GENETIC AND ENVIRONMENTAL FACTORS ASSOCIATED WITH MILK YIELD IN BEEF CATTLE

By

James Ronald Dickey

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TABLE OF CONTENTS

Page

LIST OF TABLES

LIST OF APPENDIX TABLES

LIST OF FIGURES

Abstract of Dissertation Presented to the Graduate Council of the University of Florida in Partial Fulfillment of the Requirements for the Degree of Doctor of Philosophy

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The objectives of this study were to estimate environmental effects on milk yield of beef cows, to estimate genetic parameters associated with milk yield and cow growth traits and to estimate the direct effects of average lifetime milk yield on all traits studied.

Milk yield data (the mean of three within lactation observations obtained by the calf-nursing method after an average 16-hr separation) were recorded in 1969 and 1970 for 262 and 201 lactations, respectively, of 162 Angus cows by 46 sires and 137 Hereford cows by 39 sires. The data were analyzed by the least-squares method to estimate environmental effects within each breed. The Angus data were adjusted for the effect of cow age ($P < .01$) and the effect

of sex of calf nursed ($P < .01$). Hereford milk yield data were adjusted for the effect of cow age ($P < .05$). The cow growth traits, birth weight, weaning weight, weaning grade, yearling weight and 32-month weight were obtained from the station records.

The adjusted milk yield data of each breed were subjected to separate analyses of variance to obtain heritability and repeatability estimates by the intraclass correlation method. Heritability of single lactation 16-hr milk yield records was estimated to be $0.10 \pm .18$ and $0.03 \pm .21$, respectively, for the Angus and Hereford cows. Corresponding estimates of repeatability were $0.22 \pm .10$ and $0.49 \pm .09$, respectively.

Milk yield records (one or two in number) were averaged for each cow to obtain average milk yield per cow. Average milk yield and the cow growth traits were subjected to analyses of variance and covariance to obtain components for estimating heritability and the genetic, phenotypic and environmental correlation coefficients by the half-sib method. Heritability estimates for average milk yield, birth weight, weaning weight, weaning grade, yearling weight and 32-month weight were $0.14 \pm .30$, $0.56 \pm .33$, $0.71 \pm .34$, $0.40 \pm .32$, $1.54 \pm .34$ and $0.94 \pm .34$, respectively, for the Angus cows and $0.13 \pm .33$, $0.73 \pm .37$, $0.04 \pm .32$, $0.71 \pm .37$, $1.46 \pm .37$ and $0.80 \pm .37$, respectively, for the Hereford cows. Coefficients of correlation between milk yield and the above growth traits, respectively, were as follows from the Angus data: 0.68±0.83, 0.47±0.76, 2.39±2.23, 1.22±1.06 and 1.98±1.60 for genetic correlations; 0.13±0.09, 0.05±0.06, -.01±0.01, 0.11±0.05 and 0.24±0.05 for phenotypic correlations; and -.10±0.39, -.20±0.48, -.81±0.44, -.26±0.15 and -2.07±6.21 for environmental correlations. For the Hereford, corresponding coefficients were -.73±1.14, -6.75±25.94, -1.45±1.60, -.34±0.71 and -.08±0.77 for genetic correlations; -.07± 0.07, -.05±0.03, 0.08±0.11, 0.06± 0.63 and 0.12±0.21 for phenotypic correlations; and 0.32±0.60, 0.47±0.32, 1.04±0.86, 0.19±0.26 and 0.34±0.64 for environmental correlations.

An indirect reciprocal daughter-dam correlation method was developed to estimate genetic covariance between milk yield and growth traits and to estimate the direct effects of average lifetime milk yield on all traits. These estimates were obtained from 49 Angus and 45 Hereford daughter-dam pairs. Estimates of genetic covariance between average milk yield and the growth traits, weaning weight, weaning grade, yearling weight and 32-month weight were 0.02, 0.45, -.21 and 0.12, respectively, for the Angus cows and -.02, -.67, 0.01 and -.47, respectively, for the Hereford cows. Estimates of the direct effects of average lifetime milk yield on daughter milk yield, weaning weight, weaning grade, yearling weight and 32-month weight, expressed as standard partial regression coefficients, were 0.12, 0.25, 0.06, 0.37 and 0.14, respectively, for the Angus cows and -.27, 0.10, 0.30, 0.20 and

0.22, respectively, for the Hereford cows. Corresponding partial regression coefficients were 0.14, 7.99, 0.05, 19.00 and 7.14, for the Angus, and -.30, 2.89, 0.25, 11.98 and 13.35 for the Hereford.

INTRODUCTION

Milk yield is considered to be the most important factor affecting preweaning growth rate of beef cattle. Residual effects of milk yield on postweaning traits have also been demonstrated.

Experimental evidence of the genetic association between milk yield and growth traits in beef cattle is limited. Current evidence from genetic studies in dairy and dual-purpose cattle are not consistent and do not support the existence of a significant genetic relationship between milk yield and growth traits. Some indication of a negative genetic relationship between maternal ability and preweaning growth in Hereford and Brahman x Shorthorn cattle has been reported. A more specific genetic study is needed for elucidation of the association between milk yield and growth traits in beef cattle. Efficient estimates of genetic parameters associated with milk yield in beef cattle would help to evaluate current selection programs.

Difficulties involved in obtaining milk yield data within the environmental conditions in which beef cattle perform have contributed to limiting animal numbers for efficient genetic analysis. Utilization of the calf-nursing method makes possible the rapid collection of milk yield data on large numbers of cows maintained under pasture conditions. This method was used to collect data for analyses reported in this study.

The objectives of this study were to estimate environmental effects on milk yield of beef cows, to estimate genetic parameters associated with milk yield and cow growth traits and to estimate the direct effects of average lifetime milk yield on all traits studied.

LITERATURE REVIEW

Environmental Factors and Phenotypic Associations

As early as 1913 research was initiated to ascertain the milk yield of beef cattle. Gowen (1918) and Cole and Johansson (1933) reported average milk yields in Angus cows which ranged from 1,066 to 3,849 pounds per lactation. Since these early studies much work has been conducted to define the phenotypic relationships between milk yield and the factors which are either affected by or affect milk yield. The relative importance of milk consumption and other sources of nutrients to preweaning calf growth was demonstrated by Knapp and Black (1941). Simple correlations between average daily gain (ADG) and the three nutritive components, milk consumption, grain consumption and hay consumption were 0.52, 0.21, and 0.12, respectively, suggesting that milk consumption had the closest association with calf growth.

The dependence of calf growth on milk yield was indicated by Drewry, Brown and Honea (1959) and by Neville (1962) who found highly significant partial regression coefficients for preweaning calf gain on the dam's milk yield. Neville (1962) reported lower coefficients for cattle on higher nutritional levels than for cattle on lower plains of nutrition, indicating less dependence of calf gains on milk supply as nutrition improves. A positive phenotypic relationship between beef-cow milk yield and preweaning calf growth has been indicated by the simple correlations reported in numerous studies (Gifford, 1953; Heyns, 1960; Caldwell, 1962; Neville, 1962; Pope et al., 1963; Howes, 1964; Christian, Hauser and Chapman, 1965b; Klett, Mason and Riggs, 1965; Totusek and Arnett, 1965; Schwulst et al., 1966; Wistrand and Riggs, 1966; Melton et al., 1967, Gleddie and Berg, 1968; Rutledge, Robinson and Legates, 1970 and Wilson et al., 1970). Sixty-nine simple correlation estimates from these studies ranged from 0.01 to 0.88 with an unweighted mean of 0.49. The mutual dependence of milk yield and growth on environmental conditions, breed composition of the cattle studied and genotype within breeds were suggested as factors influencing these correlation estimates. Milk yield and growth were usually more highly correlated in the earlier months of lactation than just prior to weaning.

A portion of the weight differences present at weaning tends to be carried through to slaughter, thereby affecting economic value. Evidence suggests that calves receiving the most milk in early life weigh more and rate higher in other slaughter traits as compared to calves receiving less milk. Neville et al. (1962) reported simple correlations between milk yield and average daily gain on stocker test, average daily gain on fattening test, weight per day of age at slaughter and slaughter grade to be 0.17, -.17, 0.73 and 0.38, respectively. Simple correlations between calf slaughter grade and total milk yield at 180 and 250 days of lactation were found to be 0.55 and 0.37, respectively, by Caldwell (1962). Cook et al. (1942) reported negative correlation estimates of -.07, -.17 and -.20 between milk yield of Milking Shorthorn cows and three steer traits: efficiency of gain, percent carcass fat and grade of steer.

Many factors have been found to affect beef-cow milk yield in varying degrees. Among those having been well documented in previous studies are year, season, nutritional status, breed, cow age, day of lactation, estimation method, and separation interval. Other factors affecting milk yield in some studies, but usually not being significant, are cow size, early growth rate of cow, sex of calf and calf birth weight.

A brief description of some of the more prominent early studies and most recent work are presented along with part of their results which support the above-mentioned effects. Gifford (1953) studying milk yield and associated factors in 57 Hereford, 12 Angus and 13 Shorthorn lactations estimated 8-month average milk yield of 1,303, 1,972 and 1,983 pounds, respectively, for the three breeds. Yield declined at a relatively constant rate from the first to the eighth month. Milk yield was significantly correlated ($P<.01$) with offspring weight at 8, 12, 24, and 36 months. Correlation coefficients were 0.82, 0.69, 0.53 and

0.55, respectively. Gifford pointed out that other factors such as "mothering" and genetic influence may have been partly responsible for these correlations. Calf capacity was considered a limiting factor on milk yield of high producing cows during the first 6 weeks of lactation. Gleddie and Berg (1968) also reported calf capacity as a limiting factor in early lactation. Neville (1962) and Christian, Hauser, and Chapman (1965b) failed to find this limitation due to young small calves.

Over a 2-yr period Drewry, Brown and Honea (1959) estimated milk yield in 48 lactations of Angus cows. Daily milk yield collections made during the first, third and sixth month of lactation averaged 14.1 ± 3.7; 16.0 ± 3.9; and 9.0 ± 2.5 pounds, respectively. Cows giving the most milk tended to have superior mothering ability when defined as attentiveness to the newborn calf. The effect of calf birth weight on milk yield was positive, but significant only in the third month. Heyns (1960) found a significant correlation between birth weight of calf and milk yield of 24 Africander cows; whereas, no significant effect was observed in Hereford cattle by Christian, Hauser and Chapman (1965b).

Milk production in 135 Hereford cows was shown by Neville (1962) to vary with level of nutrition. As measured by the calf-nursing method, the 8-month milk yield estimates were 2,520, 2,304 and 1,944 pounds, respectively, for cows on high, medium and low nutritional levels. Caldwell (1962) studying milk yield in 48 Angus, 53 Hereford, 20 Shorthorn and 14 crossbred cows at 30, 60, 90, 180 and 250 days of lactation found highest yields in the Angus cows. Peak production was reached in the first month of lactation followed by a slow decline until the 180th day, after which the decline was more rapid. Cow weight change during lactation was negatively correlated with milk yield, while a positive association between cow weight and milk yield was noted.

Pope et al. (1963) reported findings from milk production data on 300 beef cows over a 3-yr period; however, most of the correlations reported were based on data from 49 4-yr-old cows. Correlations between 24-hr milk yield, obtained by the calf-nursing method, and various measures of cow size were generally low and nonsignificant. Cows in earlier lactation and those nursing male calves produced significantly more milk at the first collection and higher total average milk yield. The association of birth weight with milk yield was slightly positive, but nonsignificant. Level of supplementation and season significantly affected milk yield. The high level supplemental group was less affected by the winter season. Cows calving in February and March maintained a near constant milk yield through June, then declined sharply until weaning in September. April yields were 9.8, 11.7 and 11.6 pounds for 2-, 3- and 4-yr-old cows, respectively. These same groups averaged 6.5, 7.1 and 7.8 pounds, respectively, in September. Other workers have reported comparable nutritional and seasonal effects on milk yield (Montsma, 1960 and

1962; Nelson, Furr and Velasco, 1961; Furr and Nelson, 1964; Howes, 1964; and Deutscher, Whiteman and Webb, 1970).

