 lb of butterfat per year or about .3 percent of

the annual production. The expected genetic progress from the direct-selection technique was 16 kg, or 2.5 percent of the herd average per year in a closed Hariana herd (Acharya and Lush, 1968).

A steady increase in The University of Guelph Holstein and Ayrshire herds with respect to each breed for milk yield was observed by Burnside, Rennie and Bowman (1968). The improvement was expressed as breed-age-class average (BCA) points. The genetic gain in milk yield in the Holstein and Ayrshire breeds were .01 and .3 BCA points, respectively. The significant positive rate of genetic improvement for milk yield in the Ayrshire herd was attributed to more extensive use of AI sires with high breeding values for milk production.

Repeat-Mating Technique

Smith (1962) estimated ΔG in a purebred swine herd based on the difference in rate of change in performance of the population and full-sib progeny. Over a period from 1950 to 1958 he found the average annual genetic changes as follows: age at slaughter in days, 0.66 ± .16; carcass weight (lb), -1.36 ± 0.58; dressing percentage, -0.45 ± 0.17; carcass length (mm), 4.93 ± 1.40; fat depth mid-back (mm), -1.06 ± 0.31.

Harville and Henderson (1967) calculated estimates of the intra-herd environmental trends of 108 ± 32 kg of milk and 3.3 ± 1.5 kg of fat per year and a genetic trend of 68 ± 33 kg of milk and 3.0 ± 1.6 kg of milk fat per year. Of these, 2273 were first records of full-sisters. Burnside and Legates (1967) analyzed 34,380 full-sister Holstein records to obtain least-squares estimates of year constants. Regression of these constants on year estimated the environmental trend in the population. Comparison of the environmental trend with total change provided

an estimate of 45 ± 16 kg for milk and .018 ± .003 percent fat for the annual genetic trend.

Flower, Brinks, Urick and Wilson (1964) evaluated the selection intensity in three closed lines of Herefore cattle. Intensity of selection was defined as the annual selection differential or the average performance of the animal used as parents minus the average performance of the group of animals in which they were born. Selection differentials for pre-weaning traits were computed for sires and dams; the resulting selection intensity was greater in males. The ΔG estimated was positive and ranged from 2.16 lb to 6.51 lb for weaning weight and from -.04 to 1.71 for birth weight. Scarsi (1971) used repeat-mating data to determine environmental trends in the Fort Royal herd and reported positive genetic trends in weaning weight in the selection lines ranging from 2.9 to 4.9 lb per year.

Fahmy and Lalande (1973) used birth and weaning records of 892 Shorthorn calves (progeny of 249 cows and 19 sires) born 1951 to 1969 at the Lennoxville Research Station to study genetic and environmental trends. The sires used were introduced from other herds to avoid inbreeding. They were all selected for high rate of gain. At the time of the analysis, birth and weaning records of only six bulls were available, and they were all above Lennoxville herd average. Most bulls were used from 2 to 4 consecutive years; only one bull was used for 5 years and eight bulls were used for 1 year each. The $\Delta\hat{P}$ in birth weight observed (.14 kg/yr) was partitioned as .11 ± .06 of genetic origin and .053 ± .04 kg due to improved environment. For weaning weight, however, although there was an estimated genetic gain of .48 ± .27 kg per year, there was a negative environmental change of -.58 ± .28 per year.

Powell and Freeman (1974) used two estimators of intra-herd ΔG with the repeat-mating technique. The estimates of ΔG for milk and milk fat were 133.4 ± 54.7 and 5.07 ± 1.91 kg, respectively, when the ΔE was estimated within sire and dam. The estimates of ΔG for milk and milk fat were 142 ± 54.5 and 4.52 ± 1.85 kg, respectively, when the environmental trends were estimated within full-sister families of deviations from the adjusted population mate average on time.

Repeat-Record Technique

Selection pressures exerted on cows in the Iowa State University Holstein herd during a 29 year period (1930-58) theoretically resulted in an average annual increase in genetic merit of .6 percent of the herd average (Walton and Lush, 1962). Similar results were estimated by the ML technique.

Arave and Laben (1963) estimated yearly environmental effects in 12 dairy herds and annual genetic progress by ML method by the regression of yield on time after correcting for year effects. The estimates varied from 16.4 ± 54.8 to 186.2 ± 30.1 lb of milk. Yearly environmental effects were estimated by Arave, Laben and Mead (1964) in the same 12 herds using a ML method and annual ΔG was expressed as the linear regression of FCM yield on year. The average $\Delta\hat{G}$ for all herds was 74 lb FCM annually. The $\Delta\hat{G}$ within individual herds ranged from -51 ± 52 to 145 ± 21 lb FCM per year.

Bailey, Harvey, Hunter and Torell (1971) estimated ΔG and ΔE in five closed lines of Hereford cattle where single trait selection for post-weaning gain, feed efficiency, or yearling conformation score had been practiced. Responses in the lines under selection were 3.64 ± 2.09

and 4.77 ± 1.70 lb per year for gain, 0.09 ± 0.07 and 0.08 ± 0.08 lb gain per 100 lb TDN, while type score decreased at the rate of -.094 ± 0.110 lb per year.

Generation-Number Technique

Brinks, Clark and Rice (1961) reported that constants obtained for year effects in a study of line 1 Herefords showed a strong upward trend over years, but generation constants were relatively constant after generation two for birth weight, gain and weaning weight. When genetic gain was expressed in terms of the progeny's most probable producing ability (MPPA), Arave, Laben and Mead (1964) found genetic improvements per generation in Jersey cows to be 112 lb FCM or 28 lb RCM per year assuming a generation interval of four years.

CHAPTER III

PROCEDURE

I. SOURCE OF DATA

The records available for evaluating and comparing the techniques for estimating the genetic, environmental, and phenotypic trends considered in this study were collected from the purebred Angus herd of Ames Plantation, a field station of The University of Tennessee. They are the same records described by Holbert (1975) with the addition of those collected in 1975. Ames Plantation is located in West Tennessee approximately 60 miles east of the Mississippi River and 10 miles north of the Mississippi state line. The climate is humid and temperate. The mean seasonal temperature varies from approximately 42 degrees Farenheit in winter to 78 degrees in the summer. The normal growing season averages 209 days. The soils at Ames Plantation are fertile and excellent for forage production.

The herd was established in 1912 by Mr. Hobart Ames. From 1912 to 1955 the management of the herd was similar to that of most beef herds in Tennessee with little emphasis directed to improvement in growth and type at weaning. The University of Tennessee and the trustees of the Hobart Ames Foundation entered into an agreement in 1955, where the Animal Science Department staff (project leaders) would provide leadership for management of the herd. In 1955, the Angus breeding program was expanded and an intensive performance testing program was initiated. However, very little selection pressure, if any, was exerted

with respect to replacement females prior to 1965. In the fall of 1965, 123 cows were culled due to inadequate performance and/or poor reproduction. During the last 10 years, female numbers have been sufficient to allow annual selection among both replacement heifers and older breeding females. Preliminary selection of replacement heifers has been based primarily on adjusted 205-day weight with secondary emphasis placed on weaning type. Preliminary selection was conducted at weaning and final selection made the following spring. Approximately 80 percent of all heifers weaned in the herd were retained as replacements during the period in which the records were collected. Culling of dams was on the basis of both reproductive and progeny performance. Cows diagnosed open in the fall following failure to calve the previous spring were usually culled. Records of individual dams were the average performance of all their progeny.

Sire selection criteria were similar to those used for selection for replacement heifers. All prospective sires raised in the herd were evaluated with respect to adjusted 205-day weight and type at weaning, and at the end of a post-weaning performance test. Prospective sires from outside sources were selected at weaning on the basis of their weaning record and were usually evaluated in a post-weaning performance test at Ames Plantation.

From 1955 to the present time, the herd had access to orchardgrass and ladino clover pastures during the spring and early summer, and lespedeza pastures in the late summer and fall. During the winter months the herd received corn silage, grass legume hay and protein supplement as required.

For breeding purposes, the females of the herd were classified on the basis of age and past performance of their progenies' records, then randomly assigned to sire groups with a small amount of selective mating in the latter years. Females were bred in single sire groups and were reassembled into large groups following the breeding season. The females were so exposed to provide progeny born in both spring and fall.

Progeny were weaned between 120 and 300 days of age. Weaning information was normally recorded in September; however, it was usually October when the progeny were actually weaned. This allowed time for processing of the records so they could be used in selection at weaning.

Weaning records collected at Ames Plantation included identification of calf, dam and sire, birth dates of calf and dam, birth year of sire, birth weight, sex, weaning date, weight, type and condition scores, and management system used. From the records collected the Agricultural Experiment Station performed the following calculations: numerical date of weighing; numerical date of birth; weaning age; weight gain and average daily gain. The average daily gain for each calf was calculated by subtracting an actual birth weight from the recorded weaning weight and dividing this weight by age in days. Weaning weight was then expressed as adjusted 205-day weight by the procedure used in The Tennessee Beef Cattle Improvement Program (TBCIP) to remove the effects of sex of calf, age of calf and age of dam on performance. Available for this study were 3,218 205-day records collected over the 19 year period from 1957 to 1975.

