The effect of dam milk production on daughter maternal ability in Hereford cattle
by William Andrew Reed

A thesis submitted in partial fulfillment of the requirements for the degree of Master of Science in Animal Science
Montana State University

Abstract:
The selection of replacement beef heifers based on their weaning weight performance has been inaccurate due to a demonstrated negative correlation between preweaning gain and maternal performance as measured by amount of calf produced at weaning. Milk production has been shown to be an important component of maternal performance. It was the objective of this thesis to investigate the role of milk production in the negative correlation between dam and daughter maternal ability.

The data set contained 880 cow/calf records from Hereford cows and calves located at the Northern Agricultural Research Center near Havre, Montana from the years 1970 to 1987 and included milk production measurements and calf weaning weights. Milk production was measured during two periods. The first averaged 39 d and the other averaged 131 d postpartum. Milk productions and weaning weights were tested for the effects of year, age of cow, sex of calf and age of calf and adjusted for those effects found to be significant. Production was then averaged over years for each cow. Correlations between weaning weight and milk production variables were calculated. They were found to be positive. Data were organized into 67 dam-daughter-granddaughter sets and the maternal lines grouped by relative milk production or weaning weight production of generation 1 cows into high, moderately high, moderately low and low groups. The groups were then compared between generations and between groups and trends noted. The data were reorganized into 171 dam-daughter sets and correlations and regressions were calculated.

Analyses of the three generation data subset revealed a trend of dams with above average milk production producing daughters with below average milk production and dams with below average milk production produced daughters with above average milk production. Regressions of daughter traits on dam traits performed on the two generation data subset were generally not significantly different from zero.

Combined results from all analyses, however, indicated that dam milk production had a negative effect on daughter milk production and daughter weaning weight produced. The data also suggested that the dam's second milk production period had more influence on the daughter's subsequent maternal ability than did the first milk production period.

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MATERNAL ABILITY IN HEREFORD CATTLE

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William Andrew Reed

This thesis has been read by each member of the thesis committee and has been found to be satisfactory regarding content, English usage, format, citations, bibliographic style, and consistency, and is ready for submission to the College of Graduate Studies.

7/27/88 D D Kress

Date Chairperson, Graduate Committee

Approved for the Major Department

7-28-88

Date Head, Major Department

Approved for the College of Graduate Studies

August 10, 1988 Henry L Parsons

Date Graduate Dean

STATEMENT OF PERMISSION TO USE

Signature William C. Reid

Date July 28, 1988

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ABSTRACT

The selection of replacement beef heifers based on their weaning weight performance has been inaccurate due to a demonstrated negative correlation between preweaning gain and maternal performance as measured by amount of calf produced at weaning. Milk production has been shown to be an important component of maternal performance. It was the objective of this thesis to investigate the role of milk production in the negative correlation between dam and daughter maternal ability.

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INTRODUCTION

Commercial producers who sell beef calves at weaning by weight or purebred breeders trying to attain the most rapid gain in calves to a year of age are under economic pressure to provide a preweaning environment which can produce high weaning weights. Improved pasture management (Holloway et al., 1979; Holloway and Butts, 1983), creep feed (Cross, 1983), and dams with higher milk production (Clutter and Nielsen, 1987) have been effective in achieving this goal. However, there is evidence that high preweaning gain in heifer calves can have a detrimental effect on their subsequent production for amount of calf weaned. A negative effect of high preweaning gain due to environment on subsequent weaning weight production also reduces the ability to accurately select replacement individuals of high genetic merit for calf weaning weight. In the applied sense, this makes selection of beef replacement females by weaning weight very difficult.

The preweaning environment provided by the dam has been termed "maternal effect" and is realistically measurable only in the phenotype of her offspring (Willham, 1972b). However, research has shown that milk production is a major portion of the maternal effect (Neville, 1962; Rutledge et al, 1971; Clutter and Nielsen, 1987). This portion of the maternal effect can be measured directly.

The objective of this study was to investigate the role of milk production in the demonstrated negative correlation between dam and daughter weaning weight performance (Mangus and Brinks,1971; Kress and Burfening, 1972).

LITERATURE REVIEW

General

Maternal effects have been recognized for centuries as an important factor in the growth and health of young mammals (Robison, 1981) but they have been identified with certain negative correlations only within the past 35 years. A negative correlation between litter size of rearing and litter size produced has been demonstrated in mice (Falconer, 1960) and swine (Revelle and Robison, 1973). Ahlschwede and Robison (1971a, 1971b), using crossfostering techniques, reported numerous negative correlations between direct and maternal effects for swine traits including backfat thickness and preweaning rate of gain after the fifth week postpartum.

Crossfostering is the technique of separating two dams and offspring immediately after birth and allowing them to raise each other's offspring. It has not been feasible with beef cattle (Koch, 1972), so other methods have been employed to estimate maternal effects. Work with reciprocal crosses by Gaines et al. (1966), Gregory et al. (1965) and Pahnish et al. (1969) demonstrated significant breed differences for weaning weight. This would indicate that there are differences in maternal ability among breeds.

Quantification of the maternal effect, however, requires study of relationships between relatives. The correlation of maternal half sibs with paternal half sibs and comparison of actual values with theoretical values gives an estimate of the maternal effect acting on the trait in question. A large maternal half sib correlation compared to a smaller paternal half sib correlation suggests a large maternal effect (Koch, 1972).

Relationship Between Dam Milk Production and Their Calf's Weaning Weight

The positive correlation between dam milk production and calf preweaning gain or calf weaning weight has been well established. Correlating calf weight with milk production at five different stages of lactation, Kress and Anderson (1974) calculated a value of 0.49. Christian et al. (1965) found significant simple correlations between milk yield and butterfat production and weaning weight of calf. Correlations of 0.46 and 0.48 between weaning weight of calf and milk yield per d at 0 to 60 and 60 to 240 d postpartum , respectively, were reported. When the effects of birth weight, creep feed consumption and sex of calf were accounted for, however, milk yield ceased to be significant and butterfat production from 0 to 60 days was the only significant milk production trait. Hand milking one side of the udder while the calf nursed on the other was the method used to measure milk production. Neville (1962) reported correlations between milk production and daily gain ranging from 0.74 to 0.59 over a 240 d lactation period. The highest correlation occurred during the first 60 d postpartum, and the lowest occurred at 180 d postpartum. Daley et al. (1987), in a study of Bos indicus cross cattle, reported correlations at 60, 105 and 150 d postpartum of 0.45, 0.36 and 0.41, respectively. Totusek et al. (1973) found a very high correlation (0.88) for calf weight at 210 d and daily milk production to 210 d postpartum, while Chenette and Frahm (1981) found a much lower (but still positive) correlation (0.20) for the same relationship. Positive correlation between milk traits and birth to preweaning weight traits have also been reported for sheep (Slen et al., 1963) and goats (Ehoche et al., 1983; Misra et al., 1985).

A trend was evident in studies which sampled milk production several times during lactation. Early milk production was most highly correlated to weaning weight followed by a drop to relatively low correlation anytime between 100 d (Daley et al, 1987) and 180 d (Neville, 1962) postpartum. Melton et al. (1967) showed a significant correlation between average daily milk yield and average daily gain only during the first 77 d postpartum (0.58) followed by a decline to 0.01 at 137 d and an insignificant increase to 0.27 by 196 d of age.

When comparing gains within periods to milk intake within period for range cattle, Ansotegui (1986) found a significant correlation only for gain and milk intake over the entire period 66 d to 153 d of age and then for only one of the two study years (1984). He attributed the lack of correlation within periods of lactation and overall time, birth to weaning, in the second year (1985) to the compensatory forage intake by calves nursing poor milking dams. He did note an increase in milk intake in 1984 at approximately 140 d postpartum although the level was not significantly different (P>.10) from the previous period.