Milk yield for 175 days was estimated to be 664, 784 and 581 kg for 15 Angus, 15 Charolais and 15 Hereford cows, respectively (Melton et al., 1967). Total milk and solids yields were significantly affected by both breed and age of dam, whereas percent butterfat and percent solids were not significantly affected. A slight milk yield advantage for dams nursing male calves was nonsignificant. Milk yield declined in all breeds as lactation advanced. The estimated partial regression coefficient for daily milk yield (kg) on calf age in days within each period studied ranged from -.020 (ns.) to -.031 ($P < .01$).

Breed, age of dam, month of collection and day of lactation were considered important effects on milk yield of 8 Galloway, 8 Angus, 8 Charolais x Angus, 5 Angus x Galloway and 5 Hereford cows studied by Gleddie and Berg (1968). The average milk yield estimate was 7.7 ± 2.39 kg as measured by the oxytocin-machine milking method. Milk consumption measured by the calf-nursing method was 6.5 ± 2.36 kg. Milk yield declined an average of 0.02 kg per day of lactation.

Todd, Fitzhugh and Riggs (1969) reported estimates of 24-hr milk yield obtained by the oxytocin-machine milking method in 58 Hereford, 33 Brahman, 32 Hereford x Brahman, 65 Brahman x Hereford, and 48 Angus x (Brahman x Hereford) cows during April and June over a 3-yr period. Yields for the breed groups were 7.7, 9.4, 13.9, 13.8 and 15.4 pounds, respectively, in April; and 6.8, 9.8, 12.6, 12.8 and 13.8 pounds, respectively, in June. Age of dam had a curvilinear effect on milk yield. Production increased from age 3 to 6, remained constant from 7 to 9, and declined slightly in dams 10 years and older.

A study of milk yield estimated by the calf-nursing method in 279 lactations of 193 Hereford cows was reported by Rutledge (1970). Mean monthly 24-hr milk yield for the winter calving cows was 5.8, 5.7, 5.5, 5.1, 4.8, 4.4 and 4.0 kg, respectively, for the first through the seventh month. Average total milk yield obtained over the seven collections was 35.3 kg. The estimated linear partial regression of total milk yield on calf birth weight was 0.51. Year of record, cow weight and sex of calf significantly affected milk yield. Age of cow had a significant ($P<.01$) curvilinear effect on milk yield with a maximum yield at 8.4 years of age. Both cow age and year of record were reported by Dawson, Cook and Knapp (1960) to have significant effects on milk yield in Milking Shorthorn cattle.

Turner, Ragsdale and Brody (1923) reported that milk yield of dairy cows varied with nutritional level, but that it followed a fairly consistent curve upward the first 2 months, then a decline each month to approximately 94 percent of the previous month until the end of lactation. Cows in advanced stages of gestation declined more rapidly in the last 2 months of lactation. Similar declines with advancing lactation were reported by Cannon, Frye and Sims (1942).

A liberal grain fattening ration fed to one of each of seven sets of Jersey twins from approximately 8 months to 24 months of age reduced milk yields in the first and second lactation as compared to their twins which were fed a normal ration (Swanson, 1957). Poor lobule-alveolar development was observed in the fattened group. Preweaning nutritional level, as estimated by weaning weight, was found to be negatively associated with milk yield of Hereford cows studied by Christian, Hauser and Chapman (1965b). Utilizing "Most Probable Producing Ability" as a measure of maternal ability of Hereford cows, and their own weaning weight as a measure of preweaning nutritional level, Mangus and Brinks (1971) found strong evidence of a negative association. A cyclic effect was observed from generation to generation, with heavy weaning cows producing lower weaning calves, who in turn, tended to produce higher weaning calves. Holtz, Erb and Hodgson (1961) working with dairy cattle, and McClure and Meacham (1968) working with Angus and Angus x Hereford cattle, failed to demonstrate a relationship between milk yield and ADG or nutritional level in the cows' early life. Martin et al. (1962) reported a phenotypic correlation of 0.30 between gain from birth to one year and subsequent first lactation milk yield of 659 dairy cows.

The early estimates of milk yield in beef cows were obtained under dairy management conditions (Gowen, 1918 and Cole and Johansson, 1933). That is, cows were separated from the calves in the first few days of lactation, then hand-milked twice daily in the same manner as dairy cows. Calves were usually raised on nurse cows. These dairy management conditions are not normal for the typical range beef cow; therefore, the estimates may have limited value. The need of removing the calf under dairy conditions eliminates the usual calf effect on milk yield and calf growth.

Gifford (1953) used a modified hand-milking method to estimate milk yield. Cows and calves were run together on pasture with the exception of 3 days per month during the 8-month lactation. On the second and third days of separation alternate sides (two quarters) were hand-milked and the other side suckled by the calf morning and afternoon. The 4 milk collections for the 2 days were summed to make an estimate of 24-hr milk yield. Calves were weighed and measured each month during the 3-day separation for calculation of correlations between milk yield and growth traits. Howes (1964) maintained cows and calves on pasture except for 1-1/2 days per month. Cows and calves were put in drylot after noon one day, then separated until after completion of two hand-milkings, morning and afternoon of the next day. Oxytocin injections (40 I. U.) were administered before each milking.

The oxytocin-machine milking method has been used by several researchers in studies of milk yield in beef cows. Anthony et al. (1959) and Gleddie and Berg (1968) explain that the cow and calf are separated, the cow injected with oxytocin, machine- and/or hand-milked to empty udder, then after a 12-hr period the cow is injected again with oxytocin and milked to obtain an estimate of milk produced during the period. This is sometimes repeated after another 12-hr period to complete a 24-hr milk yield estimate.

Knapp and Black (1941), Drewry, Brown and Honea (1959), Neville (1962), Pope et al. (1963) and Rutledge (1970) report data where the calf-nursing method has been used to estimate milk yield in beef cattle. Drewry et al. described the technique to be somewhat like the oxytocin-machine milking method except the calf is used to extract the milk. The calf is weighed immediately before and after nursing to estimate milk yield by taking the difference of the two weights. The natural stimulus of the calf negates the need of oxytocin injections; therefore, a step is eliminated. Pope et al. points out that nursing can be in groups of 6 to 10 pairs, thereby increasing the number of cattle which can be worked in a given period.

Average milk yield estimates obtained from one morning collection by the calf-nursing method on 2 or 3 days was considered by Neville (1962) to be comparable to estimates from two collections per day on 4 days. The phenotypic correlation between milk yield and calf weight when milk yield was estimated by two daily collections on 4 days was 0.81, as compared to 0.80, 0.77, 0.75 and 0.69 for one daily collection on 4, 3, 2 and 1 day, respectively. Neville and Cullough (1969) used the multiplicative correction factor of 1.38, obtained in a previous study, for converting 14-hr milk yield to a 24-hr basis. Rutledge (1970) found that morning and evening collections three times during lactation gave almost the same milk yield estimates as were obtained over seven collections. He reported correlations of 0.87 to 0.91 between total milk yield over seven monthly collections and various predictions of total milk yield based on three collections.

The calf-nursing method has been compared to variations of the oxytocin-machine milking method and the hand-milking method in several studies (Chow, 1964; Totusek and Arnett, 1965; Schwulst et al., 1966; Wistrand and Riggs, 1966; Gleddie and Berg, 1968; Lamond, Holmes and Haydock, 1969; and Wilson et al., 1969 and 1970). Estimates obtained by the calf-nursing method were usually lower than those by the other methods; however, the variation and order of the observations from the different methods were similar.

The estimation of 305-day or total lactation milk yield from limited measurements has long been of interest to the dairyman. To avoid the expense, etc., of every day weighing and because of the close agreement of predictions from limited measurements and actual 305-day milk yield, the limited system has been commonly used in the dairy industry. Prediction of 305-day milk yield from bi-monthly estimates has been recommended by Cannon, Frye and Sims (1942), Van Vleck and Henderson (1961), Singh and Acharya (1969), Balaine, Gill and Acharya (1970) and Keown and Van Vleck (1970 and 1971) based on the highly significant correlations they found between predictions and actual production.

Genetic Studies

The study of genetic parameters associated with milk yield in beef cattle has apparently been limited to two investigations which dealt with heritability. Others have reported estimates of repeatability which can be considered the upper limit of heritability. Genetic studies of dual-purpose and dairy cattle have indicated that the most probable range for heritability of milk yield is between 0.20 and 0.40, and that genetic correlations between milk yield and beef traits are slightly positive, but near zero.

Estimates of heritability for milk yield obtained by two different methods were 0.33 and 0.86 for Angus, and 0.46 and 0.79 for Hereford (Caldwell, 1962). The first estimate for each breed was calculated by the intrasire correlation method and was considered the most reliable by the author. Christian, Hauser and Chapman (1965a) estimated heritability of milk yield to be 0.50 and 0.88 by two methods using identical and fraternal

Hereford twins. Estimates from twin sources tend to be larger than nontwin sources. Rutledge (1970) reported repeatability estimates between lactations of 0.38±.09 for total milk yield over seven observations, and 0.31±.10 and 0.27±.01 for predicted milk yield based on three observations. Repeatability of milk yield between lactations varied with breed group from 0.00 to 0.77, whereas the repeatability between observations taken within 6 days was 0.92 (Caldwell, 1962). Other estimates of repeatability of daily milk yield within lactation of beef cows are 0.60, 0.16 and 0.75 to 0.96, respectively, by Pope et al. (1963), Melton et al. (1966) and Gleddie and Berg (1968).

Yao, Dawson and Cook (1954) studying 163 Milking Shorthorn cows estimated heritability of milk yield to be 0.28±0.32 by the intrasire correlation method. When the same method was used on a reduced number of cows (123) the estimate was 0.14±0.35. The reduced estimate was attributed to more uniformity among sires of the 123 cows due to selection. Also, the 40 cows removed were not considered a random sample of the herd. Using the intrasire regression of daughter on dam with the reduced number of cows the estimate was 0.71±0.30. This inflated estimate was attributed to maternal effects (including cytoplasmic effects), epistatic effect, selection influence and error. Other estimates of heritability of milk yield of dual-purpose cattle are 0.27 by Mason (1964) and 0.54±.32 by Martin and Starkenburg (1965). Both studies used the intrasire correlation method for estimation of heritability

Thirty estimates of heritability of milk yield in dairy cattle taken from published reports averaged 0.36 with a range from 0.05 to 0.71 (Lasley, 1963). Johansson and Rendel (1968) reviewing previous studies of milk yield heritability listed a range from 0.08 to 0.43 with reported standard errors ranging from 0.04 to 0.05. The predominance of estimates reviewed were between 0.20 and 0.40.

Reviewed estimates of repeatability of milk yield between lactations of dairy cows ranged from 0.13 to 0.76 (Johansson, 1950; Rendel et al., 1956; Wilcox et al., 1962; Salazar, 1970; and Verde et al., 1970). Most estimates were between 0.30 and 0.60.

Studies of the genetic association between milk yield and various beef traits in dairy and dual-purpose cattle have resulted in nonsignificant and inconsistent correlations as is concluded in the review articles of Johansson (1964), Nichols and White (1964), and Tyler (1970). A slightly positive genetic correlation between milk yield and beef traits is indicated, but because of the progress limitation a second trait exerts on the first, beef traits are usually excluded from selection programs in dairy cattle. However, Soller, Bar-Anan and Pasternak (1966) found the inclusion of live-weight-forage in the selection index along with milk yield increased progress in economic value of Israeli dairy cattle.

Tyler (1970) in his review of several European studies reported estimates of genetic correlations between milk yield and beef traits of dairy and dual-purpose cattle which ranged from -.05 to 0.27. Martin and Starkenburg (1965) reported genetic correlation estimates between milk yield and total gain and feed efficiency of 0.16 and 0.41, respectively, in dual-purpose cattle.

Touchberry (1951), Blackmore, McGilliard and Lush (1958), Miller and McGilliard (1959), Clark and Touchberry (1962) and Wilk, Young and Cole (1963) reported genetic correlation estimates between milk yield and various beef traits in dairy cattle which ranged from -.66 to 0.43. Most estimates were not significantly different from zero.