II. PREPARATION OF DATA

Due to the unbalanced nature of field records, Smith (1962) presented several conditions that should be met before applying techniques that are dependent on replicated genotypes if the most accurate estimates of genetic and environmental trends are to be obtained. Therefore, the following restrictions were placed on the records used in this study:

1. All sires must have sired progeny in more than one year;
2. More than one sire must have been used each year;
3. There must have been an overlap in time of progeny by different sires;
4. There must have been a minimum of three offspring per sire;
5. There must have been both full- and half-sib offspring within each sire group.

Since the restrictions associated with the other techniques were not as demanding as those of replicated genotypes and since all restrictions appropriate for all other techniques are included in the restrictions listed above, this set of restrictions was used with all techniques studied.

In addition to the restrictions above four more were imposed in this study:

1. There must have been complete information on all records through weaning;
2. Only records of non-creep fed calves were considered;
3. Records were divided according to birth year of progeny;
4. Adjusted 205-day weight was the only trait studied.

After imposing the above restrictions, additional adjusted 205-day weights were calculated using Robertson's (1974) W7 method. In the W7 method adjustments were made for the effects of age of calf, age of dam and sex of calf with an additional adjustment made for the over-adjustment of younger and older calves. Then the adjusted 205-day weights calculated by the two methods (TBCIP, W7) were regressed on those sources of fixed environmental variation for which they were adjusted. The records finally used for evaluating the techniques considered in this study met all of the criteria above and were adjusted by the W7 method.

III. DESCRIPTION OF DATA

After all restrictions were imposed, records of 2606 progeny were available for the analysis. The mean, median and mode of the number of records per year (1957-1975) were 137, 137 and 128, respectively. The mean adjusted 205-day weight (205 Wt) of the 2606 progeny was 426 ± 47 lb. The mean adjusted 205-Wt was lowest (386 ± 43 lb) in 1959 and highest (460 ± 38 lb) in 1972. The distribution of progeny, mean and standard deviation of adjusted 205-day weights are presented in Table 1.

The 36 sires represented a total of 165 sire years with a mean of 4.58 years per sire. Service of individual sires ranged from 3 to 11 years. The distribution of progeny within sire and year are shown in Table 2. There was a mean of 72 progeny per sire, ranging from a low of 19 to a high of 228. The low mean adjusted 205-day weight for the progeny of an individual sire was 365 ± 33 lb, and the high was 458 ± 46 lb. The distribution of progeny, mean and standard deviation of adjusted 205-day weights by sire are presented in Table 3.

There were 526 full-sib progeny with a mean of 14.61 full-sib

TABLE 1

DISTRIBUTION OF PROGENY, MEAN AND STANDARD DEVIATION OF ADJUSTED 205-DAY WEIGHT WITHIN YEAR

Year	Number of Progeny	Adjusted 205-Day Weight[a]	
		Mean	Standard Deviation
1957	23	425.65	49.09
1958	73	413.54	63.35
1959	85	386.37	42.67
1960	129	391.76	44.47
1961	190	420.17	41.59
1962	128	422.86	41.69
1963	137	399.41	41.21
1964	128	396.51	33.99
1965	122	386.83	43.18
1966	113	428.39	43.52
1967	192	452.16	40.10
1968	164	433.59	33.51
1969	163	440.22	48.30
1970	160	434.80	37.65
1971	168	439.29	41.30
1972	197	459.78	37.65
1973	173	438.92	46.04
1974	159	441.10	38.29
1975	102	418.45	51.23
All	2606	426.23	47.35

[a]All weights are in lb.

TABLE 2

DISTRIBUTION OF PROGENY WITHIN SIRE AND YEAR

Sire	Year																		
	57	58	59	60	61	62	63	64	65	66	67	68	69	70	71	72	73	74	75
929554	9	28	22	23	14														
938055	6	24	19	6															
938554	8	16	19	27	18	20	8												
929155		2	16	20															
930555		3	9	7															
865757				5	19	20	8	5	9										
902558				11	33	2													
919357				9	29	11	8				2								
953757				5	24	8													
977757				16	26	40	30	12	12	2	14	26	15	7					
868858					27	15				16	14								
831060						4	12	34	9	12	9								
914858						8	15	31	11										
866060							14	17	15	11									
925760							14	19	15										
825161								6	11	2	29	24	16	6					
910262								4	20	17		18							
841262									15	14	20	19	17						
970959									9	16	5								
819262										14	18	15							
870363										1	7	1	27	26	17	6			
900962										8	34	20	15	13	12				
802363											9	23	10						
909258											32	13	29	3	2				
903166												5	10	5					
841666													14	19	9	17			
852767													10	31	27	24	22	8	
573666														14	29	14	7	5	
857767														13	23	30	25	18	12
864868														9	21	20	17		
886868														14	10	19	21	16	
900069															18	46	23	26	25
804969																20	24	12	
832070																1	7	21	20
100071																	14	26	26
871870																	13	27	19

TABLE 3

DISTRIBUTION OF PROGENY, MEAN AND STANDARD DEVIATION OF ADJUSTED 205-DAY WEIGHT WITHIN SIRE

Sire	Number of Progeny	Adjusted 205-Day Weight[a]	
		Mean	Standard Deviation
929554	96	389.19	48.07
938055	55	432.45	55.89
938554	116	402.78	44.38
929155	38	364.59	32.80
930555	19	402.09	49.21
865757	62	410.78	37.57
902558	46	415.70	41.01
919357	59	421.23	44.22
953757	37	415.71	45.94
977757	228	422.00	43.07
868858	72	426.97	40.36
831060	80	407.93	43.72
914858	65	386.44	42.50
866060	57	398.40	34.72
925760	48	388.22	34.93
825161	93	424.38	44.73
910262	59	412.74	44.19
841262	85	457.50	46.42
970959	30	426.29	44.98
819626	47	438.02	41.23
870363	85	449.20	36.93
900962	102	448.13	43.92
802363	42	438.85	32.16
909258	78	419.31	45.15
903166	20	412.84	49.10
841666	59	434.34	40.49
852767	122	444.67	34.62
573666	69	433.10	40.36
857767	121	436.74	45.16
864868	67	445.67	45.13
886868	80	436.07	41.73
900069	138	457.01	42.41
804969	56	434.64	40.13
832070	49	440.03	46.76
100071	66	435.23	51.08
871070	59	435.46	47.31

[a]All weights are in lb.

progeny per sire. The number of full-sib progeny ranged from 4 to 64 per sire. The mean adjusted 205-day weight of all full-sib progeny was 425 ± 44 lb, delineated by a low of 364 ± 26 and a high of 475 ± 34 lb. The distribution of full-sib progeny, mean and standard deviation of adjusted 205-day weight within sire are shown in Table 4.

Two hundred eighty of the 526 full-sib progeny were born in consecutive years, with a mean of 15.56 pairs between years. The lowest number of full-sib pairs born in consecutive years (4) occurred in 1957 and 1958, and the highest number (29) occurred in 1960 and 1961. The distribution of full-sib pairs, means and standard deviations of adjusted 205-day weights between consecutive years are presented in Table 5.

The records represented 704 dams with a mean of 3.70 progeny per dam and ranged from 1 to 15 progeny per individual dam.

IV. SEPARATION OF TRENDS

Four techniques and their applicable estimators for measuring phenotypic, genetic and environmental trends were either directly or indirectly applied to the restricted, adjusted records as described below.

Sires-Over-Time Technique

Two estimators of ΔP were applied. Phenotypic change (ΔP) was estimated by the regression of performance on time,

$$\Delta\hat{P} = b_{P.T}, \qquad (1)$$

which represented the total change (t + g). This regression estimator of ΔP was used in conjunction with two regression estimators of ΔG described by Smith (1962) with the sires-over-time technique. The second estimator of ΔP was

TABLE 4

DISTRIBUTION OF FULL-SIB PROGENY, MEAN AND STANDARD DEVIATION OF ADJUSTED 205-DAY WEIGHT WITHIN SIRE

Sire	Number of Full-Sibs	Adjusted 205-Day Weight[a]	
		Mean	Standard Deviation
929554	38	398.01	50.04
938055	8	456.64	40.73
938554	23	413.58	34.18
929155	12	364.01	26.45
930555	6	437.62	26.90
865757	6	430.35	29.47
902558	14	424.84	36.48
919357	8	429.91	64.53
953757	8	385.06	30.60
977757	64	431.75	39.27
868858	12	430.72	37.67
831060	17	418.10	29.48
914858	6	369.45	28.87
866060	46	401.66	33.98
925760	17	398.38	33.59
825161	20	437.12	41.87
910262	8	372.75	50.13
841262	16	475.04	33.81
970959	6	401.75	28.95
819262	22	451.18	46.12
870363	20	448.39	38.91
900962	12	460.64	33.39
802363	8	420.43	15.78
900258	10	423.88	24.58
903166	4	393.77	74.10
841666	5	443.28	49.12
852767	23	445.71	32.59
573666	6	433.25	27.70
857767	22	432.06	43.16
864868	10	444.84	31.98
886868	9	432.39	38.88
900069	10	465.80	20.75
804969	10	426.34	25.14
832070	6	426.14	50.59
100071	8	435.58	48.85
871070	6	442.48	52.42

[a]All weights are in lb.