Day et al. (1987) reported a negative regression of nursing behavior of calves on milk production of dam. They found a decrease of

0.0038 nursing bouts per kg of milk produced. They speculated from their data and subjective observations that calves suckling cows producing low levels of milk were eating more forage.

It is likely that calf feeding behavior contributed to the wide range in correlations between milk production and weaning weight in the literature. It has been demonstrated in swine that baby pigs from large litters eat creep feed earlier and in larger amounts than do baby pigs from small litters (Robison, 1981). Preweaning gain of calves on good pasture was higher than that of their contemporaries on poor pasture even though dam milk production did not differ between the two groups (Holloway et al., 1979). Thus estimates of maternal ability could be made less accurate by feeding behavior differences among calves.

Preweaning Nutritional Levels and Maternal Ability

Negative correlations of dam preweaning gain (or weaning weight) with calf weaning weight produced has been demonstrated by several researchers. In 1960, Swanson reported on a study using identical twin Jersey and Jersey cross females reared on diets formulated to produce normal gain (controls) and high gain with fattening until first parturition. The high gain group gained much faster than the normal gain group to 11 mo of age, then nearly the same to 14 mo and at an increasingly greater rate from 14 to 24 mo of age when they began calving. At that time, twins were put on identical diets. At 24 mo, the fattened group weighed 409 kg and the controls 310 kg, a difference of 99 kg. Although not all twins were started on the study at the same age, the high gain group produced less milk over two lactations than their normal gain sisters. The high gain group yielded 5.5 and 6.8 kg/d of milk and the control group yielded 6.6 and 7.5 kg/d of milk during 245 d lactations for their first and second lactations, respectively. Examination of dissected udders at the conclusion of the trial revealed voids in the tissue of most members of the high gain group. The voids corresponded to areas normally filled with alveolar-secreting tissue. The normal gain group had normal udders. These data also suggested that earlier fattening depressed milk production more than later fattening (the twins were started on treatments anywhere from 4 to 12 mo of age). The numbers of cows, however, were too low to be conclusive on this point.

Swanson did not believe that the entire difference between twins could have been caused by udder damage and hypothesized that weight changes during the first lactation could have been indicating metabolic differences. Fattened cows lost weight during the first lactation in a manner similar to mature heavy milking cows but did not convert that weight loss into milk, whereas, the control cows grew rapidly throughout this lactation. The weight difference at the end of the first lactation was only 34 kg in favor of the fattened group. Swanson indicated that differences in growth hormone levels during the first lactation could have been responsible for some of the differences between the two groups but that this factor should have disappeared by the second lactation.

Martin et al. (1981) reported results of a 21-yr study using creep feed in rearing Angus calves. They wrote, "creep feeding of replacement heifers had a detrimental effect on their performance as cows, as measured by number of calves weaned, calf birth weight, calf 120-d weight, calf 210-d weight, and lifetime productivity" even though they were heavier themselves at weaning than non-creep fed contemporaries.

An experiment performed in Australia by Johnsson and Obst (1980) on Hereford heifers revealed that high "preweaning" (to 8 mo) gain on diets consisting of milk replacers, grain, and hay resulted in no difference in weight at 14 mo of age but lower subsequent production of weaned calf weight and milk than those with low preweaning gain. A follow up study was conducted by Phillips et al. (1982). Heifers that gained 0.67 kg/d from 0 to 5 mo, 0.47 kg/d 5 to 8 mo and 0.56 kg/d 8 to 14 mo produced significantly more milk and weaned heavier calves than heifers that gained 0.68 and 0.67, 1.12 and 0.36, and 0.33 and 0.45 kg/d from 0 to 5, 5 to 8, and 8 to 14 mo, respectively. They concluded that low to moderate weaning weights and moderate to high premating weights produced heifers with good fertility and maternal ability.

Relationships Between Dam and Daughter

Mangus and Brinks (1971) followed most probable producing ability for weaning weight (MPPA) and weaning weight (WW) in maternal lines of Hereford cattle over four generations. When they partitioned the first generation into high, medium and low groups based on WW, they found that the high WW group produced calves with low WW which, in turn, produced calves with high WW. When MPPA was analyzed using the same grouping, the high WW group had an average MPPA for the first generation, high MPPA in the second generation and low MPPA in the third generation. It was postulated that the patterns seen were due to the nutritional intake of the preweaning calves. No milk production data was reported for this study set. Assuming the herd investigated by Mangus and Brinks had a dam milk production to calf weaning weight correlation somewhere near the average for the literature reviewed by Kress and Anderson (1974) of 0.55, milk intake could be assigned more specifically as a major agent responsible for the results. There is, in fact, evidence for this in their report. Females raised by young cows produced heavier calves at weaning than did those raised by normally heavier milking mature cows.

Koch (1972) described three paths in dam-daughter relationships which could contain the negative correlation demonstrated in the above examples. The first would have a negative environmental covariance between individual and maternal effects, i.e., an environment beneficial to phenotype for early growth would be detrimental to phenotype for maternal ability. The rearing data by Martin et al. (1981) and Swanson (1960) described above help elucidate this path. Further evidence was furnished through a study by Vesely and Robison (1971). Data on weaning weight and birth weight from Herefords were analyzed for heritability by three relationships: paternal half-sib, maternal half-sib and dam-offspring. Unless the covariance between additive genetic and maternal genetic effects is relatively high and negative, heritability estimates using dam-offspring analysis should be highest of the three since the relationship is closer between dam and offspring than between half-sibs. In an analysis of Holstein data, which, due to normal dairy rearing methods, contained no post-partum maternal effects, Van Vleck and Bradford (1966) found this to be the case for the first two lactations. (However, the differences between methods of estimation disappeared in the third lactation.) That was not the case for Vesely and Robison's (1971) data wherein calves were reared by their dams. Dam-offspring analysis instead yielded the lowest heritability estimate (0.31); paternal half-sib relationships gave the highest estimate (0.50). These finding would indicate that there is a negative covariance between additive genetic and maternal genetic effects.

Other research using similar methods supported the findings of Vesely and Robison (1971). Koch (1972) reviewed four reports published between 1955 and 1971 and found all negative values and an average value of -.55 for the genetic correlation between maternal and direct effects (r_G). Bertrand and Benyshek (1987) reported a covariance between direct and maternal effects for Limousin and Brangus cattle to be -.17 and -.39, respectively. Cantet et al. (1988) found estimates of r_G between -.57 and -.79 from analyses of Hereford data.

Irgang et al. (1985) studying effects of selection on two Hereford lines, one chosen for high preweaning growth and the other for postweaning growth, found that both selection criteria resulted in increased herd average milk production and concluded that r_G was positive. They felt the positive value agreed with Sejrsen (1978) who postulated that since high growth rates are associated with high levels of growth hormone which increased udder tissue growth, it should result in higher milk production. Dickey et al. (1972) used reciprocal daughter-dam correlation coefficients between dam milk yield and daughter growth traits in Hereford and Angus cattle to obtain the corresponding genetic covariance estimates. They found positive genetic correlations for Angus and negative genetic correlations for Herefords between milk yield (a component of maternal ability) and pre- and postweaning weight gain.