Two methods of estimating genetic correlations yielded widely differnet estimates between milk yield and body measurements of Holstein cows (Blackmore, McGilliard and Lush, 1958). When the method using the reciprocal correlations between daughter and dam traits was used in the numerator as presented by Hazel (1943), positive genetic correlations were usually obtained between milk yield and all body measurements at 6 months, 1 year and 2 years of age. However, when only the correlation between daughter's milk production and dam's measurements were used in the numerator all estimates were reduced, several below zero. The higher estimates derived from the first method were deemed less reliable because prenatal maternal effect was considered to be confounded in the calculations, causing a bias upward. Though not significantly different from zero, phenotypic correlations between dam's production and daughter's size were consistently larger than the reciprocal correlations between dam's size and daughter's production, thus supporting the presence of a maternal effect. It was concluded that inclusion of growth triats in a selection program would retard genetic progress in milk yield.

A study of carcass data of 45 Holstein steers and their mean estimated breeding value (EBV) for milk production estimated from their parents indicated a negative association of -.38 ($P<.05$) between EBV and carcass yield; while positive correlations ($P<.05$) of 0.11, 0.21 and 0.36, respectively, were found between EBV and carcass grade, marbling score, and conformation (Suess et al., 1968).

The genetic correlations between maternal ability and maternally affected traits and the effect of maternal environment on heritability and genetic correlation estimates were studied in beef cattle by Koch and Clark (1955b, c). These authors state, "Of the maternal environment, differences in milking ability are the most important elements, since milk is the major source of nutrient during the early months of growth." Estimates of genetic parameters from paternal half-sib correlations are shown by path coefficients to be free of maternal effects. Whereas, estimates from maternal half-sib correlations and daughter-dam correlations are inflated by the maternal effect of the dam and the grandam. The use of sire-offspring correlations reduces the estimate inflation to that portion coming through the grandam. Results from the Koch and Clark (1955c) study indicated a negative association between maternal ability and preweaning performance traits in Hereford cattle. Similar negative associations have been reported by Hill, Legates and Dillard (1966) and Hohenboken and Brinks (1971) in Hereford cattle; Deese and Koger (1967) in Brahman x Short-horn cattle; and Dickerson and Grimes (1947) in swine. Postweaning gain and maternal effects were reported to be positively associated in the study by Koch and Clark (1955c). Legates (1970) found a slightly positive genetic correlation between maternal performance and weight of mice.

Deese and Koger (1967) failed to find a relationship between maternal ability and growth in a group of Brahman cattle. They reasoned that the sire and dam variances of the crossbred cattle may have been overestimated causing a false appearance of negative covariance. Hill et al. (1966) also expressed limited confidence in their negative estimate due to the small number of cattle involved (717 calves and 141 offspring-dam pairs).

Hohenboken and Brinks (1971) reported estimates of -.28 and -.79 for the genetic correlation between preweaning growth and maternal performance computed from equations utilizing offspring-sire and offspring-dam covariance, respectively.

The larger negative estimate was attributed to the deflationary effect of the negative maternal environment (reported by Mangus and Brinks, 1971) on the offspring-dam covariance estimate. They noted that similar previous studies (Koch and Clark, 1955c; Hill et al., 1966; and Deese and Koger, 1967) reporting negative estimates within the same range have also used daughter-dam covariance in their computations. Hohenboken and Brinks concluded that the larger negative estimates were probably biased and that only a weak genetic antagonism between offspring and maternal effects on weaning weight was likely, perhaps in the order of their smaller negative estimate, r_G=-.28.

EXPERIMENTAL PROCEDURE

Materials

Milk yield data were collected from Angus and Hereford cattle over a 2-yr period at the Brooksville Beef Cattle Research Station, Brooksville, Florida. The Angus herd, established in 1954, is composed primarily of station born cows with a portion having been purchased in other eastern states as weanlings or yearlings. Data were obtained on 119 Angus cow-calf pairs in 1969 and 143 in 1970. A total of 162 Angus cows by 46 sires were observed through at least one lactation during the study. Included in this number were 49 daughter-dam pairs.

The Hereford herd is part of a genotype x environment interaction study which includes groups of cattle of two origins maintained at each of the two origin locations, Brooksville, Florida and Miles, City, Montana. The Brooksville herd is composed of approximately 36 percent Brooksville line cows which were mostly station born and 64 percent Montana line cows of which about 37 percent were Montana born and 63 percent were born at Brooksville. The Brooksville line was established in 1952, while the Montana line was introduced in 1962 and 1963 from the Miles City Station herd which has been closed since 1934. Data were collected from 105 Hereford cow-calf pairs during 1969 and from 96 pairs in 1970. One hundred and thirty-seven Hereford cows by 39 sires produced at least one record during the 2 years. Forty-five daughter-dam pairs were included.

The linebred Montana cattle were more closely related on the average than the Brooksville cattle. Pahnish et al. (1964) reported the average relationship of the half-sibs in the Montana line to be 0.28 rather than the usual 0.25 for outbred cattle. No adjustment was made for this relationship; therefore, the estimates of heritability in the Hereford cattle may be slightly inflated.

Each of the 262 Angus and 201 Hereford milk yield records is an average of three collections taken following an average 16-hr separation interval in early, mid and late lactation. The observations recorded at each collection included milk yield, calf weight, and separation interval. Cow weight and calf grade and ultrasonci backfat score was recorded at weaning. The previous weights and grades for cows were obtained from the station records. Birth weight was not available on some of the older cows. These few cells were filled with the average birth weight to make possible the estimation of parameters involving birth weight. Equipment used for collection of the data consisted of a good set of corrals and a scale which was considered accurate to the nearest half pound. The analyses of data were facilitated by the personnel and equipment of the University of Florida data processing center.

Procedures

Milk Yield Measurements

Observations were made in mid April, June and August of 1969 and 1970 to obtain estimates of milk yield in early, middle and late lactation. A variation of the calf-nursing method as described by Drewry, Brown and Honea (1959) was used. Cows and calves were brought to the pens and separated about noon on the day before collection of data. After 4 to 5 hours of separation, or between 5 and 6 pm, they were reunited with the objective of obtaining uniform nurse-out of all cows. The cows and calves were then separated for the night, leaving the calves in pens without water or feed and putting the cows in large pens or adjacent traps containing water but having limited grass. The overnight stay in or near the pens was convenient and provided a uniform treatment of all cows. Work by Munford et al. (1964) indicated that limited grazing reduced milk yield of dairy cows the following day; however, the variability apparently was not affected. The reduction in milk yield which the treatment may have caused is not considered a serious problem, assuming that the relative variation was basically unchanged.

The following morning, beginning at 7:00 am, groups of 8 to 12 calves were separated from remaining calves, weighed individually and turned into a nursing pen adjacent to the cows.

While a calf was being weighed his dam was being cut from the cow herd into the same adjacent nursing pen. Four to six cow-calf pairs were placed in each of two pens. Approximately two minutes were required to weigh each calf and locate the dam; therefore, the first pen of calves usually had been nursing about 10 minutes when the last cow and calf of the second pen were paired.

An effort was made to maintain a minimum nursing time of 10 minutes; however, some groups were separated earlier due to apparent loss of suckling interest by most calves. Excretory loss was feared to be a problem if nursing time was allowed to extend past 20 to 25 minutes. Observed excretion was recorded and calf weight was adjusted upward 0.5 pound. Few such observations were noted.

When suckling interest appeared to be lost or minimal in all calves of a group they were separated as a group and immediately reweighed individually. The difference between the prenursing and postnursing weight was recorded as the milk yield estimate. The overnight separation interval was determined by difference between the nurse-out time the day before collection and the prenursing-weight time.

This process was repeated until approximately 115 pairs were worked. The collections were usually completed by about 11:00 am, in time to prepare for the second half of the cattle to be measured the next day.

Personnel needed included two men to pen, separate and recombine cows and calves for nursing on the day before collection. On the day of collection eight men were utilized. Two pushed calves to the scale; one worked the scale gate and read identification numbers; one weighed and recorded; one recorded time, worked the exit gate and assured proper pairing; while three turned the cows to the calves and later separated them.

The three observations were averaged to obtain one observation for each lactation. These milk yield data are the subject of the following analyses.

Analyses and Adjustments for Environmental Effects

The identification of environmental effects on milk yield of the cow is important within itself and would be expected to account for a large portion of the variance. Since the primary purpose of this study was to estimate genetic parameters, the elimination of these environmental effects to obtain unbiased estimates of genetic parameters was of major concern. Part of the temporary variation would be expected to be removed by the simple averaging of the three within lactation observations to obtain the one lactation record. The milk yield data were subjected to least-squares analyses (Harvey, 1960) to determine the significance of certain environmental effects and to obtain least-squares constants for adjustment of significant ($P < .05$) effects.

Model A was used to analyze the milk yield records for each breed.

$$Y_{ijk} = u + y_i + s_j + ys_{(ij)} + b_1(X_{1_{ijk}} - \overline{X_1}) + b_1'(X^2_{1_{ijk}} - \overline{X^2_1}) + b_2(X_{2_{ijk}} - \overline{X_2}) + b_2'(X^2_{2_{ijk}} - \overline{X^2_2}) + b_3(X_{3_{ijk}} - \overline{X_3}) + b_3'(X^2_{3_{ijk}} - \overline{X^2_3}) + e_{ijk} \qquad [A]$$

where

Y_{ijk} = the dependent variable, milk yield for the ijkth lactation,

u = the overall least-squares mean,

y_i = the effect of the ith year of record,

s_j = the effect of the jth sex of calf,

$ys_{(ij)}$ = the effect of the specific year by sex combinations or the year by sex interaction,

X_1 = cow age unique to the Y_{ijk}th lactation,

X_2 = calf age at first lactation unique to the Y_{ijk}th lactation,

X_3 = average separation interval unique to the Y_{ijk}th lactation,

$b_{1,2,3}$ = partial linear regression coefficients for specific independent variables,

$b'_{1,2,3}$ = partial quadratic regression coefficients for these same variables, and

e_{ijk} = residual error.

A more complete model including sires and cows within sires would have been preferable; however, the available least-squares computer program was unable to handle such large numbers. Variation due to sires and cows, consequently, was included in the error term. This may have slightly biased the test of significance of other variables; however, such bias was assumed to be small.

Based on the results of these least-squares analyses milk yield records were adjusted for significant environmental effects within each breed. Model B exemplifies those used to adjust the data.

$$\text{Adjusted 16-hr milk yield} = Y_{ik} - a_i - [b(X_{ik} - \overline{X})] - [b'(X_{ik}^2 - \overline{X^2})] \quad , \qquad [B]$$

where

Y_{ik} = the actual milk yield record for the ik^{th} lactation,

a_i = a constant for a discrete effect,

X_{ik} = a value of a continuous effect specific to the Y_{ik}^{th} lactation,

b = the partial linear regression coefficient determined for the continuous effect X, and

b' = the partial quadratic regression coefficient determined for the square of the continuous effect X.

Heritability and Repeatability

Within each breed being studied there were cattle of different origins (previously described) with possibly differential effects on production that could not be specifically labeled genetic or environmental. Therefore, for the following analyses sires were nested within origin in order to remove this variation which may have tended to inflate the sire variance. The origins in the Angus herd were identified as 1 for cows introduced from outside herds, and 2 for cows born locally. Hereford origin was identified as 1 for Miles City line cows introduced to Florida, 2 for Miles City line cows born locally and 3 for Brooksville line cows born locally.

Year of cow birth was ignored in these and in the other genetic analyses. Partial confounding of year of cow birth and sire of cow may have tended to inflate the sire variance; however, this was assumed to be minimal.

The nested analysis of variance used to determine the variance components for cows and sires is presented in table 1. Nested analysis of variance and the associated statistical calculations (table 2) are discussed in Snedecor (1956). Formulas for calculating the k values for lactations per cow and for cows per sire were developed by Swiger et al. (1964) and altered by Becker (1967) to accommodate nested analyses.

Estimates of heritability and repeatability of milk yield were calculated by the paternal half-sib method discussed by Brinks et al. (1962).