TABLE 5

DISTRIBUTION OF FULL-SIB PROGENY, MEAN AND STANDARD DEVIATION OF ADJUSTED 205-DAY WEIGHT BETWEEN CONSECUTIVE YEARS

Years	Number of Pairs	Adjusted 205-Day Weight[a]			
		Year 1		Year 2	
		Mean	Standard Deviation	Mean	Standard Deviation
1957-1958	4	438.78	41.62	428.30	59.09
1958-1959	18	425.41	46.42	400.14	58.10
1959-1960	18	393.09	36.38	378.86	39.28
1960-1961	29	412.78	53.43	428.01	36.25
1961-1962	12	435.79	45.76	428.12	35.96
1962-1963	7	435.74	38.82	421.27	37.37
1963-1964	26	401.91	44.19	400.80	34.06
1964-1965	22	394.74	24.14	394.17	31.05
1965-1966	13	401.44	39.42	431.46	39.09
1966-1967	18	434.23	36.16	466.47	47.10
1967-1968	19	462.56	52.12	439.83	35.51
1968-1969	17	440.24	29.55	431.62	35.50
1969-1970	16	444.06	28.93	425.35	48.12
1970-1971	14	447.92	24.73	450.18	47.34
1971-1972	9	448.50	31.06	458.50	17.66
1972-1973	15	447.67	42.66	426.19	27.60
1973-1974	18	424.40	42.58	440.76	37.97
1974-1975	5	453.94	42.02	415.04	56.96

[a]All weights are in lb.

$$\Delta\hat{P} = \Sigma(\overline{X}_{Ty} \overline{X}_{To})/Y, \quad (2)$$

and was used with the difference between means-over-time estimator.

Reliability of $\Delta\hat{P}$'s derived by the regression estimator was calculated by the expression

$$S_{\Delta\overline{P}} = \sqrt{[1/(N-2)][(\sigma^2_P/\sigma^2_T) - b^2_{P.T}]}, \quad (3)$$

where

N = number of progeny in the regression,

σ^2_P = variance of performance,

σ^2_T = variance of time,

$b_{P.T}$ = the regression of performance on time (Everett, Meadows and Gill, 1967).

No unbiased estimator of the variance component of the estimate of ΔP derived by the means estimator was available; therefore a standard error was not calculated.

Genetic change was estimated by the sires-over-time technique as a comparison of the performance of successive progeny groups on a within sire basis with change in the entire population (Smith, 1962). Application of the sires-over-time technique involved the assessment of one-half ΔG in a sire's progeny in one year by the expression

$$.5g = (t + g) - (t - .5g), \quad (4)$$

where

t + g = phenotypic change: environmental (t) plus genetic (g);

t + .5g = change in performance of successive groups of progenies of individual sires.

Genetic change in any sire was considered to be zero; thus genetic change in the female population was actually estimated.

Three estimators of genetic change were used with the sires-over-time technique: two were associated with regression of performance on time, and the other was calculated as the difference in means-over-time. The regression of performance on time ($b_{P.T}$) estimated the phenotypic change (t + g), while the regression within sire ($b_{P.T/S}$) included t plus one-half g, the dam's contribution to the genetic change. The first estimator of ΔG was

$$\Delta\hat{G} = 2(b_{P.T} - b_{P.T/S}). \qquad (5)$$

Application of this estimator involved two regression analyses to determine (1) the coefficients of regression of adjusted 205-day weight (205 Wt) on time, and (2) regression of 205-day weight on time within sire. The following models were fitted to obtain estimates of these effects:

$$Y_{ij} = a + bT_i + e_{ij},$$

where

Y_{ij} = observed 205 Wt of the ij progeny,

a = intercept,

bT_j = effect of the i^{th} year, i = 1, 2, . . . 19,

e_{ij} = random error, and

$$Y_{ijk} = a + bTS_{ij} + e_{ijk},$$

where

Y_{ijk} = observed 205 Wt of the ijk^{th} progeny,

a = intercept,

bTS_{ij} = effect of the i^{th} sire, i = 1, 2, . . . 36, within the j^{th} year, j = 1, 2, . . . 19,

e_{ijk} = random error.

In these models and all subsequent models involving the regression of performance on time, year was used as a continuous variable.

Following the procedure outlined by Smith (1962), an attempt was made to avoid year-to-year changes in the environment by applying a second estimator,

$$\Delta\hat{G} = -2b_{(P-\bar{P}).T/S}, \qquad (6)$$

which was twice the pooled within sire regression of the deviation of the records of the sire's progeny on time: $b_{(P-\bar{P}).T/S} = (t + .5g) - (t + g)$. Each record was expressed as a deviation from the population mean (mean of all progeny performing in the same birth year). The deviated records were subjected to a regression analysis to determine the coefficient of regression of 205 Wt for sire within year effects. The following model was fitted to obtain the coefficient of regression of $\Delta\hat{G}$ performance deviation on time needed for calculation by this estimator,

$$Y_{ijk} = a + bTS_{ij} + e_{ijk},$$

where

Y_{ijk} = deviation of 205 Wt of the ijk^{th} progeny from the population mean,

a = intercept,

bTS_{ij} = effect of the i^{th} sire, $i = 1, 2, \ldots 36$, within the j^{th} year, $j = 1, 2, \ldots 19$,

e_{ijk} = random error.

A modification of Smith's (1962) mean-difference estimator was used as the third estimator. Genetic change was determined by the expression,

$$\Delta\hat{G} = \frac{\Sigma\left[\frac{\Sigma 2[(\bar{X}_{Ty} - \bar{X}_{To}) - (\bar{X}_{Sy} - \bar{X}_{So})]}{y-1}\right]}{Y}, \qquad (7)$$

where

$\bar{X}_{Ty}$ = population mean for the y^{th} year,

$\bar{X}_{To}$ = population mean for the o^{th} year,

$\bar{X}_{Sy}$ = continued sire mean for the y^{th} year,

$\bar{X}_{So}$ = continued sire mean for the o^{th} year,

y = number of years service for each sire,

Y = number total years.

The initial difference between the $(\bar{X}_{Ty} - \bar{X}_{To})$ and $(\bar{X}_{Sy} - \bar{X}_{So})$ was assumed to be zero. The expressions $(\bar{X}_{Ty} - \bar{X}_{To})$ and $(\bar{X}_{Sy} - \bar{X}_{So})$ represented t + g and t + .5g, respectively.

Standard error of the estimate of ΔG obtained by regression of actual performance on time (equation 5) was calculated as described by Everett, Meadows and Gill (1967):

$$s_{\Delta\bar{G}} = 2\sqrt{[1/(N-2)][(\sigma^2_P/\sigma^2_T) - b^2_{P.T}] + 1/\Sigma_i[N-2]/[(\sigma^2_P/\sigma^2_T) - b^2_{P.T/S_i}]} \quad , (8)$$

and standard error of the estimate of ΔG obtained by regression using deviation of individual progeny performance from the population mean on time (equation 6) was calculated as

$$s_{\Delta\bar{G}} = 2\sqrt{[1/(N-2)][(\sigma^2_P/\sigma^2_T) - b^2_{P.T}] + 1/\Sigma_i[N-2]/[(\sigma^2_P/\sigma^2_T) - b^2_{(P-\bar{P}).T/S_i}]} \quad , (9)$$

where

N = number of progeny in the regression,

σ^2_P = variance of performance,

σ^2_T = variance of time,

$b_{P.T}$ = regression of performance on time,

$b_{P.T/S_i}$ = regression of performance of progeny of sire i on time,

$b_{(P-\bar{P}).T/S_i}$ = regression of the deviation of the records of progeny of sire i on time (Everett, Meadows and Gill, 1967).

No unbiased estimator of the variance component of the estimate of ΔG derived by the means estimator was available; therefore, no standard error of the estimate was calculated.