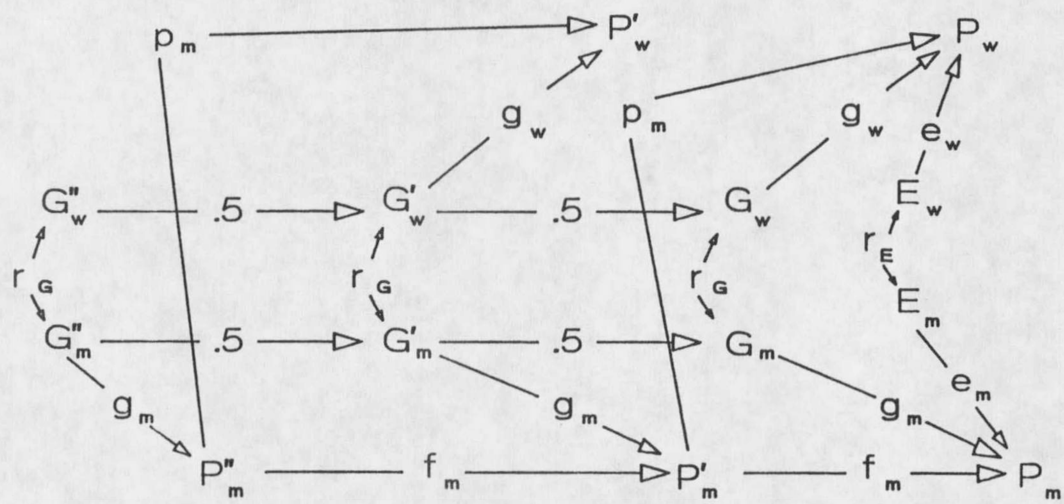
The possibility exists that dams having high genetic potential for depositing body fat have low genetic potential for either depositing fat in the milk or producing milk in high quantity (Willham, 1972a). Rutledge et al. (1971) concluded from a study with Herefords that fat proportion in milk had no significant effect on calf 205-d weight which implies that if Willham's hypothesis is basically sound, the effect must be on overall milk production.

The second path described by Koch (1972) involves a negative dominance deviation of individual and maternal effects. Few data have been analyzed which quantify this path. Koch (1972) was unable to isolate maternal dominance from permanent environmental effects in the data from Fort Robinson Beef Cattle Research Station , Nebraska when analyzed using paternal half-sib verses maternal half-sib estimates. Cantet et al. (1984) proposed that epistasis confounds the dominance covariance between direct and maternal effects.

The third path is a direct influence of dam maternal phenotype on daughter maternal phenotype which could be negative. Total evaluation of this path would require the summation of this effect over generations of maternal lines. Mangus and Brinks (1971) and Kress and Burfening (1972) showed that the negative influence of dam maternal phenotype on their daughter's subsequent maternal ability was environmental in origin. All environmental sources of variation tested by Kress and Burfening (1972) on relationships between various measures of early growth rate and subsequent MPPA (year of birth of cow, age of dam and regression on birth date) were negative. Mangus and Brinks (1971), using most probable producing ability for weaning weight (MPPA) as the dependent variable found birth year of cow, line of sire, actual weaning weight, and cow inbreeding to be significant effects using a model that also included age of dam, line of sire of dam and weaning age. Correlations of MPPA (most probable producing ability for weaning weight) with birth year of cow and cow inbreeding were negative. The correlation of MPPA with actual weaning weight was positive but small (0.026). The line of sire with MPPA correlation varied with line but they found a high positive relationship between actual weaning weight means and MPPA values by line of sire which suggested that concurrent increases could be made in these traits using sire line evaluation.

The third path deserves special attention when applied to livestock systems where females of the species provide the environment for raising the offspring. In order to select replacement females with high direct effects for preweaning gain, negative maternal effects must be accounted for. The contribution of dam maternal phenotype to daughter maternal phenotype by the direct path (f_m) (Falconer, 1965) (figure 1; after Koch, 1972) was estimated by Koch (1972) to be in the range of -.1 to -.2. He wrote, "such values lead to estimates of

Figure 1.
Relationships between dam and daughter.



Legend:

- E = environment
- G = genotype
- P = phenotype
- m = for maternal ability
- w = for weaning weight
- " = of grandam
- ' = of dam
- f_m = standard partial regression coefficient of offspring phenotype for for maternal ability on dam phenotype for maternal ability
- g_m = standard partial regression coefficient of phenotype for maternal ability on genotype for maternal ability
- g_w = standard partial regression coefficient of phenotype for weaning weight on genotype for weaning weight
- p_m = standard partial regression coefficient of offspring phenotype for weaning weight on dam phenotype for maternal ability
- r_E = the environmental correlation between direct and maternal effects
- r_g = the genetic correlation between direct and maternal effects

environmental covariance which satisfy observed correlations and regressions." (Koch, 1972) A recent estimate of f_m has been made by Cantet et al. (1988) using eighteen different (co)variances among relatives for birth weight and weaning weight. Their estimate of f_m for weaning weight was -.25, a more negative value than Koch's (1972) estimate. The genetic and environmental background of the cattle used by Cantet et al. (1988) was similar to that used in these analyses. Vesely and Robison (1971) did not explore the possibility of a negative f_m in their estimation of heritability by different relationships described above. Since f_m has no influence on paternal half-sib analysis but does on dam-offspring analysis, a negative value for f_m could account for their findings.

Other Factors Influencing Maternal Phenotype

Although they are beyond the scope of this thesis, two other factors associated with maternal effects, maternal transmission of substances either *in utero* or through milk and cytoplasmic inheritance, should not be ignored and could form the basis for further study. In cattle, it would seem that the greatest opportunity for substances in the milk to effect the calf would be within the first 48 hr after parturition when the digestive tract is less selective of compounds absorbed (Stormont, 1972). Immunity to organisms through colostrum is known to last at least 3 mo (Koger, 1972), so it is conceivable that other substances could be absorbed which could directly or indirectly effect rate of preweaning gain adversely or advantageously.

Tess et al. (1987) reported important differences in preweaning growth and milk production existed among maternal lines of Herefords in two herds in North Carolina higher milk production was responsible for higher preweaning growth. They cited several studies in dairy cattle including one by Bell et al. (1985), who used a similar statistical technique, which supported their conclusion that important cytoplasmic genetic effects may exist in beef cattle. Since mitochondria have been shown to be maternally inherited in humans (Giles et al., 1980) and rats (Hayashi et al., 1978) and are generally regarded as the power plants of the cell (Wagner, 1972), this could be related to the metabolic differences noted by Swanson (1960).

MATERIALS AND METHODS

Study Area and Feed Resources

The data used in this study were gathered at the Northern Agricultural Research Center (NARC) located 17.7 km southwest of Havre, Montana at 48°34'N latitude and 109°40'W longitude and at approximately 762 m above sea level. The cattle were held at this location from mid-autumn to late spring. During autumn, feed consisted of grazing on regrowth alfalfa/grass hay fields. Hay, corn silage, grass/alfalfa haylage and straw (both ammoniated and nonammoniated) were fed during winter. All were used in various combinations to provide a balanced ration based on the then current National Research Council (NRC) recommendations. In the spring, the cattle grazed range consisting of crested wheatgrass (*Agropyron desertorum* and *A. cristatum*) and some blue gramagrass (*Bouteloua gracilis*) and needle-and-thread (*Stipa comata*) (Williams, 1977).

From early June to weaning in early October cow/calf pairs were kept on leased summer range whose location changed through the years of the study. At weaning, calves were moved to NARC and cows remained on the summer range into November. From 1968 to 1975, the stock were grazed on the Rocky Boy Indian Reservation south-southwest of NARC. From 1976 to 1977, range on the Fort Belknap Indian Reservation 64 km south of Harlem, Montana was used. And from 1978 to 1987 mountain foothill range of the Webster Thackeray Ranch 24 km southeast of the research center near the northeast end of the Bear Paw Mountains was rented. The habitat on the Thackeray lease was of the rough fescue/bluebunch wheatgrass (Festuca scabrella/Agropyron spicatum) type with some ponderosa pine (Pinus ponderosa) overstory (Casebolt, 1984). Elevation is 1,300 m and average rainfall 48 cm per year (Funston, 1987).

Livestock

All cows and calves were straight bred Hereford. Foundation cows were born in 1968 and 1969 as the result of all possible reciprocal crosses and straightline matings of five closed lines of Herefords. Line 1 was polled and Lines 2 through 5 were horned. All lines were unrelated when they were initially closed and subsequent inbreeding resulted not from a deliberate effort to mate relatives but from genetic isolation of the lines. Inbreeding coefficients for lines 1 through 5 for sires and dams averaged 22 and 13, 12 and 11, 15 and 11, 4 and 2, and 7 and 10% respectively (Kress et al., 1979). The Havre line 4 herd resulted from the upgrade in 1939 of existing commercial Herefords at NARC using Miles City Line 1 bulls developed at the Livestock and Range Research Station, Miles City, Montana (Kress et al., 1979). Line 4 is currently being maintained at NARC and two maternal lines in this study came from that herd. Further details on the closed lines were described by Flower et al. (1963). The crossline herd is currently kept primarily for use as foundation and control animals in crossbreeding studies.