The sire and cow variance components were estimated by the following formulas, respectively,

$$V_s = \frac{MS_s - (MS_w + k_2V_c)}{k_3} \quad , \text{ and}$$

$$V_c = \frac{MS_c - MS_w}{k_1} \quad .$$

TABLE 1. NESTED ANALYSIS OF VARIANCE

Source	df	SS	MS	EMS
Total	N-1			
Origin	O-1	SS_o	MS_o	$V_w + k_4\Theta^2$
Sires/Origin	S-O	SS_s	MS_s	$V_w + k_2V_c + k_3V_s$
Cows/Sire/Origin	C-S	SS_c	MS_c	$V_w + k_1V_c$
Within Cows	N-C	SS_w	MS_w	V_w

$$k_1 = \frac{N - \Sigma \frac{\Sigma n_{ij}^2}{n_{i.}}}{C - S}$$

$$k_2 = \frac{\Sigma \frac{\Sigma n_{ij}^2}{n_{i.}} - \frac{\Sigma\Sigma n_{ij}^2}{N}}{S - 1}$$

$$k_3 = \frac{N - \frac{\Sigma n_{i.}^2}{N}}{S - 1}$$

k_4 = number of origins

N = total number of records

$n_{i.}$ = number of records for the i^{th} sire

n_{ij} = number of records for the ij^{th} cow

TABLE 2. STATISTICAL CALCULATIONS TO OBTAIN SUMS OF SQUARES FOR THE NESTED ANALYSES OF VARIANCE

Correction Factor = CF = $X^2 \ldots / N$

Total SS = $\Sigma X^2_{ijkl} - CF$

Origin SS = $\Sigma (X^2_{i\ldots} / n_{i\ldots}) - CF$

Sires/Origin SS = $\Sigma (X^2_{ij..} / n_{ij..}) - \Sigma (X^2_{i\ldots} / n_{i\ldots})$

Cows/Sire/Origin SS = $\Sigma (X^2_{ijk.} / n_{ijk.}) - \Sigma (X^2_{ij..} / n_{ij..})$

Within Cow SS = $\Sigma X^2_{ijkl} - \Sigma (X^2_{ijk.} / n_{ijk.})$

Heritability and repeatability of milk yield were estimated by the following formulas, respectively,

$$h^2_s = \frac{4V_s}{V_s + V_c + V_w} \quad , \text{ and}$$

$$t = \frac{V_s + V_c}{V_s + V_c + V_w} \quad .$$

Approximate standard errors of the heritability and repeatability estimates were calculated by the formulas presented by Swiger et al. (1964):

$$SE_{(h_s^2)} = 4\sqrt{\frac{2(N-1)(1-t_s)^2[1+(k_3-1)t_s]^2}{k_3^2(N-S)(S-1)} \quad \frac{N-1}{N}},$$

and

$$SE_{(t)} = \sqrt{\frac{2(N-1)(1-t_s)^2[1+(k_1-1)t]^2}{k_1^2(N-C)(C-1)} \quad \frac{N-1}{N}}.$$

Heritability and Genetic, Phenotypic and Environmental Correlations

The following analyses necessitated a single observation for each cow. Consequently, the average for the lactation records by each cow was employed. There were 62 Angus and 73 Hereford cows with single records, while 100 Angus and 64 Herefords had two lactations each. Therefore, the milk yield studied in the following analyses are referred to as average milk yield. The growth traits which were studied along with milk yield included birth weight, weaning weight, weaning grade, yearling weight and 32-month weight.

Harvey's (1963) "least-squares and maximum likelihood general purpose program" which employed method 1 of Henderson (1953) was used to estimate genetic parameters. The program computed approximate standard errors for heritability and genetic correlation coefficients by a modification of the formula by Swiger *et al.* (1964). Approximate standard errors for phenotypic and environmental correlation coefficients were calculated with a desk calculator using the methods presented by Scheinberg (1966). The expectations for sire components of variance and covariance as presented by Henderson (1953) are shown in table 3 along with the formula by Swiger *et al.* (1964) for calculating the k value for unequal numbers per sire.

TABLE 3. NESTED ANALYSES OF VARIANCE AND COVARIANCE

Source	df	MS(X)	MCP	MS(Y)	EMS	EMCP
Total	N-1					
Origin	O-1					
Sires/Origin	S-O	MS_s	MCP_s	MS_s	$V_w + kV_s$	$Cov_w + kCov_s$
Within Sires	N-S	MS_w	MCP_w	MS_w	V_w	Cov_w

$$k = \frac{N - \dfrac{\Sigma n_i^2}{N}}{S - 1}$$

n_i = number of cows for the i^{th} sire.

The computer program utilized the intrasire correlation method described by Dickerson (ASAP, 1960) to estimate heritability as:

$$h_s^2 = \frac{4V_s}{V_w + V_s},$$

and the half-sib correlation method presented by Hazel *et al.* (1943) to estimate the genetic correlation coefficients where:

$$r_{G_xG_y} = \frac{Cov_{xy_G}}{\sqrt{V_{x_G}\ V_{y_G}}} = \frac{Cov_{xy_s}}{\sqrt{V_{x_s}\ V_{y_s}}}$$

Phenotypic and environmental correlation coefficients also were calculated by the computer program. One environmental correlation was recalculated by hand (Falconer, 1954) due to apparently erroneous computer results caused by an inflated heritability estimate. An inflated sire variance will cause a reduction in magnitude of the genetic correlation coefficient estimate, while the sign will not be affected as will the sign of the environmental correlation estimate. The weighted average heritability estimate for that trait reported by Petty and Cartwright (1966) was substituted into Falconer's formula to estimate the environmental correlation coefficient.

Genetic Covariance and Direct Effects of Milk Yield by the Indirect Reciprocal Daughter-Dam Correlation Method

The conventional daughter-dam covariance method presented by Hazel (1943) to estimate genetic correlations is not appropriate when maternal effects are present. Koch and Clark (1955b, c) compared the relative usefulness of several methods and concluded that only the paternal half-sib correlation method was free of confounding with maternal effects when working with maternally influenced traits.

An alternative method, patterned after the methods presented by Koch and Clark (1955c), was developed to utilize available daughter-dam relationships to estimate genetic parameters and the direct effects of milk yield. Ideas were also gained from the works of Willham (1963 and 1964), Hill, Legates and Dillard (1966), Deese and Koger (1967) and Eisen (1967).

The path diagram in figure 1 adapted from Koch and Clark (1955c) was used for the development of the following equations which were utilized for estimation of additive genetic covariances and direct effects of milk yield. The symbols are: P_i = phenotype for the i^{th} trait; G_i = genotype for the i^{th} trait; h_i = square root of the heritability of the i^{th} trait; u = direct prenatal environmental effect on birth weight; m_i = direct effect of milk yield on the i^{th} trait; r = genetic correlation between each pair of traits; the absence of a prime = daughter generation; one prime = dam

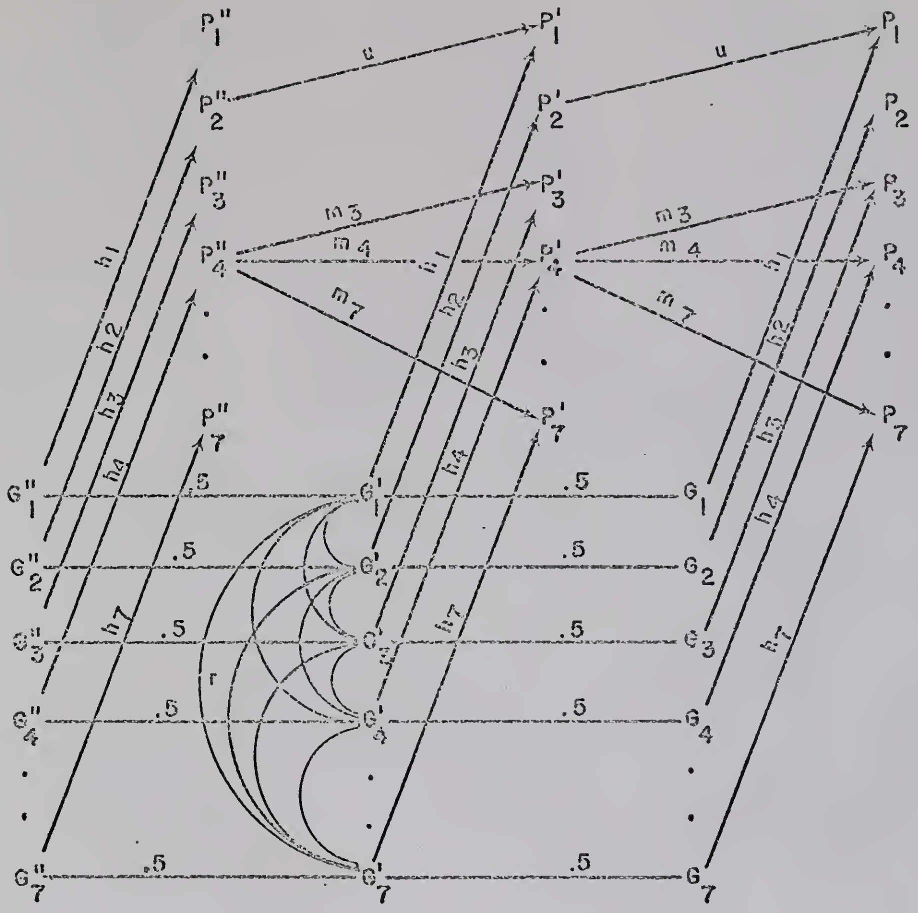

Figure 1. Relationship between offspring, dam and maternal grandam. Where traits 1 through 7 are birth weight, prenatal maternal environment, weaning weight, milk yield, weaning grade, yearling weight, and 32-month weight, respectively.

generation; and two primes = grandam generation. The .5 represents the relationship between generations. The cow traits referred to in the path diagram and others included in subsequent calculations were birth weight (1), prenatal environment (2), weaning weight (3), milk yield (4), weaning grade (5), yearling weight (6) and 32-month weight (7).

Subsequent calculations were made with the following assumptions: the direct effect of calf birth weight on milk yield of the dam was negligible; prenatal and postnatal maternal environment, other than effects of milk yield, had negligible effects on the traits studied; epistatic effects were negligible; and other environmental and genetic effects were randomly distributed. Average milk yield for the 2-yr study was used as an indication of average lifetime milk yield. Since estimated lifetime yield was utilized in place of lactation yield corresponding to the growth traits, the above direct effect of milk yield (m_i) is equal to the product of repeatability (t) and direct effect of the lactation yield ("m_i"). That is, $m_i = t$ "m_i" . The equations and procedures used to obtain estimates of genetic covariance between milk yield and the growth traits, and the direct effects of milk yield by the indirect daughter-dam method, are subsequently presented. Birth weight was not included in these analyses due to missing data on some dams.

Reciprocal daughter-dam phenotypic correlation coefficient estimates were calculated between milk yield and each growth trait. Theoretical causal components of the phenotypic correlation coefficient estimates were determined by following all paths of the path coefficient diagram between the two traits involved as described by Wright (1934). Equations 1 and 2 show the theoretical causal components of the reciprocal daughter-dam phenotypic correlations between milk yield (4) and the growth traits (i).

$$r_{P'_4P_i} = .5\, h_4 h_i r_{G_4G_i} + m_i + .25\, m_4 h_4 h_i r_{G_4G_i} \quad [1]$$

$$r_{P_4P'_i} = .5\, h_4 h_i r_{G_4G_i} + .25\, m_i h_4^2 + m_4 h_4 h_i r_{G_4G_i} \quad [2]$$

Equations 1 and 2 were then reduced by their last component $.25\, m_4 h_4 h_i r_{G_4G_i}$ and $m_4 h_4 h_i r_{G_4G_i}$, respectively. These components were calculated from the best available estimates of milk yield and growth trait heritabilities, genetic correlation coefficients and direct dam milk yield effect on daughter milk yield (m_4). The sources of these parameter estimates were: milk yield heritability and genetic correlation coefficients--from the half-sib analyses of these data (plus or minus one was used if the estimates exceed these limits); growth trait heritabilities--from the weighted average estimates reported by Temple (1963) or Petty and Cartwright (1966); and direct dam milk yield effect on daughter milk yield (m_4)--from the indirect daughter-dam correlation method using equation 3.

$$m_4 = (r_{P_4P'_4} - .5\, h_4^2) / (1 + .25\, h_4^2) \quad , \qquad [3]$$

where

$$r_{P_4P'_4} = .5\, h_4^2 + m_4 + .25\, m_4 h_4^2 \quad , \text{ and}$$

h_4^2 = heritability of milk yield estimated from these data by the intrasire correlation method (free of maternal effects).