Two estimators of environmental trend were used with the sires-over-time technique. An unbiased regression estimator presented by Harville and Henderson (1967) was used with the regression of the performance on time estimate where the environmental change t was estimated as

$$\Delta\hat{E} = b_{P.T} - \Delta\hat{G}. \tag{10}$$

The environmental change (ΔE) was estimated as the difference in the estimates of ΔP and ΔG for their respective means estimator. The standard errors for the estimates of ΔE obtained by the regression estimator (equation 11) was calculated by the following expressions derived from equalities presented by Everett, Meadows and Gill (1967):

$$s_{\Delta\bar{E}} = \sqrt{[1/(N-2)][(\sigma^2_P/\sigma^2_T) - b^2_{P.T}] + 4\left[[(\sigma^2_P/\sigma^2_T) - b_{P.T}/(N-2)] + 1/\Sigma_i[(N-2)/(\sigma^2_P/\sigma^2_T) - b^2_{P.T/S_i}]\right]}, \tag{11}$$

and

$$s_{\Delta\bar{E}} = \sqrt{[1/(N-2)][(\sigma^2_P/\sigma^2_T) - b^2_{P.T}] + 4\left[[(\sigma^2_P/\sigma^2_T) - b^2_{P.T}/(N-2)] + 1/\Sigma_i[(N-2)/(\sigma^2_P/\sigma^2_T) - b^2_{(P-\bar{P}).T/S_i}]\right]}, \tag{12}$$

where

N = number of progeny in the regression,

σ^2_P = variance of performance,

σ^2_T = variance of time,

$b_{P.T}$ = regression of performance on time,

$b_{P.T/S_i}$ = regression of performance of progeny of sire i on time,

$b_{(P-\bar{P}).T/S_i}$ = regression of the deviation of the records of progeny of sire i on time (Everett, Meadows and Bill, 1967).

Repeat-Mating Technique

Repeated matings of sires and dams was the second technique used in estimating phenotypic, genetic and environmental changes. Phenotypic change (ΔP) was estimated as the linear regression of performance on time ($b_{P.T}$) and represented the total change t + g in the population (equation 1).

The reliability of the estimate of ΔP was established by calculating an appropriate standard error by equation 3.

Genetic change was estimated by comparing $\Delta\hat{E}$ and $\Delta\hat{P}$. Smith (1962) stated that the genic material of full-sibs was alike and any difference in their performance between years reflected $\Delta\hat{E}$. ΔE was estimated by the comparison of the performance of full-sibs born in different years. The genetic change g in the population in one year was estimated as the difference in the change in the performance of the population (t + g) and t; thus

$$\Delta\hat{G} = g = \Delta\hat{P} = \Delta\hat{E} = (t + g) - t. \qquad (13)$$

Flower, Brinks, Urick and Wilson (1964) suggested the following regression estimator of ΔG:

$$\Delta\hat{G} = b_{P.T} - b_{(PF_2 - PF_1).T}. \qquad (14)$$

The regression of the differences in the performance of full-sibs born in consecutive years on time,

$$\Delta\hat{E} = b_{PF_2 - PF_1).T}, \qquad (15)$$

estimated the environmental change t. The following models were fitted in the analysis to obtain coefficients of regression of adjusted 205-day weight and deviated performance of full-sib pairs for year effects in the total and full-sib populations:

$$Y_{ij} = a + bT_i + e_{ij},$$

where

Y_{ij} = observed adjusted 205-day weight of the ij^{th} progeny,

a = intercept,

bT_i = effect of the i^{th} year, $i = 1, 2, \ldots 19$,

e_{ij} = random error

and

$$Y_{ij} = a + bT_i + e_{ij},$$

where

Y_{ij} = observed difference in the performance of the ij^{th} full-sib pair,

a = intercept,

bT_i = effect of the i^{th} year, $i = 2, 3, \ldots 19$,

e_{ij} = random error.

Standard error of $\Delta\hat{G}$ was calculated by the following equation derived from estimates of variance components suggested by Everett, Meadows and Gill (1967):

$$S_{\Delta\bar{G}} = \sqrt{[1/(N-2)][(\sigma^2_P/\sigma^2_T) - b^2_{P.T}] + [1/(N-2)][(\sigma^2_P/\sigma^2_T) - b^2_{(PF_2-PF_1).T}]} \quad , (16)$$

where

N = number of progeny in the regression,

σ^2_P = variance of performance,

σ^2_T = variance of time,

$b_{P.T}$ = regression of performance on time,

$b_{(PF_2-PF_1).T}$ = regression of the difference in performance of full-sibs in consecutive years on time.

Standard error of the estimate of ΔE was calculated by the expression

$$S_{\Delta\bar{E}} = \sqrt{[1/(N-2)][(\sigma^2_P/\sigma^2_T) - b^2_{(PF_2-PF_1).T}]}\ , \qquad (17)$$

where

N = number of progeny in the regression,

σ^2_P = variance of performance,

σ^2_T = variance of time,

$b_{(PF_2-PF_1).T}$ = regression of the differences in performance of full-sibs in consecutive years on time.

Dams-Over-Time Technique

Smith (1962) pointed out that the within dam change could be estimated by the procedure as the within sire change outlined in the sires-over-time technique. However, a review of the literature revealed that no attempt had been made to estimate the within dam change. The within dam change was estimated in this study using a modification of one of Smith's (1962) estimators.

The phenotypic change (ΔP) was estimated by the regression of performance on time (equation 1) and represented the total change in the population (t + g).

The genetic change was obtained by the estimator

$$\Delta\hat{G} = 2(b_{P.T} - b_{P.T/D}). \qquad (18)$$

The regression of performance on time within dam estimated only t + .5g, where .5g was the sire's contribution to genetic change.

In applying this estimator, the records were subjected to regression analyses to determine the coefficient of regression of 205 Wt on year and the coefficient of regression of 205 Wt on year within dam. The following models were fitted to obtain estimates of these coefficients:

$$Y_{ij} = a + bT_i + e_{ij},$$

where

Y_{ij} = observed adjusted 205-day weight of the ij^{th} progeny,

a = intercept,

bT_i = effect of the i^{th} year, $i = 1, 2, \ldots 19$,

e_{ij} = random error

and

$$Y_{ijk} = a + bTD_{ij} + e_{ijk},$$

where

Y_{ijk} = observed adjusted 205-day weight of the ijk^{th} progeny,

a = intercept,

bTD_{ij} = effect of the i^{th} dam, $i = 1, 2, \ldots 704$, within the jth year, $j = 1, 2, \ldots 19$,

e_{ijk} = random error.

Due to the large number of dams, bTD_{ij} could not be calculated directly as were the other coefficients of regression. The records were divided into six equal groups according to the number of progeny, the number of progeny for each dam and the number of dams. All progeny of each dam was included in the same sub-group to prevent inflation of the among dam variance. A new variable performance plus time (P + T) for each progeny was calculated and consisted of the adjusted 205-day weight (P) plus year (T). The six groups of records were then subjected to the following analysis:

(1) adjusted 205-day weight (P) was regressed on dam, with dam held constant, to obtain the residual sum of squares for adjusted 205-day weight;

(2) year (T) was regressed on dam, with dam held constant, to obtain the residual sum of squares for year; and

(3) adjusted 205-day weight plus year (P+T) was regressed on dam, with dam held constant, to obtain the residual sum of squares of (P+T).

Bartlett's Test for homogeneity of variances was imposed on the variances of the above regressions to determine whether the sum of squares could be pooled. The coefficient of regression ($b_{P.T/D}$) was calculated as

$$\frac{\text{overall residual cov PT.}}{\text{overall residual SS T}}$$

The overall residual cov (PT) was calculated as the sum of the residual cov (PT) for each group. The cov (PT) for each group was calculated as

$$\frac{\text{residual SS (P + T) - residual SS (P) - residual SS (T)}}{2}$$

because of the relationship

$$\sigma^2_{(P+T)} = \sigma^2_P + \sigma^2_T + 2 \text{ cov PT}$$

$$2 \text{ cov PT} = \sigma^2_{(P+T)} - \sigma^2_P - \sigma^2_T$$

$$\text{cov PT} = \frac{\sigma^2_{(P+T)} - \sigma^2_P - \sigma^2_T}{2}.$$

The overall residual SS(T) was calculated as the sum of the residual sum of squares for each group because of the following relationship

$$\sigma^2_T = \sigma^2_{T_1} + \sigma^2_{T_2} + \sigma^2_{T_3} + \sigma^2_{T_4} + \sigma^2_{T_5} + \sigma^2_{T_6}.$$

The standard error for $\Delta\hat{G}$ was calculated by the expression

$$S_{\Delta\bar{G}} = 2\sqrt{[1/(N-2)][(\sigma^2_P/\sigma^2_T) - b^2_{P.T}] + 1/\Sigma_i[N-2]/[(\sigma^2_P/\sigma^2_T) - b_{P.T/D_i}]} \quad , \qquad (19)$$

where

N = number of progeny in the regression,

σ^2_P = variance of performance,

σ^2_T = variance of time,

$b_{P.T}$ = regression of performance on time,

$b_{P.T/D_i}$ = regression of performance or progeny of dam i on time (Everett, Meadows and Gill, 1967).