All heifers weaned were kept as replacements. Heifers were culled without producing a calf only if they were determined to be not pregnant by rectal palpation in October of their second year. Subsequent culling decisions were made based on pregnancy status, soundness and age. After 1971, Hereford bulls were selected from the Havre Line 4 herd and other herds available through artificial insemination on the basis of above average yearling weight.

All cows in this herd that had daughters with production records were evaluated for this thesis. The data set contained 880 individual calves born from 1970 to 1987 and 284 individual cows born from 1968 to 1985. There were 171 dam-daughter sets. Of the 171, 93 included a milk production measurement in early lactation (period 1), 95 included a milk production measurement in mid-lactation (period 2) and 170 included average weaning weight produced for both dam and daughter. In addition, 76 contained a dam milk production measurement during period 1 and 76 contained a dam milk production measurement during period 2 for years when their daughters who subsequently had these measurements were born. Also, there were 67 dam-daughter-granddaughter sets.

Data

Typically, data collected included birth weight, birth day, sex of calf at weaning (bull, steer or heifer), weaning weight, weaning day, calf condition score at weaning and two milk production measurements. The mean, standard deviation (SD), range and number of records (N) containing each variable are shown in table 1. These statistics are over all years. Within year variation for milk production data collected was not as great as it was overall. For example, the overall SD of age of calf during period 1 was 10.3 d; within years it averaged 8.7 d.

Table 1. Means, standard deviations (SD), ranges and numbers of records (N) for each variable in the data set.

Variable	Mean	SD	Min	Max	N
Cow age, yr	4.6	2.4	2	13	880
Calf birth wt, kg	36.0	5.7	19.5	54.4	877
Calf birth day, julian	92.6	16.1	40	138	880
Actual calf weaning wt, kg	185.8	28.2	97.7	261.4	876
Calf weaning day, julian	275	1.1	271	278	877
Calf cond. score at weaning, 1-9	5.8	1.1	1.5	8.7	713
Calf age at weaning, d	183	16.3	138	235	877
Separation time MP1, h	11.0	4.7	6.0	17.0	284
Calf age MP24HR1, d	39.0	10.3	14	80	412
MP24HR1, kg	7.3	2.5	0	17.2	367
Adj. MP1, kg	7.7	2.0	0.3	15.5	367
Separation time MP2, h	12.1	5.1	6	19	203
Calf age MP24HR2, d	131.0	14.0	83	160	350
MP24HR2, kg	4.7	2.3	0	20.0	367
Adj. MP2, kg	5.7	2.0	0.3	15.2	367

see page 63 for a glossary of variables.

Most records contained one or more missing measurements for some variable or variables. Rather than deleting entire records for these missing values, SAS (1985), the computer statistical package used for all analyses, assigned a "." to that variable for that record and ignored the record for any calculation involving the missing value. The program was able to use, therefore, incomplete records whenever needed variables were present.

Milk production data were collected from 1972 to 1987 with the exception of 1979. From 1976 to 1987, milk production was measured twice during a lactation targeting 20 to 50 d (MP1) and 110 to 150 d (MP2) postpartum for the first and second measurements, respectively. Although the mean age some years fell outside these ranges, there were approximately 90 d between tests in all years. During the earlier years of data collection, more than two tests were performed during a lactation. In some cases, two tests, one above and one below the target range, were averaged to get an estimate of the milk production at a time consistent with the later data. The lactation curve for Hereford cows reported by Kress and Anderson (1974) supports the feasibility of a linear estimate between points close to the limits of the target ranges. Table 2 shows those years and values which were estimated from more than one test.

Table 2. Number of tests used for each milk production period.

Year	Period 1	Period 2
1972	1	2
1973	1	2
1974	2	2
1975–1987	1	1

All milk production was estimated using the weigh-suckle-weigh technique. Calves were separated from their dams for a specified period, the separation time (SEPTIME). They were then weighed individually, returned to their mother to nurse until the udder appeared empty, and immediately reweighed. The change in weight was attributed to milk ingested. Calves were observed between weighings and any seen to urinate or defecate were noted. The cattle were handled in groups of 8 to 15 to minimize the time each calf spent in the chute waiting to be weighed and maximize the number tested per day. Day of test was chosen to avoid rain, muddy conditions or other factors which would affect accuracy.

Separation time ranged from 6 to 19 h over the course of the study. Within year variation was much less. Separation times of over 14 h were common up to 1977. At that time, results of a study (Williams et al., 1979a), using some of the same data used in this thesis, on effects of separation interval on weigh-suckle-weigh milk production estimates became available. It was concluded a 16-h separation time significantly underestimated milk production and 8-h separation time gave the best overall estimate of calf milk intake when considering natural nursing behavior, stress to the cow and calf, udder distention and precision of measurement. From 1977 to 1987, therefore, separation time was held to less than 11 h, 6 or 7 h being the most common. All milk production records were put on a 24-h basis using the equation

$$MP24HR1(2) = MP1(2) \times 24 / SEPTIME$$

where

MP24HR1 = milk production for period 1 put on a 24 h basis,

MP24HR2 = milk production for period 2 put on a 24 h basis,

MP1 and MP2 = actual weight of milk measured for period 1 and 2, respectively and

SEPTIME = the period of time to the closest hour that the cows and calves were separated.

The milk production and weaning weight variances were partitioned by the following statistical model:

$$Y_{ijkl} = u + D_i + A_j + S_k + bG_{ijkl} + e_{ijkl}$$

where

Y_{ijkl} = MP24HR1 or MP24HR2 or weaning weight (CAFWWT) observation on the l^{th} cow,

u = means of all observations,

D_i = the effect of the i^{th} year,

A_j = the effect of the j^{th} age of cow (in years),

S_k = the effect of the k^{th} sex (bull, steer or heifer),

bG_{ijkl} = the regression of milk production or weaning weight on age of calf at the time of the observation

and

e_{ijkl} = residual variation.

Cows were grouped by age in order to form larger subclasses. Among year of age comparisons were made based on the above models and those years that were not significantly different (P<.05) in all three analyses (SAS, 1985) were grouped in sequential pairs (table 3). The models were then re-analyzed substituting A'_j, the age group of the cow, for A_j.

The data were corrected for significant (P<.05) fixed effects as calculated by the GLM procedure of SAS (1985). Corrections were made

Table 3. Cow age grouping.

Age (Yr)	Age group
2	2
3	3
4	4
5 or 6	5
7 or 8	7
9 or 10	9
11+	11

additively using the formula

adjusted value = unadjusted value − the least-squares constant for the subclass.

Nelson and Kress (1981) concluded that for weaning weight in Herefords additive age of dam correction factors were preferable to multiplicative age of dam correction factors. They did not support the use of additive correction factors for sex of calf, however. The data were then corrected for a significant regression term by the formula:

$$AdjY = Y_{new} - b(CA-MCA)$$

where

$AdjY$ = milk production 1 or 2 or weaning weight adjusted for age of calf,

$Y_{new} = Y_{ijkl}$ corrected for fixed effects,

CA = calf age at the time of the observation

and

MCA = average age of all calves observed.

The resulting values for the adjusted 24-hr milk production during period 1 and period 2 (MPAJ1) and MP2 (MPAJ2) and adjusted weaning weight produced (AJCAFWWT) were added to the data set.