Subtracting the estimated last component from each appropriate correlation coefficient, equations 1 and 2 became reduced equations 4 and 5.

$$"r"_{P'_4P_i} = .5\, h_4 h_i r_{G_4G_i} + m_i \qquad [4]$$

$$"r"_{P_4P'_i} = .5\, h_4 h_i r_{G_4G_i} + .25\, m_i h_4^2 \qquad [5]$$

Then using the reduced reciprocal correlations, the direct milk yield effects (m_i) and the additive genetic covariances ($h_4 h_i r_{G_4G_i}$) were equated. The direct milk yield effects (m_i) were solved with equation 6 which was derived from equations 4 and 5 as follows.

$$\begin{array}{rrcll} & "r"_{P'_4P_i} & = & .5\, h_4 h_i r_{G_4G_i} + m_i & [4] \\ - & "r"_{P_4P'_i} & = & .5\, h_4 h_i r_{G_4G_i} + .25\, m_i h_4^2 & [5] \\ \hline \end{array}$$

$$\begin{aligned} "r"_{P'_4P_i} - "r"_{P_4P'_i} &= 0 + (m_i - .25\, m_i h_4^2) \\ &= 0 + m_i\,(1 - .25\, h_4^2) \\ &= m_i\,(1 - .25\, h_4^2) \end{aligned}$$

Thus, equation 6 is:

$$m_i = (\text{"r"}_{P'_4 P_i} - \text{"r"}_{P_4 P'_i}) \; / \; (1 - .25\, h_4^2) \quad , \qquad [6]$$

where

h_4^2 = heritability of milk yield estimated from these data by the intrasire correlation method.

The additive genetic covariance between milk yield and each growth trait was solved by equation 7 which was derived from equation 4.

$$\text{"r"}_{P'_4 P_i} = .5\, h_4 h_i r_{G_4 G_i} + m_i \quad , \qquad [4]$$

$$\text{"r"}_{P'_4 P_i} - m_i = .5\, h_4 h_i r_{G_4 G_i} \quad , \text{ thus}$$

$$\mathrm{Cov}_{G_4 G_i} = h_4 h_i r_{G_4 G_i} = 2(\text{"r"}_{P'_4 P_i} - m_i) \qquad [7]$$

RESULTS AND DISCUSSION

Environmental Effects on Milk Yield

Subclass means of unadjusted milk yield and the number of lactations per subclass are given in tables 1A and 2A, respectively, for the Angus and Hereford cows. The model for least-squares analyses of milk yield included effects for year of record; sex of calf; year x sex interaction and three continuous variables, including age of cow, age of calf at first collection and average separation interval for which both linear and quadratic effects were included. Sex of calf and age of cow, both linear and quadratic, significantly ($P < .01$) affected Angus milk yield (tables 3A and 4A). Milk yield by Hereford cows was significantly affected by age of cow (tables 5A and 6A). A more complete model including sires and cows within sires should have given a more sensitive test of significance since these effects are part of the remainder in the present model. However, the computer program available for these analyses did not have the capacity to include these variables. Effect of year of record, which approached significance in the Angus analysis, possibly could have become significant if the complete model would have reduced the error term. The remaining effects did not approach significance in either breed.

Angus cows nursing bull calves produced 0.66 pounds more ($P < .01$) milk than those nursing heifer calves. Melton et al. (1967) reported a nonsignificant increased yield in cows nursing bull calves. Gifford (1953), Melton et al. (1967) and Gleddie and Berg (1968) associated higher milk yield with the greater capacity of bull calves in early lactation. This could not be evaluated with these data.

Partial linear and quadratic regression coefficients for milk yield on cow age were $0.6092 \pm .1618$ ($P < .01$) and $-.03638 \pm .01145$ ($P < .01$), respectively, for the Angus and $0.5430 \pm .2222$ ($P < .05$) and $-.03376 \pm .01706$ ($P < .05$), respectively, for the Hereford. Maximum yield, estimated from these coefficients, was realized at 8.4 yr of age for the Angus cows and 8.0 yr of age for the Hereford cows. These estimates were obtained by setting the first derivative of the curvilinear equation equal to zero, then solving for cow age at maximum yield. Figure 2 illustrates the increase in milk yield observed from age 3 yr to the maximum near 8 yr, then the decrease as age advanced. The range of cow age was 3 to 14 yr and 3 to 12 yr, respectively, for the Angus and Hereford cows. The age distribution for each breed is given in table 8A. These results are in close agreement with work reported by Todd, Fitzhugh and Riggs (1969) and Rutledge (1970). Dawson, Cook and Knapp (1960) and Melton et al. (1967) evaluating effect

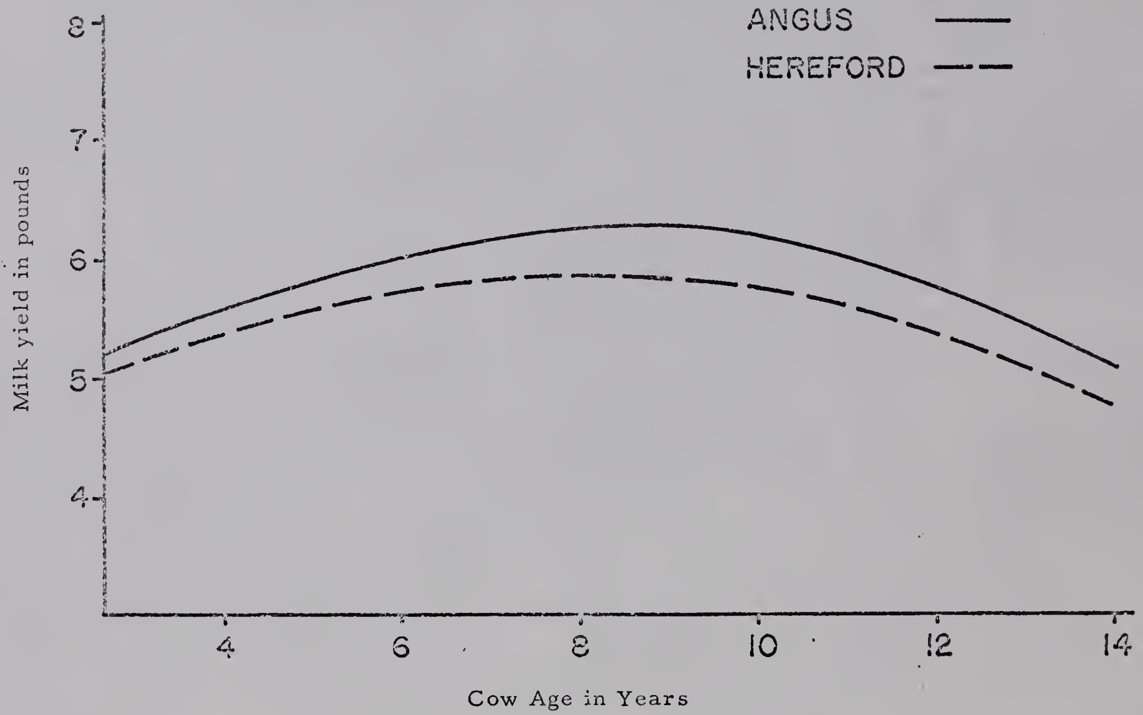

Figure 2. Effect of cow age on milk yield.

of age as a discrete variable reported maximum yields at 7 to 8 yr and 5 to 10 yr, respectively. Both studies found very little change in milk yield after the maximum was reached. Similar effects of cow age on weaning weight have been reported (Koch and Clark, 1955a) which suggest that weaning weight variation attributed to cow age is probably a function of the level of milk production as has generally been assumed. Although the cow's genetic potential remains constant, her physiological ability to realize the full potential varies with age.

The least-squares mean milk yield was $5.66 \pm .09$ pounds and $5.49 \pm .10$ pounds, respectively, for the Angus and Hereford cows. These yields were projected linearly [using the partial regression coefficient 0.34 obtained from a preliminary analysis reported by Dickey et al. (1970)] to estimate 24-hr yields of 8.6 pounds and 8.3 pounds (205-day yields of 1,763 pounds and 1,702 pounds), respectively, for the Angus and Hereford cows. Although extrapolation of estimates past the actual range of observations can give erroneous results, research in dairy cattle has shown that limited observations are usually good indicators of total production. The majority of the published beef cattle milk yields have been reported as 24-hr or total lactation yields, usually estimated from limited observations.

The yield estimates of the present study are similar to those reported by Gifford (1953), Montsma (1960 and 1962), Caldwell

(1962), Neville (1962), Pope et al. (1963), Furr and Nelson (1964), Howes (1964), Christian, Hauser and Chapman (1965b), Melton et al. (1967) and Todd, Fitzhugh and Riggs (1969). Most other estimates in British cattle differed very little from this study. However, substantially higher estimates have been obtained in studies of dual-purpose, dairy-beef crossbred and Brahman derivitive breeds.

Genetic Effects

Heritability and Repeatability

Milk yield records were adjusted for significant ($P < .05$) environmental effects prior to genetic analyses, using the within breed constants presented in tables 4A and 6A. The Angus data were adjusted for the effects of sex of calf and age of cow, while the Hereford data were only adjusted for the effect of cow age. The average values of the continuous effects are presented in table 7A for each breed. The data were adjusted to the average cow age for each breed.

Analyses of variance with sires nested within origin, cows within sires and records within cows were used to obtain the components of variance for estimating both heritability and repeatability of milk yield for each breed by the intraclass correlation method. The nested analyses of variance are presented in table 9A for the

Angus and Hereford cows. Cow effect was significant ($P<.05$) in the Angus analysis and highly significant ($P<.01$) in the Hereford analysis. The effect of sires was not significant in either breed.

Heritability of milk yield was estimated to be $0.10 \pm .18$ and $0.03 \pm .21$, respectively, for the Angus and Hereford breeds (table 4). Although these estimates are not statistically different from zero, a low level of heritability is indicated. Previous studies have usually reported higher levels of heritability both for beef cattle (Caldwell, 1962 and Christian, Hauser and Chapman, 1965a) and for dual-purpose cattle (Yao, Dawson and Cook, 1954; Mason, 1964; and Martin and Starkenburg, 1965). The estimates of this study approach the lowest estimates for heritability of milk yield in dairy cattle as summarized by both Lasley (1963) and Johansson and Rendel (1968).

The environmental stress to which a beef cow is subjected, especially in the subtropics of Florida, may tend to mask the genetic potential for milk production. As is indicated by the low heritability estimates of this study, environmental factors apparently are responsible for most of the variation in milk yield among these cows.

TABLE 4. ESTIMATES OF HERITABILITY AND REPEATABILITY OF MILK YIELD OF THE ANGUS AND HEREFORD COWS

Breed	Heritability $\pm$ SE	Repeatability $\pm$ SE
Angus	0.10$\pm$.18	0.22$\pm$.10
Hereford	0.03$\pm$.21	0.49$\pm$.09

Repeatability of milk yield was estimated to be 0.22$\pm$.10 and 0.49$\pm$.09, respectively, for the Angus and the Hereford cows. Based on the standard errors of these estimates, they are both significantly different from zero, and differ significantly from each other, being more than 2 standard deviations separated.

The Angus estimate is in the lower range of the repeatability estimates reviewed and agrees closely with those reported by Melton et al. (1966), working with beef cattle in Texas. Salazar (1970) and Verde et al. (1970) reported similar estimates for dairy records in Columbia and Venezuela. Due to the many stresses cattle are subjected to in the more tropical areas, especially under range conditions, temporary environmental variance is probably substantially expanded. Therefore, low repeatability estimates may be normal for these conditions.