The environmental change was estimated as

$$\Delta\hat{E} = b_{P.T} - \Delta\hat{G} \quad , \qquad (20)$$

the difference in the phenotypic change, estimated as $b_{P.T}$, and the genetic change (ΔG) (Harville and Henderson, 1967). The standard error for $\Delta\hat{E}$ was calculated by the expression

$$S_{\Delta\bar{E}} = \sqrt{[1/(N-2)][(\sigma^2_P/\sigma^2_T) - b^2_{P.T}] + 4\left[[(\sigma^2_P/\sigma^2_T) - b^2_{P.T}/(N-2)] + 1/\Sigma_i[(N-2)/(\sigma^2_P/\sigma^2_T) - b_{P.T/D_i}]\right]} \quad , \qquad (21)$$

where

N = number of progeny in the regression,

σ^2_P = variance of performance,

σ^2_T = variance of time,

$b_{P.T}$ = regression of performance on time,

$b_{P.T/D_i}$ = regression of performance of progeny of dam i on time (Everett, Meadows and Gill, 1967).

Sires-and-Dams-Over-Time Technique

The final technique for estimating the phenotypic, genetic and environmental change in the population under study is the continued use

of sires plus continued use of dams. The phenotypic change ΔP was estimated as the linear regression of the population performance on time (equation 1).

The genetic change in the population was estimated by comparing the change in performance of successive progeny groups, within sire and within dam, with change in the entire population. The technique involved the assessment of one-half the genetic change in a sire's progeny and one-half the genetic change in a dam's progeny in one year by the expression

$$g = [(t + g) - (t + .5gs)] + [(t + g) - (t + .5gd)]. \quad (22)$$

where

$t + g$ = phenotypic change (P): environmental (t) plus genetic (g),

$t + .5gs$ = change in performance of successive groups of progenies of individual sires,

$t + .5gd$ = change in performance of successive groups of progenies of individual dams.

Genetic change in the population was estimated as $\Delta\hat{G}$ due to selection of dams (equation 5) plus $\Delta\hat{G}$ due to selection of sires (equation 18). All assumptions associated with these individual estimates applied also to the estimates by sires-and-dams-over-time technique. This estimator was symbolized by

$$\Delta\hat{G} = [(b_{P.T} - b_{P.T/S}) + (b_{P.T} - b_{P.T/D})] \quad (23)$$

and the components were calculated by regression equations discussed earlier.

The standard error for ΔG estimated by the sires-and-dams-over-time technique was calculated by the following expression which was a

combination of procedures used to calculate SE of ΔG estimated by the sires-over-time technique (equation 8) and the dams-over-time technique (equation 19),

$$s_{\Delta\bar{G}} = \sqrt{\left[2[1/(N-2)][(\sigma^2_P/\sigma^2_T) - b^2_{P.T}] + 1/\Sigma_i[N-2]/[(\sigma^2_P/\sigma^2_T) - b^2_{P.T/S_i}] + 2[1/(N-2)][(\sigma^2_P/\sigma^2_T) - b^2_{P.T}] + 1\Sigma_i[N-2]/[(\sigma^2_P/\sigma^2_T) - b^2_{P.T/D_i}]\right]} , \quad (25)$$

where

N = the number of progeny in the regression,

σ^2_P = variance of performance,

σ^2_T = variance of time,

$b_{P.T}$ = regression of performance on time,

$b_{P.T/S_i}$ = regression of performance of progeny of sire i on time,

$b_{P.T/D_i}$ = regression of performance of progeny of dam i on time (Everett, Meadows and Gill, 1967).

The environmental change (t) was estimated as

$$\Delta\hat{E} = b_{P.T} - \Delta\hat{G},$$

the difference in phenotypic change, estimated as $b_{P.T}$, and genetic change (ΔG) (Harville and Henderson, 1967). The standard error associated with this estimate of ΔE was calculated by the following expression which was derived from equations 11 and 21:

$$s_{\Delta\bar{E}} = \sqrt{[1/(N-2)][(\sigma^2_P/\sigma^2_T) - b^2_{P.T}] + 2\left[[1/(N-2)][(\sigma^2_P/\sigma^2_T) - b^2_{P.T}] + 1/\Sigma_i[N-2]/[(\sigma^2_P/\sigma^2_T) - b^2_{P.T/S_i}] + [1/(N-2)][(\sigma^2_P/\sigma^2_T) - b^2_{P.T}] + 1/\Sigma_i[N-2]/[(\sigma^2_P/\sigma^2_T) - b^2_{P.T/D_i}]\right]} , \quad (26)$$

where

N = number of progeny in the regression,

σ^2_P = variance of performance,

σ^2_T = variance of time,

$b_{P.T}$ = regression of performance on time,

$b_{P.T/S_i}$ = regression of performance of progeny of sire i on time,

$b_{P.T/D_i}$ = regression of performance of progeny of dam i on time

(Everett, Meadows and Gill, 1967).

CHAPTER IV

RESULTS AND DISCUSSION

I. METHODS OF ADJUSTMENT

The records used in this study were adjusted for the effects of age at weaning, age of dam and sex on progeny performance by two methods. These three sources of fixed environmental variation, with the addition of season of birth, were regressed on adjusted 205-day weight to provide some reliability of the accuracy of the two methods of adjustment. The analysis of variance of the effects of age at weaning, age of dam, sex and season of birth on adjusted 205-day weight for both methods of adjustment are presented in Table 6. The regressions indicated that the method described by Robertson (1974) as the regression of calculated 205-day weight on weaning age (W7) was more efficient in removing differences due to these fixed effects. The W7 method and the TBCIP method (procedures used in the Tennessee Beef Cattle Improvement Program) removed 97 and 89 percent of the variation, respectively. Changes in R^2 (ΔR^2) for the aforementioned sources of variation in adjusted 205-day weight, resulting from sequentially adding elements to the model, are shown in Table 7. The changes in R^2 indicated that the W7 method removed more of the variation due to difference in sex, and weaning age on adjusted 205-day weight. Differences in R^2 for weaning age by the two methods would be more pronounced as the range in weaning age increased. Thus, the differences in the two methods would become more apparent in populations under less rigid management, especially in herds with prolonged breeding season. These findings were in agreement with those of Robertson (1974).

TABLE 6

ANALYSIS OF VARIANCE OF THE EFFECTS OF SEX, AGE OF DAM, AGE AT WEANING AND SEASON OF BIRTH ON ADJUSTED 205-DAY WEIGHT BY METHOD OF ADJUSTMENT

Source	Degrees of Freedom	Mean Square	
		TBCIP Method	W7 Method
Sex	2	130435.88***	20863.60***
Age of Dam	13	9298.48***	8507.78***
Age at Weaning	1	341041.12***	31436.07***
Season of Birth	3	21382.78***	18246.35***
Residual	2586	2442.08	2173.71

***P < .001.

TABLE 7

VARIATION IN ADJUSTED 205-DAY WEIGHT EXPLAINED BY SEQUENTIALLY ADDING ELEMENTS TO THE MODEL

Elements				ΔR^2	
				205-Day Weight Adjusted by	
Sex	Age of Dam	Age at Weaning	Season of Birth	TBCIP	W7
x				.04	.00
x	x			.01	.03
x	x	x		.05	.00
x	x	x	x	.01	.00
Total R^2				.11	.03

II. ESTIMATES OF TRENDS

Sires-Over-Time Technique

Three estimators of phenotypic, genetic and environmental trends were compared using the sires-over-time technique. Two of these estimators were associated with regression procedures and one with comparison of means over time. Phenotypic change estimated by the regression estimator ($b_{P.T}$) was 2.89 ± .18 lb per year, while the phenotypic change obtained with the difference in means-over-time estimator was -.38 lb per year. The differences in the estimates of phenotypic change by the regression estimator and the means estimator are in agreement with the findings of Zabel (1973). In his study, estimates of phenotypic change in adjusted 205-day weight showed a positive trend (.6 lb per year) when calculated by the regression estimator, but a negative trend (-1.2 lb per year) resulted from the means estimator.

Differences were also observed in the estimates of genetic trend by these estimators. Estimates of ΔG obtained by the regression estimators $2(b_{P.T} - b_{P.T/S})$ and $-2b_{(P-\bar{P}).T/S}$ were 4.14 ± .37 and 2.58 ± .36 lb per year, respectively. The means estimator provided an estimate of 2.67 lb per year. Other authors have reported differences in estimates of genetic trend by these estimators. Harville and Henderson (1967) reported estimates of ΔG by the two regression estimators to be -12 ± 38 and 58 ± 23 kg per year for milk and -.1 ± 1.4 and 1.6 ± 8 kg per year for milk fat, respectively. Acharya and Lush (1968) found estimates of annual ΔG of -2.90 and -1.48 months in age at first calving, 30.7 and 10.3 kg for milk and -.66 and -.29 months in age at first calving interval, by the two regression estimators, respectively. Powell and Freeman (1974) reported

that estimates of ΔG by these estimators were 84.8 ± 29.9 and 81.9 ± 28.5 kg per year for milk and 1.94 ± 1 and 1.54 ± .97 kg per year for milk fat, respectively. Zabel (1973) reported estimates from the regression of performance deviation-on-time estimator and the means estimator of -.34 and -.20 lb per year, respectively, for adjusted 205-day weight.