The arguement could be advanced that the milk data should not have been adjusted. If the expression of a cow's genetic potential for milk production was being decreased by the intake of a particular quantity of milk or energy or protein or other environmental component correlated to actual feed intake, it would have been most enlightening to deal with absolute amounts. Adjusting for year and age of dam effects clearly removed a portion of the environmental variation influencing a calf. In analyzing his data from Fort Robinson, Nebraska, Koch (1972) regressed the offspring's weaning weight on the age of dam correction factor and found that cows out of dams younger than 6 and older than 8 yr produced calves that gained more to weaning than did cows from dams 6 to 8 yr old. However, by correcting for known environmental effects, comparisons can be made across these effects without confounding. Also, it is conceivable that heifers with a higher genetic potential for growth would be able to consume more milk without having a negative impact on their subsequent maternal ability. Since sire selection was for above average yearling weight, uncorrected data would have masked an effect due to genetic improvement for rate of gain.

Correction resulted in being able to use greater numbers of measurements which should more accurately predicted the genetic component of trait relationships. If a trend not predicted by genetic theory was evident in data corrected for known environmental effects, either the theory is inadequate or additional environmental effects must be causing the unexplained trends. Koch (1972) had available to him 4060 calf records over a span of 5 yr. In contrast, this study had a maximum of 880 records over 17 yr for this thesis.

A lifetime average production value for adjusted MP1 (MPAJ1), MP2 (MPAJ2) and weaning weight (AJCAFWWT) was calculated by taking the mean across years for each cow. They were assigned the names AVMP1, AVMP2 and AVCAFWWT, respectively. A further averaging was performed on milk production. The mean of AVMP1 and AVMP2 was calculated resulting in a daily milk production estimate from 39 to 131 d postpartum (AVMP).

Once the data were adjusted, the 171 dam-daughter and the 67 dam-daughter-granddaughter data sets were assembled to analyze milk production and weaning weight relationships. In the three generation data set, 1st generation cows often appeared in the pedigree of more than one 3rd generation cow. Therefore, although there were 67 granddaughters, only 46 individual cows constituted the first generation. A similar situation existed in the two generation data set where there were 131 individual cows in the 1st generation and 171 in the 2nd generation.

Maternal lines of the three generation data set were assigned to one of four groups based on AVMP1, AVMP2, AVMP or AVCAFWWT of the first generation cows: high (HIGH), moderately high (MODHIGH), moderately low (MODLOW) and low (LOW). Groups were made to contain as near to equal numbers as possible.

Statistical Analyses

For the three generation data set, two-factor plus interaction least-squares analyses of variance using the GLM procedure of SAS (1985) were performed using the following model:

$$Y_{ijk} = u + g_i + p_j + gp_{ij} + e_{ijk}$$

where

Y_{ijk} = AVMP1, AVMP2, AVMP or AVCAFWWT of the k^{th} cow,

u = the overall mean,

g_i = the i^{th} generation,

p_j = the j^{th} group,

gp_{ij} = interaction of the i^{th} generation with the j^{th} group

and

e_{ijk} = residual variation.

Weaning weight was the dependent variable in models which included the three milk production groups (from periods 1 and 2 and the average period) and weaning weight groups as p_j. When the milk production variables were used as the dependent variable only the respective milk production groups were used for p_j.

Pearson correlation coefficients were calculated by the CORR procedure of SAS (1985) for all relationships among 24 h milk production during the first period adjusted for year, age of dam and age of calf (AJMP1); 24 h milk production during the second period adjusted for year and age of dam (AJMP2); and calf weaning weight produced adjusted for year, age of dam, age of calf and sex of calf (AJCAFWWT) within each record. All cow records in the 880 original data set that contained milk production measurements were included in these analyses. The numbers of records involved were as follows:

AJCAFWWT, 874 records;

MPAJ1, 367 records

and

MPAJ2, 367 records.

Regression analyses were performed on the two generation data set using the GLM procedure of SAS (1985). All relationships were analyzed with linear, quadratic and cubic models to determine the best fit. The following regressions were calculated:

daughter's AVMP1 (DTAVMP1)	on AVMP1,
DTAVMP1	on MPAJ1,
daughter's AVMP2 (DTAVMP2)	on AVMP2,
DTAVMP2	on MPAJ2,

and

daughter's weaning weight production (DTCAFWWT)	on AVCAFWWT.

Also, Pearson correlation coefficients were calculated for all pairs of AVMP1, MPAJ1, AVMP2, MPAJ2, AVCAFWWT, AJCAFWWT, DTAVMP1, DTAVMP2 and DTCAFWWT (daughter's average adjusted calf weaning weight produced). See page 63 for a complete summary of variable definitions.

RESULTS AND DISCUSSION

Adjustments to Data

In the initial analyses of the data correction model, the year and age of cow were significant sources of variation for MP24HR1, MP24HR2 and CAFWWT; sex of calf was significant only for CAFWWT and the regression on age of calf was significant for MP24HR1 and CAFWWT. (See page 63 for a glossary of variables.) A significant year effect was expected due to year to year environmental variation and that of age of cow is in agreement with the literature (Christian et al., 1965; Melton et al., 1967; Vesely and Robison, 1971; Neville et al., 1974). Effect of sex of calf on milk production has been demonstrated in some studies (Pope, et al. 1963; Melton et al., 1967; Rutledge et al., 1971; Daley et al., 1987) but not in others (Christian et al., 1965; Neville et al., 1974). It did approach significance ($P<.10$) for MP24HR2.

Based on the results of among age of cow comparisons, it was decided to group cow age according to table 3 and re-analyze the data. Doing this increased the error sum of squares (SS) slightly in all models but did not change the P-value of the main effects appreciably. The milk production of 4 yr-old cows did not differ significantly from 5 yr-old cows. However, weaning weight differences did approach significance ($P<.10$). Comparison of 3 yr-olds to 4 yr-olds yielded significant differences for MP24HR1 and CAFWWT but not for MP24HR2. Based on these comparisons and previous research (Christian et al., 1965; Neville et al., 1974), it was decided to retain the 4 yr-old cows in a separate age group. The analysis of variance (ANOVA) tables are given in tables 4 through 6. Based on these analyses, CAFSEX was dropped from the data correction model for MP24HR1, and CAFSEX as well as age of calf (AGEMP2) were dropped from the data correction model for MP24HR2 before calculation of least-squares constants (table 7) and regression coefficients on age of calf (tables 8 and 9).

Table 4. ANOVA of 24 h milk production in period 1 (MP24HR1).

Source	DF	SS	MS	F	P
Model	21	783.1	37.3	8.47	<.01
YRRECD	14	437.9	31.3	7.10	<.01
CAFSEX	2	10.5	5.3	1.20	.30
AGEGRP	4	214.0	53.5	12.20	<.01
AGEMP1	1	43.6	43.6	9.91	<.01
Error	345	1519.5	4.4		
Total	366	2302.6			

see page 63 for a glossary of variables

Table 5. ANOVA of 24 h milk production in period 2 (MP24HR2).

Source	DF	SS	MS	F	P
Model	20	413.8	20.7	5.19	<.01
YRRECD	14	272.7	19.5	5.26	<.01
CAFSEX	2	20.0	10.0	2.50	.08
AGEGRP	4	45.4	11.4	2.85	.02
AGEMP2	1	2.9	2.9	.72	.40
Error	328	1308.0	4.0		
Total	349	1721.8			

see page 63 for a glossary of variables

Table 6. ANOVA of calf weaning weight (CAFWWT).

Source	DF	SS	MS	F	P
Model	26	366833.5	14109.0	36.60	<.01
YRRECD	17	57584.8	3387.3	8.79	<.01
CAFSEX	2	22536.3	11268.2	29.23	<.01
AGEGRP	6	73237.3	12206.2	31.66	<.01
CAFAGE	1	176652.5	176652.5	458.19	<.01
Error	847	326553.4	385.5		
Total	873	693386.9			

see page 63 for a glossary of variables

Table 7. Least-squares constants (kg) for year, age of dam (AGEGRP) and sex of calf (CAFSEX) effects.