The repeatability estimate obtained for the Hereford data was near the average of the published estimates reviewed, and comparable to the estimate of 0.38$\pm$.09 reported for Hereford cattle

(Rutledge, 1970). Repeatability is the percentage of total variance which can be accounted for by genetic and permanent environmental factors. Since heritability was low for Hereford milk yield, the genetic portion of variance might be similarly low. Therefore, permanent environmental sources of variation would be expected to be large to account for the higher repeatability. Evidence has been found in this study and earlier studies by Totusek (1968) and Mangus and Brinks (1971) which suggests that preweaning nutritional status may influence subsequent milk yield or maternal ability. This may tend to increase the permanent environmental variance, thus increasing repeatability above that observed for the Angus data. Results of this study, subsequently discussed, suggest that this preweaning influence may be stronger in the Hereford than the Angus cattle at the Brooksville Station.

Heritability of average milk yield and of the growth traits studied in association with milk yield was estimated by the half-sib method. The analyses of variance are given in table 10A. Variance components for sire effects (table 11A) were used to calculate the heritabilities shown in table 5. Means, standard deviations and coefficients of variation for these traits are presented in table 12A.

The estimates of heritability for average milk yield of $0.14 \pm .30$ and $0.13 \pm .33$, respectively, for the Angus and Herefords were slightly higher than the corresponding estimates for single lactation records as would be expected. Due to the large standard errors, however, these differences were not significant. Averaging more than one record, nevertheless, tends to remove a portion of the temporary environmental variance, thus reducing total variance. Genetic variance would not be expected to be affected by averaging; therefore, the genetic portion would tend to constitute a larger percentage of the total variation.

Most of the heritability estimates for the growth traits (table 5) were slightly higher than the weighted average estimates presented by Temple (1963) and Petty and Cartwright (1966). The estimates for heritability of yearling weight for both breeds exceeded any of the estimates reviewed by these authors. Considering the large standard errors, which were expected with the relatively small number of cattle studied, estimates in this study do not differ statistically from the published weighted average heritability estimates. Partial confounding of year of cow birth and sire of cow probably tended to inflate sire variance estimates for growth traits. These traits would be expected to be influenced more by year of cow birth than would subsequent milk yield.

TABLE 5. ESTIMATES OF HERITABILITY OF AVERAGE MILK YIELD AND GROWTH TRAITS OF THE ANGUS AND HEREFORD COWS

Traits	Angus $h^2 \pm$ SE	Hereford $h^2 \pm$ SE
Average milk yield[a] (4)[b]	0.14±.30	0.13±.33
Birth weight (1)	0.56±.33	0.73±.37
Weaning weight (3)	0.71±.34	0.04±.32
Weaning grade (5)	0.40±.32	0.71±.37
Yearling weight (6)	1.54±.34	1.46±.37
32-month weight (7)	0.94±.34	0.80±.37

[a] average 16-hr milk yield estimated from one or two lactation records, averaging 1.6 and 1.4 records, respectively, for the Angus and Hereford

[b] trait code number in parentheses.

Genetic, Phenotypic and Environmental Correlation Coefficients

Estimates of genetic, phenotypic and environmental correlation coefficients between average milk yield and growth traits are listed in table 6 for the Angus and Hereford cattle. These estimates were computed from the components of variance and covariance obtained from the half-sib analysis. The approximate standard errors were large for all correlation estimates as would be expected with this small volume of data. Small numbers increase the possibility of

TABLE 6. COEFFICIENTS OF GENETIC, PHENOTYPIC AND ENVIRONMENTAL CORRELATION BETWEEN AVERAGE MILK YIELD AND GROWTH TRAITS OF THE ANGUS AND HEREFORD COWS

Growth traits	Average Milk Yield (4)[a] $r_{G_4G_i} \pm SE$	$r_{P_4P_i} \pm SE$	$r_{E_4E_i} \pm SE$
	ANGUS		
Birth weight (1)	0.68±0.83	0.13±0.09	-.10±0.39
Weaning weight (3)	0.47±0.76	0.05±0.06	-.20±0.48
Weaning grade (5)	2.39±2.23	-.01±0.01	-.81±0.44
Yearling weight (6)	1.22±1.06	0.11±0.05*	-.26[b]±0.15
32-month weight (7)	1.98±1.60	0.24±0.05**	-2.07±6.21
	HEREFORD		
Birth weight (1)	-.73±1.14	-.07±0.07	0.32±0.60
Weaning weight (3)	-6.75±25.94	-.05±0.03	0.47±0.32
Weaning grade (5)	-1.45±1.60	0.08±0.11	1.04±0.86
Yearling weight (6)	-.34±0.71	0.06±0.63	0.19[b]±0.26
32-month weight (7)	-.08±0.77	0.12±0.21	0.34±0.64

[a] trait code number in parentheses

[b] recalculated substituting the weighted average heritability of yearling weight 0.41 (Petty and Cartwright, 1966) for the estimated heritability

* (P<.05) ** (P<.01)

sampling error which can lead to erroneous and possibly inflated results. This might partially explain the correlation estimates which exceeded the possible range of ± 1. The between and within sire components of variance and covariance from which the estimates were calculated are listed in table 11A for both breeds.

The coefficients of genetic correlation between milk yield and the growth traits were all positive for the Angus and all negative for the Herefords. This suggests a possible breed difference. With the large standard errors, however, the corresponding estimates for the two breeds were not statistically different from each other or from zero. The rather erratic results and large standard errors obtained in this study are typical of the non-conclusive previous genetic correlation studies in dairy and dual-purpose cattle, as summarized by Johansson (1964), Nichols and White (1964) and Tyler (1970). The lack of consistency in the results of these studies might suggest that genetic correlations may not be the same for all breeds nor the same within breeds under different environments. The three reviews agree that genetic correlations between milk yield and various measures of growth or size are probably positive but near zero.

Meaningful comparisons might be made with beef cattle studies which have estimated the genetic association between maternal ability (assumed to be primarily an expression of milk yield) and growth traits (Koch and Clark, 1955c; Hill, Legates and Dillard, 1966; Deese and Koger, 1967; Hohenboken and Brinks, 1971; and Vesely and Robinson, 1971). Hereford cattle were studied by Koch and Clark, Hill et al., Hohenboken and Brinks and Vesely and Robinson; therefore, their results may be more relative to the Hereford estimates of our study. Koch and Clark (1955c) reported negative coefficients of genetic correlation between maternal ability and preweaning gain which ranged from -.65 to 0.68, and between maternal ability and weaning score which ranged from -.32 to -.39. The range in these estimates was due to different values assumed for heritability and the direct effect of maternal environment, which were necessary to complete the estimation equation. Positive coefficients of correlation between maternal ability and the postweaning traits, yearling gain and yearling score were found. These preweaning estimates agree in sign with the estimates from the Hereford data in this study. The postweaning estimates did not agree, but those of the present study were near zero.

Hohenboken and Brinks (1971) estimated genetic correlations of -.28 and -.79 between maternal ability and preweaning growth. The best estimate was said to be -.28. These authors suggested that their large negative estimate as well as the negative estimates reported by Koch and Clark (1955c), Hill, Legates and Dillard (1966) and Deese and Koger (1967) were biased in a negative direction by a common factor. This reasoning might also be applied to the negative genetic covariance recently reported by Vesely and Robinson (1971) between maternal ability and growth potential in Hereford cattle. The common element suggested was that of the offspring-dam covariance, used to estimate genetic correlation between maternal ability and growth, being biased downward by a negative environmental effect of preweaning growth rate on subsequent maternal performance as reported by Mangus and Brinks (1971). Offspring-sire covariance which is free of the negative bias was used to obtain their best estimate. Deese and Koger (1967) reported a negative covariance between the additive components for maternal ability and preweaning growth in a Brahman x Shorthorn herd, while the covariance was estimated to be zero in the Brahman herd studied. They pointed out that other artifacts in estimates, such as an over-estimate of sire effects, could result in a negative estimate for the relationship. They questioned whether the relationship could be generally negative in view of the characteristics of several breeds.

Genetic studies of this type on other beef breeds have not been found in the literature. Nevertheless, the deviation of the Brahman estimates from the consistent negative estimates from the Hereford and crossbred data supports the possibility that the genetic association may differ between breeds. Comparison of the Angus and Hereford coefficients from this study give further evidence of this possibility. While the magnitude of the standard errors do not substantiate a real difference between coefficients for the two breeds, these estimates along with other reports suggest the need for further study to better define specific breed parameters. Conclusions relative to the genetic association between beef cattle growth and milk yield should be reserved pending further research.

Most of the phenotypic correlation coefficients were non-significant (table 6), but usually larger than those reported in previous studies with dairy and dual-purpose cattle. The analysis of the Angus data gave significant positive phenotypic correlation estimates between milk yield and the growth traits, yearling weight ($P<.05$) and 32-month weight ($P<.01$). No significant phenotypic correlations were found for the Hereford data.

Environmental correlation (the correlation of the environmental deviations plus the non-additive genetic deviations) between milk yield and each growth trait is shown also in table 6. These estimates differ in sign with the corresponding genetic coefficient indicating one of two possible conditions. First, if the estimates are accurate, the difference in sign shows that genetic and environmental sources of variation affect the traits through different physiological mechanisms (Falconer, 1961). For example, a high level of nutrition directly affects both growth and milk production favorably, while there is evidence that high nutritional levels during the early growth period are antagonistic to subsequent milk production (Swanson, 1957). Swanson found that heifers grown on a fattening ration deposited fat in the udder which apparently limited milk production. Other papers (Thomas, Sykes and Moore, 1959; Crichton, Aitken and Boyne, 1960; and Swanson, 1967) have reported that subsequent milk yield was not affected by rate of gain within the normal range for developing dairy heifers. The other possibility is that of error in estimation. The large standard error estimates make the latter a more likely explanation for these data. Replicate studies, preferably with larger numbers of uniform cattle, should be conducted before confident conclusions could be made concerning the environmental correlations.

Genetic Covariance and Direct Effects of Milk Yield Estimated by the Indirect Reciprocal Daughter-Dam Correlation Method

Estimates of reciprocal daughter-dam phenotypic correlation coefficients between average milk yield and cow traits (excluding birth weight which was not recorded for some dams) are listed in table 7. Only the correlations between the dam's milk yield and the daughter's weaning grade and yearling weight for Angus pairs were significant ($P < .05$). These estimates were obtained from small

TABLE 7. COEFFICIENTS OF RECIPROCAL DAUGHTER-DAM PHENOTYPIC CORRELATION BETWEEN AVERAGE MILK YIELD AND ALL TRAITS OF THE ANGUS AND HEREFORD COWS

Cow traits	Dam Milk Yield $r_{P'_4 P_i}$	Daughter Milk Yield $r_{P_4 P'_i}$
	ANGUS	
Weaning weight (3)[a]	0.26	0.03
Weaning grade (5)	0.30*	0.26
Yearling weight (6)	0.28*	-.06
32-month weight (7)	0.21	0.10
Daughter milk yield (4)	0.20	1.00
	HEREFORD	
Weaning weight (3)	0.10	0.05
Weaning grade (5)	-.02	-.27
Yearling weight (6)	-.22	0.07
32-month weight (7)	0.00	-.15
Daughter milk yield (4)	-.21	1.00

[a] trait code number in parentheses

* $(P < .05)$

numbers (49 Angus and 45 Hereford daughter-dam pairs) which minimizes confidence in observed differences. Suggestive trends, however, were apparent. In both breeds, milk yield and daughter growth traits were more closely correlated than were the reciprocal coefficients. This suggested that maternal effects were involved, usually affecting the relationship positively. Hereford coefficients of correlation between milk yield and daughter growth traits were smaller than the corresponding Angus estimates, while the reciprocal correlations for both breeds were similarly small. The large breed differences in the coefficients of correlation between milk yield and daughter milk yield (table 7) suggest that strong opposite forces affect this relationship in the two breeds. Applying equation 3, and using the heritability estimates for average milk yield of 0.14 and 0.13 (obtained by the intrasire correlation method) for Angus and Herefords, respectively, the direct effect of dam's milk yield on daughter's milk yield (m_4) was calculated for each breed. These estimates, along with those for the direct effects of milk yield, are reported in table 8 in terms of standard partial and partial regression coefficients.