Estimates of ΔE calculated as the differences between ΔP and ΔG estimated by the regression of individual performance on time within sire, by the regression of deviated performance from the population mean and as the difference in means-over-time procedure were -1.25 ± .41, .31 ± .40 and -3.05 lb per year, respectively. Considerable differences existed in the estimates obtained by the three estimators. Harville and Henderson (1967) also reported differences in the estimates of environmental trend using these estimators. They reported estimates of environmental trend by the two regression estimators of 188 ± 39 and 118 ± 24 kg per year for milk and 6.4 ± 1.4 and 4.8 ± .9 kg per year for milk fat, respectively. Zabel (1973) reported estimates of ΔE in adjusted 205-day weight from the latter regression estimator and from the means estimator of 1.1 and -1.0 lb per year, respectively. The various estimates of ΔP, ΔG and ΔE obtained in this study by the various sires-over-time estimators, along with their standard errors, are presented by each estimator in Table 8.

Phenotypic trend associated with both regression estimators was estimated as the regression of performance over time. However, the estimate of phenotypic trend was extremely underestimated by the means estimator. This difference was due to the greater accuracy of the regression procedure.

The estimate of genetic trend calculated as the regression of performance on time within sire was larger than those obtained by the

TABLE 8

ESTIMATES OF PHENOTYPIC, GENETIC AND ENVIRONMENTAL TRENDS IN ADJUSTED 205-DAY WEIGHT BY TECHNIQUE AND ESTIMATOR

Technique	ΔP		ΔG		ΔE	
	Estimator	Estimate	Estimator	Estimate	Estimator	Estimate
Sires-Over-Time	$b_{P.T}$	2.89±.18	$2(b_{P.T}-b_{P.T/S})$	4.14±.37	$b_{P.T}-\Delta\hat{G}$	-1.25±.41
	$b_{P.T}$	2.89±.18	$-2b_{(P-\bar{P}).T/S}$	2.58±.36	$b_{P.T}-\Delta\hat{G}$	.31±.40
	$(\bar{X}_{Ty}-\bar{X}_{To})/Y$	-.38	$\Sigma\left[\frac{\Sigma 2[(\bar{X}_{Ty}-\bar{X}_{To})-(\bar{X}_{Sy}-\bar{X}_{So})]}{y-1}\right]$ / Y	2.67	$(\bar{X}_{Ty}-\bar{X}_{To})/Y-\Delta\hat{G}$	-3.05
Repeat-Mating	$b_{P.T}$	2.89±.18	$b_{P.T}-b_{(PF_2-PF_1).T}$	2.83±.61	$b_{P.T}-\Delta\hat{G}$	.06±.59
Dams-Over-Time	$b_{P.T}$	2.89±.18	$2(b_{P.T}-b_{P.T/D})$	1.40±.36	$b_{P.T}-\Delta\hat{G}$	1.49±.40
Sires-And-Dams-Over-Time	$b_{P.T}$	2.89±.18	$(b_{P.T}-b_{P.T/S})+(b_{P.T}-b_{P.T/D})$	2.77±.36	$b_{P.T}-\Delta\hat{G}$	.12±.40

other two estimators. The analysis of variance of the effect of year on adjusted 205-day weight and the analysis of variance of the effect of year, with sire held constant, on adjusted 205-day weight indicated that both regressions were significant ($P < .001$). The analysis of variances of both regressions are presented in Appendix Tables 9 and 10. The use of the deviation of individual performance from the population mean instead of individual performance per se resulted in a more reliable estimate of ΔG because this procedure tended to eliminate year-to-year fluctuation in environment. The analysis of variance of the effect of year within sire on deviated adjusted 205-day weight is shown in Appendix Table 11. This regression was significant ($P < .001$). These results were in agreement with those of Acharya and Lush (1968) and Powell and Freeman (1974). The estimator $-2b_{(P-\overline{P}).T/S}$ was more reliable in the estimation of genetic trend than the means estimator. This was due to the increased accuracy of the regression procedure and the initial difference between $\overline{X}_{To}$ and $\overline{X}_{So}$ was not zero as was assumed for the means estimator. The results of the comparison of these estimators were in agreement with those of Zabel (1973).

Estimates of environmental trend from the estimators above were dependent on the estimates of phenotypic and genetic trends. Therefore, when the estimate of genetic trend was obtained by $2(b_{P.T} - b_{P.T/S})$, which overestimated ΔG, the estimate of environmental trend was extremely underestimated. The estimate of environmental trend was also underestimated when the phenotypic trend was obtained by the means estimator.

Henceforth, in this study, whenever reference is made to the sires-over-time technique, estimates obtained by the regression of deviations of individual performance from the population mean on time $-2b_{(P-\overline{P})/T.S}$

is implied. These estimates of phenotypic, genetic and environmental trend were 2.89 ± .18, 2.58 ± .36 and .31 ± .40 lb, respectively.

When the change was assessed by the sires-over-time technique, Zabel (1973) found positive phenotypic, genetic and environmental trend for adjusted weaning grade. Holbert (1975) found a positive genetic trend for adjusted average daily gain from birth to weaning. Anderson (1975) reported positive genetic trends in three breeds with respect to adjusted 205-day weight. Reports by these authors are not in agreement with the results of this study when the sires-over-time technique was applied. Zabel (1973) reported a negative genetic trend in adjusted 205-day weight. Anderson (1975) also reported a negative genetic trend in one breed for adjusted 205-day weight.

Other factors and their influence on estimates of trends by the sires-over-time technique should be considered. Various non-additive effects could influence the estimate of genetic trend. A sire-year interaction is the most relevant, because it affects the within sire change over time. There were both short term and long term fluctuations in environment during this study. During short term fluctuations, a sire-year interaction was regarded as an additional error contributing to the variance of the average within sire change over time and did not bias the estimate of genetic trend. When long-term environmental change occurred, a sire-year interaction resulted in different estimates of a sire's breeding value, which was most appropriate for estimating genetic change. These results were in agreement with those of Smith (1962).

The estimate of genetic trend by the sires-over-time technique may have been influenced by environmental correlations. In a beef cattle population parental half-sibs born at about the same time may have been

subjected to similar environmental influences and this environment may have differed from that to which other half-sibs born later were subjected. This resulted in a similarity within half-sibs over and beyond that caused by the common share of genes and resulted in biased estimates of genetic trend.

Correlations between genotypes and the environmental deviations could occur in the population. This condition occurred when better genotypes were given better environments and happened from nothing more than the preferential management. This correlation could have caused bias in the estimate of ΔG when the sires-over-time technique was used. Another factor that should be considered is that not all genotypes respond in like manner when exposed to different environments. This could bias the estimates of genetic trend because many of the sires used in this study were from outside sources. No attempt was made to remove bias that could have existed due to environmental correlations, genotype and environmental correlations and genotype by environmental interaction. Finally, differences in the influence of maternal effects on pre-weaning performance of maternal half-sibs from one year to the next probably existed, but were extremely difficult to identify and eliminate.

Of the various additive effects which could influence the estimate of genetic trend, bias from selection and culling of sires was the most relevant to estimates of trends by the sires-over-time technique. This bias was negligible in this study because most sires were introduced from outside sources or they were sons of sires from outside sources. The time of selecting these sons resulted in the performance of the progeny born before and after selection of these sons in providing an accurate estimate of genetic trend.

Some sires were retained for future use on the basis of the performance of their early progeny, and some of the latter sires were possibly mated to older or genetically superior dams through selective mating; therefore, these estimates of genetic improvement may be biased slightly upward. Only six sires were used in the population after information on the performance of their early progeny was available. Only one of these was used extensively. No corrections for these possible sources of bias were made in this study. There also exists the possibility of bias in the estimates obtained by the sires-over-time technique due to sampling error and of bias in the statistical methods employed in adjusting the records and partitioning change.

The sires-over-time technique gave a smaller estimate of genetic change and was accompanied by a smaller standard error than the repeated-mating technique. Similar results were reported by Harville and Henderson (1967) and Powell and Freeman (1974). Smith (1962) and Burnside and Legates (1967) also reported close agreement in the results obtained by the two techniques and implied that they appeared equal in detecting genetic trend. Estimate of genetic trend by the sires-over-time technique was larger than the one obtained by the dams-over-time technique but the standard errors were identical. However, when the sires-over-time technique was compared to the sires-and-dams-over-time technique, the latter gave larger estimates of genetic change.

The sires-over-time technique resulted in a larger estimate of environmental trend than the repeat-mating technique and the sires-and-dams-over-time technique. However, the sires-over-time technique provided a smaller estimate of environmental trend than the dams-over-time technique.

Repeat-Mating Technique

The repeat-mating technique gave estimates of phenotypic, genetic and environmental trends of 2.89 ± .18, 2.83 ± .61 and .06 ± .59 lb, respectively. These estimates are shown in Table 8, p. 64.