Year	CAFWWT	MP24HR1	MP24HR2
1970	−25.04	.....	.....
1971	− 4.10	.....	.....
1972	.04	− .98	− .55
1973	− 3.08	−2.64	−1.25
1974	7.82	− .35	−1.12
1975	.37	.01	−1.54
1976	− 1.26	1.13	−1.42
1977	− 1.09	2.12	−2.21
1978	−15.70	− .48	.57
1979	− 3.72	.....	.....
1980	11.83	1.32	.19
1981	6.79	1.42	4.80
1982	−20.02	− .38	− .34
1983	.01	−1.95	−1.01
1984	− 1.94	− .66	.52
1985	13.98	.23	1.13
1986	13.74	− .38	.95
1987	21.30	1.54	1.47
mean	190.51	7.64	5.73

AGEGRP	CAFWWT	MP24HR1	MP24HR2
2	−19.92	−1.61	− .90
3	− 2.44	− .11	− .23
4	− 3.51	.75	− .33
5	8.26	1.04	.03
7	12.58	− .09	1.45
9	7.86	.....	.....
11	− 2.80	.....	.....
mean	190.51	7.64	5.73

CAFSEX	CAFWWT	MP24HR1	MP24HR2
bull	3.75	.....	.....
steer	3.46	.....	.....
heifer	−7.20	.....	.....
mean	190.51	.....	.....

see page 63 for glossary of variables

Table 8. AVOVA: Milk production during period 1 (MP24HR1) = age of dam (AGEGRP) + year (YRRECD) + day of age of calf (AGEMP1).

Source	DF	SS	MS	F	P	R^2
Model	19	772.6	40.7	9.22	<.01	.34
Error	347	1530.0	4.4			
Total	366	2302.6				

Parameter	Estimate	P	SE
AGEMP1	−.045	<.01	.01

see page 63 for a glossary of variables

Table 9. ANOVA: Calf weaning weight (CAFWWT) = age of dam (AGEGRP) + year (YRRECD) + sex of calf (CAFSEX) + age of calf (CAFAGE).

Source	DF	SS	MS	F	P	R^2
Model	26	366833.5	14109.0	36.60	<.01	.53
Error	847	326553.4	385.5			
Total	873	693386.9				

Parameter	Estimate	P	SE
CAFAGE	.98	<.01	.05

see page 63 for a glossary of variables.

The overall least-squares means for MP24HR1 and MP24HR2 were 7.64 and 5.73 kg, respectively. These figures are somewhat higher than those for other groups of Herefords reported on in the literature. Neville et al. (1974) estimated daily lactation over the first 210 d to be 4.5 kg. Pope et al. (1963) found averages of 5 kg/d during early lactation and 4.7 kg/d during mid-lactation. In a multi-breed study, which included Herefords, by Totusek et al. (1973), daily milk yield at 70 d post partum was 6.6 kg and at 112 d post partum, 6.4 kg. However, the milk yield results are confounded with breed effects. Herefords in Texas studied by Melton et al. (1967) had daily milk production of 4.5 kg at 77 d and 3.6 kg at 137 d postpartum. Charolais and Angus cows also were included in their investigation and both breeds had higher daily and total milk yields than did the Herefords. However, the Charolais, with the highest milk production, still produced less than the cross line Herefords from NARC used in this thesis. All the studies cited used the weigh-suckle-weigh technique.

Average milk productions after being put on a 24-h basis were plotted in figure 2. The among year variation was evident and there seemed to be an upward trend in MP24HR2. The high peak in MP24HR2 in 1981 may have been due to the fact that only four cows with Hereford calves were measured that year. The herd was involved in a crossbreeding study during the late 70's and early 80's and many of the Hereford cows were raising calves sired by other breeds and, consequently, were not included in these analyses. The slight upward trend suggested by the data could have been caused by the selection of bulls for above average yearling weight. Irgang et al. (1985) reported an increase in milk production in two herds of Herefords: one selected for high preweaning gain and the other selected for high postweaning gain.

The overall least-squares mean for calf weaning weight produced (CAFWWT) was 190.5 kg. There was an upward trend of the actual calf

Figure 2.
Unadj MP24HR1 & MP24HR2 by years.

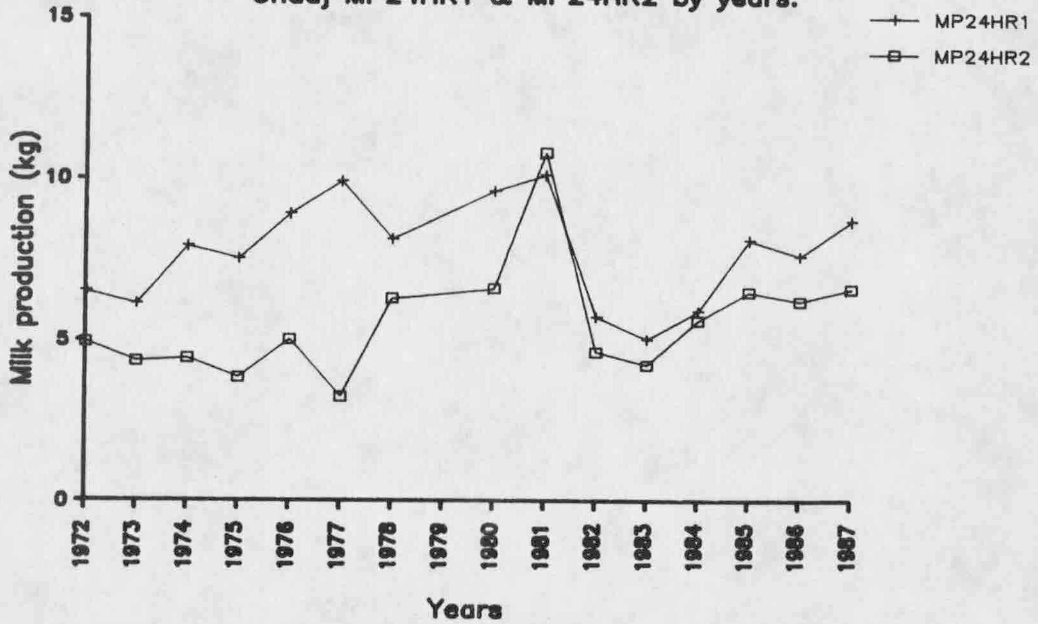
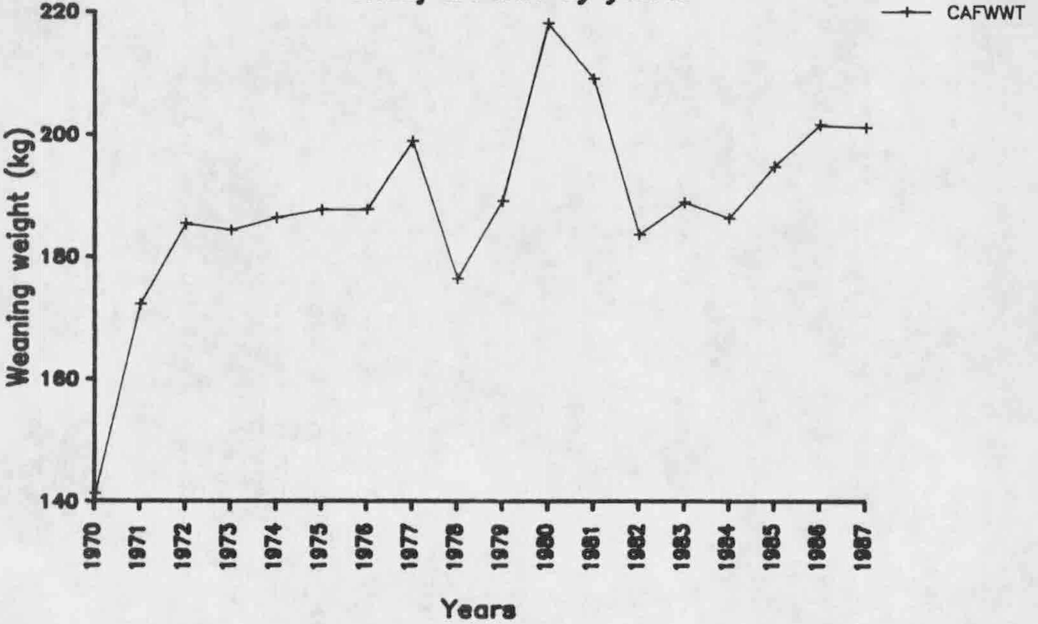


Figure 3.
Unadj CAFWWT by years.



weaning weight produced through the years of the study (figure 3). These data were subsequently corrected for year, age of cow and sex of calf. Weaning weights of bull calves did not differ significantly from weights of steers.