The negative direct effect of dam milk yield on daughter milk yield found in the Hereford data supports the findings of Mangus and Brinks (1971) who indicated that maternal ability was cyclic between generations in the Hereford cattle they studied.

TABLE 8. COEFFICIENTS OF STANDARD PARTIAL AND PARTIAL REGRESSION OF DAUGHTER TRAITS ON AVERAGE LIFETIME MILK YIELD OF THE ANGUS AND HEREFORD DAMS

Cow traits	Standard Partial Regression	Partial Regression
	ANGUS	
Weaning weight (3)[a]	0.25	7.99
Weaning grade (5)	0.06	0.05
Yearling weight (6)	0.37	19.00
32-month weight (7)	0.14	7.14
Average milk yield (4)	0.12	0.14
	HEREFORD	
Weaning weight (3)	0.10	2.89
Weaning grade (5)	0.30	0.25
Yearling weight (6)	0.20	11.98
32-month weight (7)	0.22	13.35
Average milk yield (4)	-.27	-.30

[a] trait code number in parentheses

They found that cows receiving a good preweaning environment tended to provide a poor environment for their offspring, who, in turn, provided the next generation a good environment. Totusek (1968) reported that early weaned Angus and Hereford cows produced heavier calves at weaning than normally-weaned and creep-fed normally-weaned cows. The weaning weight of Hereford cows was negatively associated with subsequent milk yield in a study by Christian, Hauser and Chapman (1965b). The conclusion of all these studies has been that high levels of preweaning nutrition tend to limit subsequent milking ability. Fat deposition in the udder, as found by Swanson (1957) in dairy heifers fattened until 24 months of age, is generally considered a limiting factor on mammary development. Other research reviewed by Swanson (1967) indicates no significant effect on milk yield due to variable nutritional levels within the normal range for developing dairy heifers. A slight, long-range production benefit from low-level feeding was indicated by the work of Crichton, Aitken and Boyne (1960).

Excessive fat in the calves was not an apparent problem under the conditions of this study. The positive association between milk yield of Angus dams and daughters indicated that such a negative effect was not a problem in the Angus herd. Angus calves observed during this study were fatter at weaning than Hereford calves as indicated by ultra-sonic backfat measurements. These findings suggest that the response of the two breeds to early environment may differ. This possibility is supported by a smaller standard partial regression of weaning grade on milk yield of 0.06 for the Angus as compared with 0.30 for the Hereford (table 8). The Hereford could be more susceptible to udder fat deposition, or the negative association may be the result of a beneficial effect from the low levels of nutrition as suggested by Crichton, Aitken and Boyne (1960). These authors reasoned that increased rumen development in cattle on the low nutritional level may have enhanced subsequent production.

The influence that the direct effect of milk yield on daughter milk yield may have had on other reciprocal correlations and the resulting estimates of direct milk yield effect and genetic covariances was not determined.

Estimates of direct milk yield effect on progeny growth traits (table 8) for the Angus were highest for the various weights, while being low for weaning grade. The Hereford estimates differed little from the Angus results except for weaning grade which was much higher. Apparently the positive effect of milk yield on preweaning traits is maintained to maturity, possibly due to early structural development. These effects might be compared most easily in the partial regression coefficients which express how many pounds or grades a growth trait changes for each pound change in average milk yield.

Regression coefficients for growth traits on milk yield which have been previously reported were estimated on milk yield and growth records resulting from the same lactation. Therefore, these previously reported coefficient estimates should be larger than those of this study which resulted from milk yield and growth records stemming from different lactations. The differences of the estimates would be a function of the repeatability of milk yield records as defined in the procedures. The previous estimates could be biased either upward or downward by the genetic effects which were not removed as they were in the present study.

Drewry, Brown and Honea (1959) reported standard partial regression coefficient estimates of 0.17, 0.60 and 0.50 for cumulative preweaning gain on milk yield at the first, third and sixth month of lactation. Estimates of partial regression coefficients of preweaning and postweaning growth triats on 100-pound units of 240-day milk yield of Hereford cows on three levels of nutrition were reported by Neville (1962) and Neville et al. (1962), respectively. The ranges of these estimates for weaning weight, slaughter weight and slaughter grade were 4.33 to 8.03, 4.18 to 9.01 and 0.005 to 0.072, respectively. The lower values of each range tended to be associated with cattle on the highest level of nutrition. Using the conversion factors utilized by Neville et al. to estimate 240-day milk yield from 14-hr milk yield, it can be shown that a one-pound unit of the present 16-hr milk yield is equivalent to approximately three 100-pound units used in the Neville studies. Therefore, the Neville and Neville et al. partial regression coefficients should be multiplied by approximately three for comparison with the current estimates.

The partial regression coefficients shown in table 8 are approximately 1/4 to 1/2 the magnitude of other published values when corrected to comparable units. However, the relative effect observed at various ages is similar. Response of weaning weight to milk yield was maintained to 32-month weight in this study and to slaughter weight in the study by Neville et al. (1962). Simple correlation coefficients reported by Gifford (1953) between milk yield and offspring weight at 8, 12, 24 and 36 months were highly significant through the 36th month, indicating a continuing association to maturity. The response of Angus grade to milk yield was comparable to that of the study by Neville et al. Grade score for Hereford was influenced more by milk yield in the present study than was the score for Angus.

Genetic covariance estimates are listed in table 9. Due to the relatively small number of daughter-dam pairs utilized and the absence of a suitable statistical test of significance, the degree of reliability of these results is not known. Nevertheless, it is of interest that the sign of the covariance estimates obtained from the daughter-dam data tend to agree within breeds with the estimates

TABLE 9. ESTIMATES OF THE GENETIC COVARIANCE BETWEEN AVERAGE MILK YIELD AND GROWTH TRAITS OF THE ANGUS AND HEREFORD COWS

Growth traits	Average Milk Yield (4)[a] $Cov_{G_4G_i}$
ANGUS	
Weaning weight (3)	0.0230
Weaning grade (5)	0.4536
Yearling weight (6)	-.2062
32-month weight (7)	0.1228
HEREFORD	
Weaning weight (3)	-.0190
Weaning grade (5)	-.6654
Yearling weight (6)	0.0092
32-month weight (7)	-.4714

[a] trait code number in parentheses

from the half-sib data. The one exception in both breeds is that of yearling weight.

The combined results of the half-sib and the daughter-dam analyses tend to suggest a positive genetic relationship between milk yield and growth traits in Angus cattle, while the relationship may be negative in Hereford cattle. Even though firm conclusions cannot be drawn from these results due to the large standard errors, these findings should elucidate the need for further research before general conclusions are made concerning the genetic association between growth and milk yield in beef cattle.

Summary

The objectives of this study were to estimate environmental effects on milk yield of beef cows, to estimate genetic parameters associated with milk yield and cow growth traits and to estimate the direct effects of average lifetime milk yield on all traits studied.

Milk yield data (the mean of three within lactation observations obtained by the calf-nursing method after an average 16-hr separation) were recorded in 1969 and 1970 for 262 and 201 lactations, respectively, of 162 Angus cows by 46 sires and 137 Hereford cows by 39 sires. The data were analyzed by the least-squares method to estimate significant environmental effects within each breed. Genetic analyses were made from the milk yield data adjusted for these

significant environmental effects. The Angus data were adjusted for the effect of cow age ($P<.01$) and the effect of sex of calf nursed ($P<.01$). Hereford milk yield data were adjusted for the effect of cow age ($P<.05$). The cow growth traits, birth weight, weaning weight, weaning grade, yearling weight and 32-month weight were obtained from the station records. These growth trait records were utilized in the genetic analyses without adjustment, except for weaning weight which had been previously adjusted for cow and calf age.

The adjusted milk yield data of each breed were subjected to separate nested analyses of variance, nesting sires within cow origin, cows within sire and records within cow, to obtain heritability and repeatability estimates by the intraclass correlation method. Heritability of milk yield was estimated to be $0.10 \pm .18$ and $0.03 \pm .21$, respectively, for the Angus and Hereford cows. Corresponding estimates of repeatability were $0.22 \pm .10$ and $0.49 \pm .09$, respectively.

Milk yield records (one or two in number) were averaged for each cow to obtain average milk yield per cow. Average milk yield and the growth traits were subjected to a nested analysis of variance and covariance, nesting sires within cow origin and cows within sires, to obtain components for estimating heritability and genetic, phenotypic and environmental correlation coefficients by the half-sib method. Heritability estimates for average milk yield, birth weight, weaning weight, weaning grade, yearling weight and 32-month weight were 0.14±.30, 0.56±.33, 0.71±.34, 0.40±.32, 1.54±.34 and 0.94±.34, respectively, for the Angus cows and 0.13±.33, 0.73±.37, 0.04±.32, 0.71±.37, 1.46±.37 and 0.80±.37, respectively, for the Hereford cows. Coefficients of correlation between milk yield and the above growth traits, respectively, were as follows from the Angus data: 0.68±.83, 0.47±0.76, 2.39±2.23, 1.22±1.06 and 1.98±1.60 for genetic correlations; 0.13±0.09, 0.05±0.06, -.01±0.01, 0.11±0.05 and 0.24±0.05 for phenotypic correlations; and -.10±0.39, -.20±0.48, -.81±0.44, -.26±0.15 and -2.07±6.21 for environmental correlations. For the Hereford, corresponding coefficients were -.73±1.14, -6.75±25.94, -1.45±1.60, -.34±0.71 and -.08±0.77 for genetic correlations; -.07±0.07, -.05±0.03, 0.08±0.11, 0.06±0.63 and 0.12±0.21 for phenotypic correlations; and 0.32±0.60, 0.47±0.32, 1.04±0.86, 0.19±0.26 and 0.34±0.64 for environmental correlations.

An indirect daughter-dam correlation method utilizing reciprocal phenotypic correlations and the path coefficient concept was developed to estimate genetic covariance between milk yield and growth traits and to estimate the direct effects of average lifetime milk yield on all traits. These estimates were obtained from 49 Angus and 45 Hereford daughter-dam pairs. Estimates of genetic covariance between average milk yield and the growth traits, weaning weight, weaning grade, yearling weight and 32-month weight were 0.02, 0.45, -.21 and 0.12, respectively, for the Angus cows and -.02, -.67, 0.01 and -.47, respectively, for the Hereford cows. Estimates of the direct effects of average lifetime milk yield on daughter milk yield, weaning weight, weaning grade, yearling weight and 32-month weight, expressed as standard partial regression coefficients, were 0.12, 0.25, 0.06, 0.37 and 0.14, respectively, for the Angus cows and -.27, 0.10, 0.30, 0.20 and 0.22, respectively, for the Hereford cows. Corresponding partial regression coefficients were 0.14, 7.99, 0.05, 19.00 and 7.14, for the Angus,and -.30, 2.89, 0.25, 11.98 and 13.35 for the Hereford.

Milk yield appears to be only slightly heritable as measured in this study; repeatability of milk yield performance is moderate to low and the genetic association between milk yield and growth is uncertain, but not statistically different from zero. A positive relationship is suggested in the Angus cattle, while the association appears to be negative in the Hereford. The direct effects of milk yield on growth is positive and relatively constant from weaning to mature weight. An antagonistic effect of dam milk yield and daughter milk yield was indicated in the Hereford, while the effect was positive in the Angus. Even though firm conclusions cannot be drawn from these results due to the large standard errors, the findings should elucidate the need for further research before general conclusions are made concerning the genetic association between growth and milk yield in beef cattle.