In studies of trends in beef cattle populations, other authors have reported positive trends resulting from the repeat-mating technique. Fahmy and Lalande (1973) reported a positive phenotypic change in birth weight of .14 kg per year. Flower, Brinks, Urick and Wilson (1964) found positive genetic trends of 2.16 to 6.51 lb for weaning weight in three closed lines of Hereford cattle. Scarsi (1971) reported positive genetic trends for weaning weight in selection lines that ranged in magnitude from 2.9 to 4.9 lb per year. Fahmy and Lalande (1973) found a positive genetic trend in birth weight of .11 ± .06 kg per year. In weaning weight, Fahmy and Lalande (1973) also reported a positive genetic trend of .48 ± .27 kg per year. Positive environmental trend of .053 ± .04 kg for birth weight was reported by Fahmy and Lalande (1973).

A few authors reported estimates of trends by the repeat-mating technique that were not in agreement with those found in this study. Flower, Brinks, Urick and Wilson (1964) reported a negative genetic trend in birth weight of beef calves. The estimates of genetic trends for birth weight ranged from -.04 to 1.71 lb between lines and crosslines (Flower, Brinks, Urick and Wilson (1964). Scarsi (1971) reported a negative genetic trend for weaning weight in Herefords. Fahmy and Lalande (1973) reported a negative environmental trend of -.58 ± .28 kg for weaning weight.

Estimates of phenotypic, genetic and environmental trends were obtained from the application of the estimator $(b_{P.T} - b_{(PF_2 - PF_1).T})$

involving regression of the difference of performance of full-sibs born in consecutive years on time. The analysis of variance of the effect of year on adjusted 205-day weight is shown in Appendix Table 9. The effect of year was significant ($P < .001$). The effect of year on the differences in adjusted 205-day weight of full-sib progeny born in consecutive years is shown in Appendix Table 12. The effect of year was non-significant, indicating that no real differences existed in the environment between consecutive years based on the comparison of the performance of full-sib progeny.

Other factors should also be considered with the application of the repeat-mating technique. The estimates of genetic trend by this technique may have been influenced by the same environmental correlations as estimates by the sires-over-time technique. Full-sibs may have been subjected to similar environmental influences that differed from those experienced by other members of the population. This possibly could cause a similarity within full-sibs greater than that caused by the likeness of genes and result in biased estimates of genetic trend.

The probability that correlations between genotypes and the environmental deviations that occur in the population was greater than in the case of half-sibs, because offspring resulting from planned repeat-matings would generally be considered superior and these offspring are more likely to receive better than average environment. This correlation could have caused bias in the estimate of genetic change by this technique.

There exists the possibility that insufficient numbers of full-sibs were available to detect the environmental change. Also, the comparison of full-sibs is only a part of an estimate of environmental variation

because genotypic difference exists through segregation and independent assortment of genes. Scarsi (1971) and Powell and Freeman (1974) stated similar results in their studies.

There also exists the possibility of bias in the estimates obtained with this technique due to sampling errors, bias in the statistical methods or failure of the mathematical models employed in adjusting the records and partitioning change.

The repeat-mating technique gave a larger estimate of genetic change, and was accompanied by a larger standard error when compared to the sires-over-time technique. Similar results were reported by Harville and Henderson (1967) and Powell and Freeman (1974). Smith (1962) and Burnside and Legates (1967) also reported that there was close agreement in the results obtained by the two techniques and that they appeared equal in detecting genetic trend. The estimate of genetic trend by the repeat-mating technique was larger than the one obtained by the dams-over-time technique, with similar standard errors. Also, the estimate of genetic trend by the repeat-mating technique was larger than the estimate by sires-and-dams-over-time technique.

The repeat-mating technique provided a smaller estimate of environmental trend than the sires-over-time technique, the dams-over-time technique and the sires-and-dams-over-time technique. However, the estimate of environmental trend by the repeat-mating technique was accompanied by the largest standard error.

Dams-Over-Time Technique

The dams-over-time technique provided estimates of phenotypic, genetic and environmental trends of 2.89 ± .18, 1.40 ± .36 and 1.49 ± .40

lb, respectively. These estimates are shown in Table 8, p. 64.

The coefficient of regression used as the estimator in this technique was calculated differently from the others. Due to limited computer capacity, the data were divided into six equal groups. The analyses of variance of the effects are presented in the Appendix Tables 13, 14 and 15. Bartlett's Test of Homogeneity of Variances reveals that there was no significant difference ($P < .05$) between groups. Estimate of one-half the genetic change of .7016 estimated on a within dam basis was considerably less than the within sire estimate. It was considered realistic because the within sire and within dam changes add to 2.77 lb which was similar to ΔG estimated by the sires-over-time and the repeat-mating technique.

The regression of performance on time was significant ($P < .001$) in all groups. The estimate of change within dam reflects the sires' contribution to genetic progress, and when this is subtracted from the overall change, indicates that the dam selection contributed less to genetic progress than selection of sires, or that there is a lag in the contributions to genetic change from dam selection.

A dam year interaction is the most relevant non-additive effect that could affect estimates by this technique because it affects the within dam change over time. Both short term and long term fluctuations in the environment during the period would result in similar influences as discussed with respect to their effect on the sires-over-time technique.

The estimate of genetic trend by this technique may have been influenced by environmental correlations. In a beef cattle population parental half-sibs, born at about the same time, may have been subjected

to similar environmental influences that differed from those experienced by other half-sibs. This possibility caused a similarity within half-sibs over and beyond that caused by the common share of genes resulting in biased estimates of genetic trend.

The possibility exists that correlations between genotypes and the environmental deviations occurred in the population. This condition occurred if better genotypes were given better environment, which sometimes happens from nothing more than partiality by the management. This correlation could have caused bias in the estimate of genetic change by this technique.

Another factor that should be considered is that not all genotypes respond in like manner when exposed to different environments. This could bias the estimate of genetic trend because many of the sires used were from outside sources. No attempt was made to remove the possible bias that could exist in the estimates obtained by environmental correlations, genotype and environmental correlations and genotype by environmental interaction. The possibility of bias exists in the dams-over-time technique because of culling of dams. But the influence of age of dams was removed so no bias should exist from this factor.

Finally, the maternal influence on preweaning performance from one year to the next is extremely difficult to identify and eliminate. There was a possibility of bias in the estimates obtained with this technique due to sampling error, bias in the statistical methods or failures of the mathematical models employed in adjusting the records and partitioning change.

The same estimator of phenotypic trend was used with all techniques.

There was a definite advantage in all of the techniques having the same estimate, because this enhanced the comparison of the techniques in partitioning genetic and environmental trends. The estimate of genetic trend by the dams-over-time technique was considerably smaller than those obtained by the other techniques applied in the study. The estimate of environmental trend obtained by the dams-over-time technique was larger than estimated by the other techniques.

Sires-and-Dams-Over-Time Technique

The sires-and-dams-over-time technique gave estimates of genetic, phenotypic and environmental changes of 289 ± .18, 2.77 ± .36 and .12 ± 40 lb, respectively. These estimates are shown in Table 8, p. 64.

When these two techniques were applied separately, the assumption was made that the genetic change occurs at the same rate in both sexes, even though there may be a lag before the change was obvious or apparent in one sex. The within sire change (genetic progress among sires) was greater than the within dam change (among dam contribution to genetic progress) and the major influence of sire selection may be due to the increased productivity of his female offspring retained in the herd. However, the combination of the two estimates at any point in time should measure the total genetic change at that particular point in time.

Other factors which should be considered with the application of sires-and-dams-over-time technique have been discussed in detail in the sections where the sires-over-time and the dams-over-time techniques were discussed individually. All factors affecting the individual estimates by each individual technique are applicable to the combination of the techniques.

The estimate of genetic trends by the sires-and-dams-over-time technique was larger than that obtained by the sires-over-time technique or by the dams-over-time technique. However, it was not as large as those obtained by the repeat-mating technique.

The estimate of environmental trend by this technique was considerably less than that obtained by the dams-over-time technique and smaller than the estimate by the sires-over-time technique. The estimate of environmental trend by this technique was larger than the estimate obtained by the repeat-mating technique.

Conclusions

Estimates of genetic trends obtained by the regression of performance on time within sire estimator was larger than those obtained by the other two estimators using the sires-over-time technique. When the deviation of individual performance from the population mean replaced individual performance per se in the regression of performance on time, the estimate of ΔG was lower and similar to the estimate obtained by the differences in progeny means over time. Since no standard error of the estimate could be calculated for the difference in the means-over-time estimate and ΔG estimated by the estimator using deviations in performance was similar to the estimates by other techniques, the regression of deviated performance on time was considered the preferred estimator of the sires-over-time technique.

The repeat-matings technique involved estimation of environmental trends by comparison of the performance of full-sibs born in consecutive years. Phenotypic change was estimated as the regression of performance on time and genetic change was estimated as $\Delta\hat{P}$ minus $\Delta\hat{E}$. The estimate

of genetic trend by the repeat-mating technique (2.83 ± .61) was similar to those obtained by the regression of deviated performance on time within sire and by the sires-and-dams-over-time technique.