Milk production during period 1 (MP24HR1) and calf weaning weight produced (CAFWWT) were adjusted for calf age at time of the measurement. The regression of MP24HR1 on age of calf at the time of the test (AGEMP1) was -.045 kg/d and was significant ($P < .01$). It was expected to be positive based on some published milk production curves (Wood, 1969; Wood, 1977; Casebolt, 1984), however, the very slight negative slope could indicate that the period 39 d plus or minus 10.3 d (one SD) encompasses the peak of the lactation curve for this herd over these years. Curves similar in shape to those suggested by Melton et al. (1967) wherein peak lactation occurred prior to 77 d post partum may fit this herd. Kress and Anderson (1974), using NARC Herefords, found a maximum predicted milk production of 7.3 kg at 20 d postpartum. They could make no prediction for less than 20 d postpartum.

The regression of CAFWWT on age of calf at weaning (CAFAGE) was 0.98 kg/d and significant ($P < .01$). This translates into the average calf weighing 236.9 kg at 205 d based on an average birth weight of 36 kg.

Three Generation Data Set

The arithmetic means and numbers of first generation cows in each group for AVMP1 (average adjusted milk production in period 1), AVMP2 (average adjusted milk production in period 2), AVMP (average of AVMP1 and AVMP2) and AVCAFWWT (average adjusted weaning weight produced) are given in table 10. The differences between means of the MODLOW (moderately low) and MODHIGH (moderately high) groups are less than between these and the HIGH or LOW groups. This was reasonable assuming that the data were approximately normally distributed and given that nearly equal numbers were assigned to each group.

Table 10. Group arithmetic means (kg) and numbers of first generation cows (N) for AVMP1, AVMP2, AVMP and AVCAFWWT.

	AVMP1		AVMP2		AVMP		AVCAFWWT	
Group	Mean	N	Mean	N	Mean	N	Mean	N
HIGH	9.9	11	8.6	11	9.1	10	210	11
MODHIGH	8.0	11	6.3	11	7.2	11	196	12
MODLOW	7.1	11	5.4	11	6.3	11	187	12
LOW	5.7	10	4.1	10	5.4	10	174	11

see page 63 for glossary of variables

Least squares means showing the effects of cow groups and generation (dam, daughter and granddaughter) are presented in tables 11 through 14 and figures 4 through 10. The overall trend from generation 1 to generation 3 was to regress to the mean. This was expected as demonstrated by Lush et al. (1941) in work with dairy cattle. However, for these data, there was also a tendency for some groups to alternate from high producing to low producing and from low producing to high producing from generation to generation. The latter trends are especially noticeable in figures 4 and 6.

When the first generation cows were grouped by AVMP1 (the average adjusted amount of milk produced on an average of 39 d postpartum), values for AVMP1 showed some significant differences between generations (table 8). For the LOW group, means alternated from below the overall mean for generation 1 to above the mean for generation 2 and back to below the overall mean for generation 3 (figure 4). For the MODHIGH group, means alternated from above the overall mean to below the mean and back up to the overall mean. The HIGH group remained above the mean for all generations. It is possible the direct effects for superior milk production in the animals in generation 1 in this group counter the negative maternal effect. The MODLOW group rose from below the mean in generation 1 to above the mean in generation 2. By the third generation there were no significant differences among groups.

Analyzing the AVCAFWWT (average calf weaning weight produced) of the cows grouped by AVMP1 (average milk production during period 1), no significant differences or general trends were found (figure 5). The HIGH group produced the heaviest calves but the LOW group was next in rank. The literature has documented a positive relationship between milk production and weaning weight produced (Neville, 1962; Melton et al., 1967; Rutledge et al., 1971; Willham, 1972a; Totusek et al., 1973; Kress and Anderson, 1974; Williams et al., 1979b; Clutter and Nielsen, 1987). This was not supported by these data except for the parallel trends of AVMP1 and AVCAFWWT through generations.

When the first generation cows were grouped by AVMP2 (the average adjusted amount of milk produced on an average of 131 d postpartum),

Table 11. Least-squares means for AVMP1 (kg) and AVCAFWWT (kg) compared among generations and among groups when generation 1 cows were grouped based on AVMP1. (plotted in figures 4 and 5)

	AVMP1			AVCAFWWT		
	Generation			Generation		
Group	1	2	3	1	2	3
HIGH	10.0^{aw}	8.8^{abw}	8.3^{bw}	203^{aw}	197^{aw}	193^{aw}
MODHIGH	8.0^{ax}	7.7^{aw}	7.5^{aw}	186^{ax}	193^{aw}	192^{aw}
MODLOW	7.1^{ax}	8.5^{bw}	7.8^{bw}	187^{ax}	192^{aw}	186^{aw}
LOW	5.7^{ay}	8.6^{bw}	6.9^{cw}	190^{ax}	193^{aw}	190^{aw}
Mean	7.7^{ax}	8.3^{aw}	7.5^{aw}	192^{ax}	193^{aw}	189^{aw}

a,b,c: significant difference ($P<.05$) within row, between columns.
w,x,y,: significant difference ($P<.05$) within column, between rows.
see page 63 for glossary of variables

Table 12. Least-squares means for AVMP2 (kg) and AVCAFWWT (kg) compared among generations and among groups when generation 1 cows were grouped based on AVMP2. (plotted in figures 6 and 7)

	AVMP2			AVCAFWWT		
	Generation			Generation		
Group	1	2	3	1	2	3
HIGH	8.3^{aw}	5.2^{bw}	5.8^{bwx}	194^{awx}	194^{awx}	191^{aw}
MODHIGH	6.3^{ax}	8.1^{bx}	5.2^{aw}	198^{ax}	198^{aw}	191^{aw}
MODLOW	5.5^{ax}	5.1^{aw}	6.9^{bx}	190^{awx}	197^{aw}	193^{aw}
LOW	4.3^{ay}	4.6^{aw}	5.4^{aw}	185^{aw}	187^{ax}	186^{aw}
Mean	6.2^{ax}	5.4^{aw}	6.0^{awx}	192^{awx}	193^{awx}	189^{aw}

a,b: significant difference ($P<.05$) within row, between columns.
w,x,y: significant difference ($P<.05$) within column, between rows.
see page 63 for glossary of variables

Figure 4.
AVMP1 groups: AVMP1 l-s means.