APPENDIX

TABLE 1A. SUBCLASS MEANS FOR MILK YIELD OF ANGUS COWS

Classification	Number of Observations	Milk Yield (Pounds)
Total	262	5.66
Year of record		
1969	119	5.80
1970	143	5.54
Sex of calf		
Male	138	6.00
Female	124	5.28
Year x sex		
1969 - Male	59	6.28
1969 - Female	60	5.34
1970 - Male	79	5.78
1970 - Female	64	5.22
Origin of cow		
Introduced	68	5.33
Local	194	5.78

TABLE 2A. SUBCLASS MEANS FOR MILK YIELD OF HEREFORD COWS

Classification	Number of Observations	Milk Yield (Pounds)
Total	201	5.51
Year of record		
1969	105	5.51
1970	96	5.50
Sex of calf		
Male	110	5.57
Female	91	5.44
Year x sex		
1969 - Male	60	5.64
1969 - Female	45	5.36
1970 - Male	50	5.48
1970 - Female	46	5.52
Origin of cow		
Miles City introduced	48	5.39
Miles City local	81	5.29
Brooksville local	72	5.82

TABLE 3A. LEAST-SQUARES ANALYSIS OF VARIANCE OF MILK YIELD FOR THE ANGUS COWS

Source	df	Means Squares	F
Total	261		
Year of record	1	6.6300	3.21
Sex of calf	1	20.9433	10.14**
Year x sex	1	1.2165	0.59
Age of cow			
-Linear	1	29.3026	14.19**
-Quadratic	1	20.8495	10.09**
Calf age at first collection			
-Linear	1	1.2024	0.58
-Quadratic	1	2.1320	1.03
Average separation interval			
-Linear	1	0.0386	0.02
-Quadratic	1	0.0498	0.02
Remainder	252	2.0657	

** ($P<.01$)

TABLE 4A. LEAST-SQUARES MEAN, CONSTANTS AND STANDARD ERRORS FOR MILK YIELD OF THE ANGUS COWS

Classification	Number of Lactations	Constant	Standard Error
Mu	262	5.66	0.09
Year of record			
1969	119	0.18	0.14
1970	143	-.18	0.13
Sex of calf			
Male	138	0.33	0.13
Female	124	-.33	0.14
Year x sex			
1969 - Male	59	0.07	0.19
1969 - Female	60	-.07	0.22
1970 - Male	79	-.07	0.18
1970 - Female	64	0.07	0.18
Partial regression coefficients			
Age of cow			
-Linear		0.6092	0.1618
-Quadratic		-.03638	0.01145
Calf age at first collection			
-Linear		0.0392	0.0514
-Quadratic		-.00029	0.00028
Average separation interval			
-Linear		-.7433	5.4406
-Quadratic		0.02676	0.17236

TABLE 5A. LEAST-SQUARES ANALYSIS OF VARIANCE FOR MILK YIELD OF THE HEREFORD COWS

Source	df	Mean Squares	F
Total	200		
Year of record	1	1.4687	0.72
Sex of calf	1	0.0690	0.03
Year x sex	1	0.0001	0.00
Age of cow			
-Linear	1	12.1722	5.97*
-Quadratic	1	7.9811	3.92*
Calf age at first collection			
-Linear	1	0.0046	0.00
-Quadratic	1	0.0080	0.00
Average separation interval			
-Linear	1	1.8994	0.93
-Quadratic	1	1.5778	0.77
Remainder	191	2.0388	

* ($P<.05$)

TABLE 6A. LEAST-SQUARES MEAN, CONSTANTS AND STANDARD ERRORS FOR MILK YIELD OF THE HEREFORD COWS

Classification	Number of Lactations	Constant	Standard Error
Mu	201	5.49	0.10
Year of record			
1969	105	0.18	0.23
1970	96	-.18	0.24
Sex of calf			
Male	110	0.02	0.14
Female	91	-.02	0.16
Year x sex			
1969 - Male	60	-.00	0.23
1969 - Female	45	0.00	0.32
1970 - Male	50	0.00	0.29
1970 - Female	46	-.00	0.27
Partial regression coefficients			
Age of cow			
-Linear		0.5430	0.2222
-Quadratic		-.03376	0.01706
Calf age at first collection			
-Linear		-.0026	0.0545
-Quadratic		0.00002	0.00034
Average separation interval			
-Linear		2.3084	2.3966
-Quadratic		-.06603	0.07506

TABLE 7A. MEANS AND STANDARD ERRORS FOR THE CONTINUOUS VARIABLES INCLUDED IN THE ENVIRONMENTAL ANALYSES OF THE ANGUS AND HEREFORD COWS

Variable	Mean	Standard Error
	ANGUS	
Age of cow	5.34	2.70
Calf age at first collection	95.91	16.14
Average separation interval	15.53	0.67
	HEREFORD	
Age of cow	5.72	2.47
Calf age at first collection	88.27	15.26
Average separation interval	16.01	1.25

TABLE 8A. NUMBER OF LACTATIONS BY AGE OF COW AND BREED

Age	Number of Lactations: Angus	Number of Lactations: Hereford
Total	262	201
3	91	57
4	52	25
5	23	18
6	21	28
7	21	24
8	17	17
9	10	13
10	9	11
11	9	6
12	4	2
13	3	0
14	2	0

TABLE 9A. NESTED ANALYSES OF VARIANCE FOR MILK YIELD RECORDS OF THE ANGUS AND HEREFORD COWS

Source	df	SS	MS	F[a]	EMS
			ANGUS		
Total	261				
Origin	1	0.2901	0.2901	0.18	$V_w + 2\Theta_o^2$
Sires/Origin	44	115.0036	2.6137	1.13	$V_w + 1.67V_c + 5.60V_s$
Cows/Sire/Origin	116	264.9694	2.2842	1.40*	$V_w + 1.59V_c$
Within Cows	100	162.6576	1.6265		V_w
			HEREFORD		
Total	200				
Origin	2	21.4073	10.7037	10.99**	$V_w + 3\Theta_o^2$
Sires/Origin	36	89.8246	2.4951	1.03	$V_w + 1.57V_c + 5.05V_s$
Cows/Sire/Origin	98	224.8575	2.2945	2.36**	$V_w + 1.43V_c$
Within Cows	64	62.3497	0.9742		V_w

[a] F test made based on ratios indicated by EMS * ($P < .05$) ** ($P < .01$)

TABLE 10A. LEAST-SQUARES NESTED ANALYSES OF SIRE VARIANCE WITHIN ORIGIN OF COW FOR EACH COW TRAIT OF THE ANGUS AND HEREFORD COWS

Source	df	Average Milk Yield		Birth Weight		Weaning Weight	
		MS	F	MS	F	MS	F
ANGUS[a]							
Total	161						
Origin	1	3.749	2.60	5.927	0.17	567.03	0.43
Sires/Origin	44	1.625	1.13	62.054	1.56*	2278.03	1.73*
Within Sires	116	1.444		39.853		1313.52	
HEREFORD[b]							
Total	136						
Origin	2	6.717	4.07*	739.932	11.76**	10909.55	6.35**
Sires/Origin	36	1.833	1.11	109.540	1.74*	1774.54	1.03
Within Sires	98	1.649		62.947		1718.84	

TABLE 10A. (CONTINUED)

Source	df	Weaning Grade		Yearling Weight		32-month Weight	
		MS	F	MS	F	MS	F
ANGUS							
Total	161						
Origin	1	7.085	8.85**	1820.26	0.71	16025.52	5.07*
Sires/Origin	44	1.215	1.38	8057.49	3.14**	6447.56	2.04**
Within Sires	116	0.880		2568.13		3158.29	
HEREFORD							
Total	136						
Origin	2	0.523	0.68	20767.48	5.44**	2096.87	0.41
Sires/Origin	36	1.317	1.72*	11115.68	2.91**	9311.05	1.83**
Within Sires	98	0.766		3819.00		5081.16	

[a] k = 3.4127 * (P<.05)
[b] k = 3.3381 ** (P<.01)

TABLE 11A. COMPONENTS OF VARIANCE AND COVARIANCE FOR AVERAGE MILK YIELD AND COW GROWTH TRAITS OF THE ANGUS AND HEREFORD COWS

Cow traits	Variance		Covariance	
	V_{s_i}	V_{w_i}	Cov_{si}	Cov_{wi}
	ANGUS			
Average milk yield (4)[a]	0.0531	1.4435	---	---
Birth weight (1)	6.5053	39.8527	0.3995	0.7096
Weaning weight (3)	282.6204	1313.5229	1.8168	0.5024
Weaning grade (5)	0.0981	0.8802	0.1725	-.1866
Yearling weight (6)	1608.4882	2568.1291	11.3083	-2.9520
32-month weight (7)	963.8200	3158.2858	14.1902	4.3051
	HEREFORD			
Average milk yield (4)	0.0552	1.6488	---	---
Birth weight (1)	13.9581	62.9468	-.6404	-.1127
Weaning weight (3)	16.6840	1718.8449	-6.4814	3.9866
Weaning grade (5)	0.1653	0.7656	-.1388	0.2430
Yearling weight (6)	2185.9063	3818.9982	-3.7566	9.3772
32-month weight (7)	1267.1716	5081.1616	-.6702	12.9599

[a] trait code number in parentheses

TABLE 12A. MEANS, STANDARD DEVIATIONS AND COEFFICIENTS OF VARIATION FOR AVERAGE MILK YIELD AND GROWTH TRAITS OF 162 ANGUS AND 137 HEREFORD COWS

Cow traits	Mean	Standard Deviation	Coefficient of Variation
	ANGUS		
Average milk yield (4)[a]	5.64	1.22	0.22
Birth weight (1)	54.69	6.77	0.12
Weaning weight (3)	369.23	39.64	0.11
Weaning grade (5)	12.04	0.98	0.08
Yearling weight (6)	649.93	65.47	0.10
32-month weight (7)	858.65	63.70	0.07
	HEREFORD		
Average milk yield (4)	5.48	1.33	0.24
Birth weight (1)	67.64	9.89	0.15
Weaning weight (3)	381.87	44.38	0.11
Weaning grade (5)	11.38	0.97	0.09
Yearling weight (6)	682.28	77.84	0.11
32-month weight (7)	954.49	78.81	0.08

[a] trait code number in parentheses

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BIOGRAPHICAL SKETCH

James Ronald Dickey was born July 21, 1934, at Bay City, Texas. In June, 1952, he was graduated from Bay City High School. In June, 1957, he received the degree of Bachelor of Science with a major in Animal Husbandry from Texas A & M University. Between 1957 and 1963 he served a year and a half as show and sales herdsman for Winrock Farms at Morrilton, Arkansas, three years as classifier for the Santa Gertrudis Breeders International at Kingsville, Texas and a year and a half as consultant and technical advisor for the Associacao Brasileira de Santa Gertrudis at Sao Paulo, Brazil. In 1963 he enrolled in the Graduate School of Texas A & M University. He worked as a graduate assistant and shepherd in the Department of Animal Science until June, 1964. He then accepted the position of livestock specialist for Texas Power and Light Company at Dallas, Texas where he worked and continued his research until 1966. In 1966 he received the Master of Science with a major in Animal Breeding. From 1966 until 1968 he served under a Texas A & M University contract as livestock production advisor to the Secretary of Agriculture of the Dominican Republic at Santo Domingo. From September, 1968, until the present time, he has been an N. D. E. A. Title IV Fellow in the University of Florida

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James R. Dickey is married to the former Mary Ann Anthony and is the father of five children. He is a member of Alpha Zeta, the American Society of Animal Science and the American Genetic Association.

I certify that I have read this study and that in my opinion it conforms to acceptable standards of scholarly presentation and is fully adequate, in scope and quality, as a dissertation for the degree of Doctor of Philosophy.

Marvin Koger

Marvin Koger, Chairman
Professor of Animal Science

I certify that I have read this study and that in my opinion it conforms to acceptable standards of scholarly presentation and is fully adequate, in scope and quality, as a dissertation for the degree of Doctor of Philosophy.

Donald E. Franke

Donald E. Franke, Co-chairman
Asst. Professor of Animal Science

I certify that I have read this study and that in my opinion it conforms to acceptable standards of scholarly presentation and is fully adequate, in scope and quality, as a dissertation for the degree of Doctor of Philosophy.

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I certify that I have read this study and that in my opinion it conforms to acceptable standards of scholarly presentation and is fully adequate, in scope and quality, as a dissertation for the degree of Doctor of Philosophy.

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I certify that I have read this study and that in my opinion it conforms to acceptable standards of scholarly presentation and is fully adequate, in scope and quality, as a dissertation for the degree of Doctor of Philosophy.

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