The estimates of ΔG by the dams-over-time technique was lower and the estimate of ΔE was higher than those by the other techniques. Since ΔG estimated by this technique reflects only the influence of dam selection, it was concluded that the estimate of ΔG by the sires-over-time technique was biased upward by the influence of the selection of daughters of superior sires.

The similar magnitude and SE of the estimates of ΔG and ΔE obtained by the sires-over-time technique, when deviation of individual performance from the population mean was regressed on time within sire, those obtained by the repeat-mating technique and the sires-and-dams-over-time technique indicate that these methods were equal with respect to their accuracy in estimating genetic and environmental trends.

CHAPTER V

SUMMARY

Data collected between 1957 and 1975 in the University of Tennessee, Ames Plantation Angus herd was used to compare two methods of adjusting weaning weight for known sources of fixed environmental variation, and four methods of estimating phenotypic, genetic and environmental trends. The method of adjusting age-constant (calculated 205-day weight) weaning weights using the coefficients of regression of weaning age on calculated 205-day weight reported by Robertson (1974) was superior to standard procedures for calculating age-constant weight in removing the effects of sex and age at weaning. The use of sex and age of dam adjustment factor described by Robertson (1974) and readjustment of calculated 205-day weight removed 97 percent of the variation in weaning weight due to sex, age at weaning and age of dam compared to 89 percent for the Tennessee Beef Cattle Improvement Program method. Differences in R^2 for weaning age by the two methods would be more pronounced as the range in weaning age increased.

Three estimators of phenotypic, genetic and environmental trends were compared in the sires-over-time technique. Two of these were associated with regression procedures and one with the comparison of means. The preferred estimator of genetic trend was minus twice the pooled within-sire regression of the deviation of progeny performance on time. Each record was deviated from the population mean. Estimates of phenotypic, genetic and environmental trends associated with the application of this estimator were 2.89 ± .18, 2.58 ± .36 and .31 ± .40 lb per

year increase in adjusted 205-day weight. This estimator was considered the preferred method because of the removal of year-to-year fluctuation in the environment. The repeat-mating technique was the second one applied in this study. Estimates of phenotypic, genetic and environmental trend were based on the performance of full-sib progeny born in consecutive years. These estimates were 2.89 ± .18, 2.83 ± .61 and .06 ± .59 lb, respectively, for adjusted 205-day weight. The third technique applied was that of dams-over-time. The estimates of phenotypic, genetic and environmental trends associated with this technique were 2.89 ± .18, 1.40 ± .36 and 1.49 ± .40 lb, respectively. The fourth technique applied was the sires-and-dams-over-time technique. Estimates of phenotypic, genetic and environmental trends by this technique were 2.89 ± .18, 2.77 ± .36 and .12 ± .40 lb.

All techniques applied showed positive phenotypic and genetic trends. However, the degree to which the technique partitioned the phenotypic change into genetic and environmental change varied. This was due in part to some sources of bias specific to each technique such as the bias that could occur in the statistical methods.

The repeat-mating technique provided the largest estimate of genetic trend but was accompanied by the larger standard error. The dams-over-time technique provided the smallest estimate of genetic change. However, all techniques reveal positive trends. Since all techniques approach the problem differently, each used in certain situations where it has advantages might be superior to the others.

Estimate of environmental trend was larger by the dams-over-time and the smallest by the repeat-mating technique. However, the estimate by the repeat-mating technique was accompanied by the larger standard error.

The estimate of ΔG by the dams-over-time technique was lower and the estimate of ΔE was higher than those by the other techniques. Since ΔG estimated by this technique reflects the influence of sire selection, it was concluded that the estimate of ΔG by the sires-over-time technique was biased upward by the influences of the selection of daughters of superior sires.

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APPENDIX

TABLE 9

ANALYSIS OF VARIANCE OF THE EFFECTS OF YEAR ON ADJUSTED 205-DAY WEIGHT

Source	Degrees of Freedom	Mean Square	F
Year	1	539322.52	264.95***
Residual	2604	2035.56	
Total	2605		

***P < .001.

TABLE 10

ANALYSIS OF VARIANCE OF THE EFFECTS OF YEAR WITH SIRE HELD CONSTANT ON ADJUSTED 205-DAY WEIGHT

Source	Degrees of Freedom	Mean Square	F
Sire	35	30965.99	16.74***
Year	1	3909.87	2.11
Residual	2569	1849.83	
Total	2605		

***P < .001.

TABLE 11

ANALYSIS OF VARIANCE OF THE EFFECTS OF YEAR WITH SIRE HELD CONSTANT ON DEVIATED ADJUSTED 205-DAY WEIGHT

Source	Degrees of Freedom	Mean Square	F
Sire	35	9288.50	5.56***
Year	1	9566.22	5.72**
Residual	2569	1671.51	
Total	2605		

***P < .001.

**P < .01.

TABLE 12

ANALYSIS OF VARIANCE OF THE EFFECTS OF YEAR ON DIFFERENCES OF ADJUSTED 205-DAY WEIGHT OF FULL-SIB PROGENY BORN IN CONSECUTIVE YEARS

Source	Degrees of Freedom	Mean Square	F
Year	1	21.71	.01
Residual	278	2228.32	
Total	279		

TABLE 13

ANALYSIS OF VARIANCE OF THE EFFECTS OF DAM ON ADJUSTED 205-DAY WEIGHT WITHIN GROUP

Source	Degrees of Freedom	Sum of Squares	Mean Square
Group 1			
Dam	116	424149.20	3656.46***
Residual	307	515080.47[a]	1677.79[b]
Total	423	939229.67	
Group 2			
Dam	116	652680.24	5626.55***
Residual	323	397469.12[a]	1230.55[b]
Total	439	1050149.36	
Group 3			
Dam	117	441346.78	3772.19***
Residual	325	564909.21[a]	1738.18[b]
Total	442	1006255.99	
Group 4			
Dam	117	487494.51	4166.62***
Residual	313	464438.27[a]	1483.83[b]
Total	430	951932.78	
Group 5			
Dam	116	462460.93	3986.78***
Residual	314	540009.51[a]	1719.78[b]
Total	430	1002470.44	
Group 6			
Dam	116	389703.53	3359.51***
Residual	320	492683.61[a]	1539.64[b]
Total	436	882387.14	

***P < .001.

[a]Residual sum of squares used in calculating $b_{P.T/D}$.

[b]Residual mean squares tested by Barlett's Test for Homogeneity of Variances (P < .05).

TABLE 14

ANALYSIS OF VARIANCE OF THE EFFECTS OF DAM ON YEAR WITHIN GROUP

Source	Degrees of Freedom	Sum of Squares	Mean Square
Group 1			
Dam	116	8350.21	71.98***
Residual	307	2665.58[a]	8.68[b]
Total	423	11015.79	
Group 2			
Dam	116	8239.85	71.03***
Residual	323	2491.69[a]	7.71[b]
Total	439	10731.54	
Group 3			
Dam	117	8002.71	68.40***
Residual	325	2976.75[a]	9.16[b]
Total	442	10979.46	
Group 4			
Dam	117	7882.31	67.37***
Residual	313	2401.93[a]	7.67[b]
Total	430	10284.24	
Group 5			
Dam	116	8237.74	71.02***
Residual	314	2610.38[a]	8.31[b]
Total	430	10848.12	
Group 6			
Dam	116	7341.22	63.29***
Residual	320	2854.45[a]	8.92[b]
Total	436	10195.67	

***P < .001.

[a]Residual sum of squares used in calculating $b_{P.T/D}$.

[b]Residual mean squares tested by Bartlett's Test for Homogeneity of Variances (P < .05).

TABLE 15

ANALYSIS OF VARIANCE OF THE EFFECTS OF DAM ON ADJUSTED 205-DAY WEIGHT PLUS YEAR WITHIN GROUP

Source	Degrees of Freedom	Sum of Squares	Mean Square
Group 1			
Dam	116	487525.10	4202.80***
Residual	307	525297.26[a]	1711.06[b]
Total	423	1012822.36	
Group 2			
Dam	116	723539.99	6237.41***
Residual	323	404733.75[a]	1253.05[b]
Total	439	1128273.74	
Group 3			
Dam	117	489273.18	4181.82***
Residual	325	479981.54[a]	1784.56[b]
Total	442	1069254.75	
Group 4			
Dam	117	543543.14	4645.67***
Residual	313	483657.88[a]	1545.23[b]
Total	430	1027201.02	
Group 5			
Dam	116	517125.76	4457.98***
Residual	314	555809.63[a]	1770.09[b]
Total	430	1072935.39	
Group 6			
Dam	116	447183.27	3855.03***
Residual	320	511457.21[a]	1598.30[b]
Total	436	958840.48	

***P < .001.

[a]Residual sum of squares used in calculating $b_{P.T/D}$.

[b]Residual mean squares tested by Bartlett's Test for Homogeneity of Variances (P < .05).

VITA

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