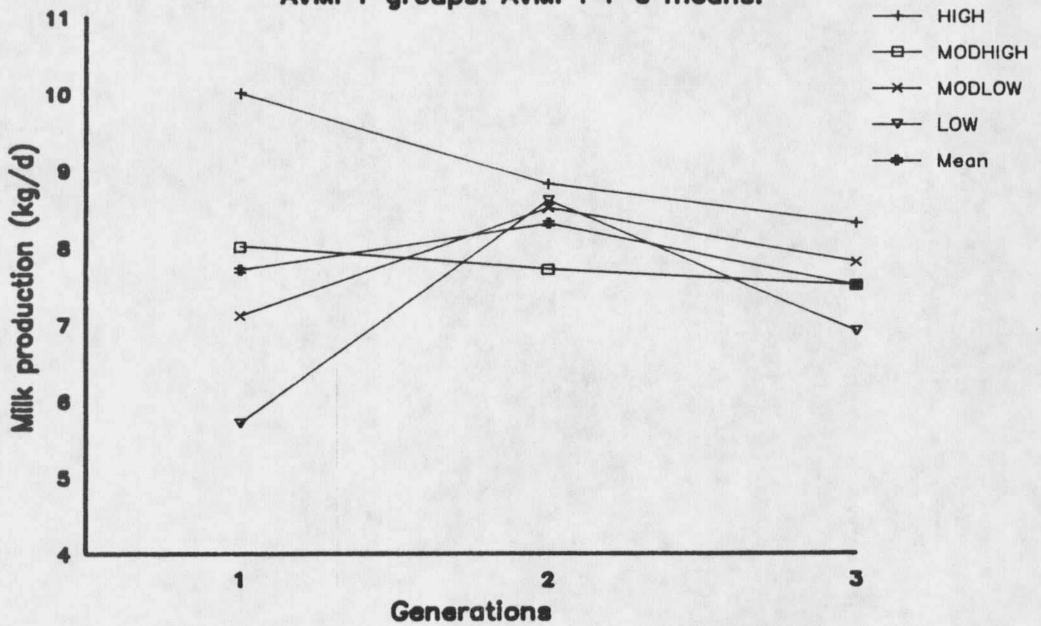


Figure 5.
AVMP1 groups: AVCAFWWT l-s means.

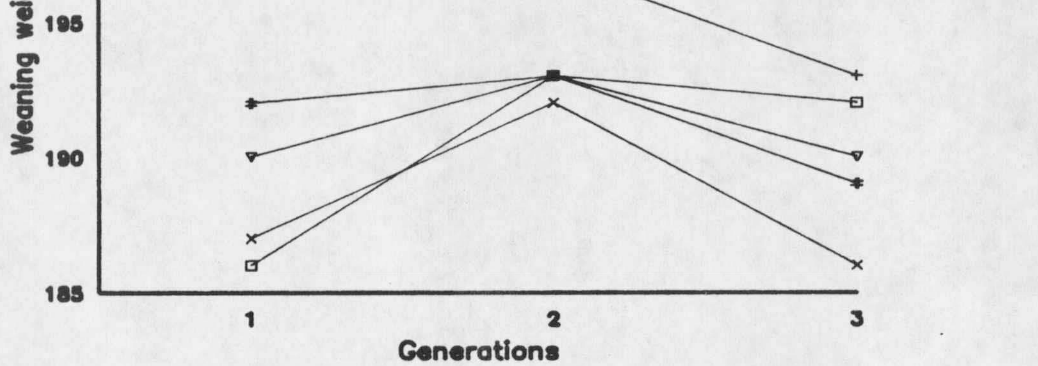


Figure 6.

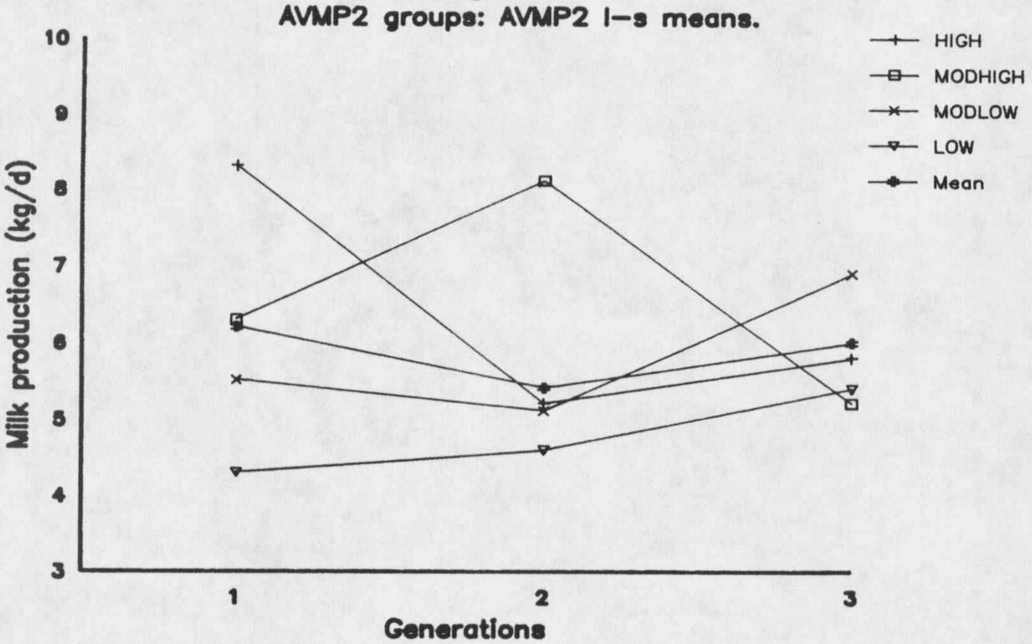


Figure 7.

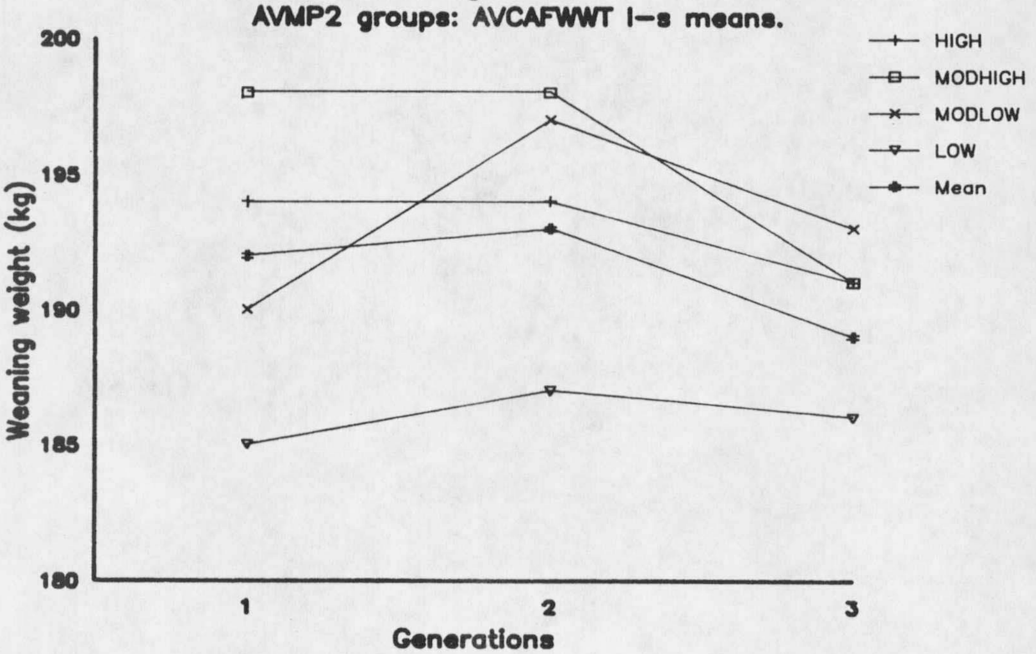


Table 13. Least-squares means for AVCAFWWT (kg) compared among generations and among groups when generation 1 cows were grouped based on AVCAFWWT. (plotted in figure 8)

	AVCAFWWT		
	Generation		
Group	1	2	3
HIGH	210[aw]	201[bw]	199[bw]
MODHIGH	196[ax]	197[aw]	192[awx]
MODLOW	187[ay]	189[ax]	184[ax]
LOW	174[az]	188[bx]	185[bx]
Mean	192[axy]	193[awx]	189[ax]

a,b: significant difference (P<.05) within row, between columns.
w,x,y,z: significant difference (P<.05) within column, between rows.
see page 63 for a glossary of variables.

Figure 8.

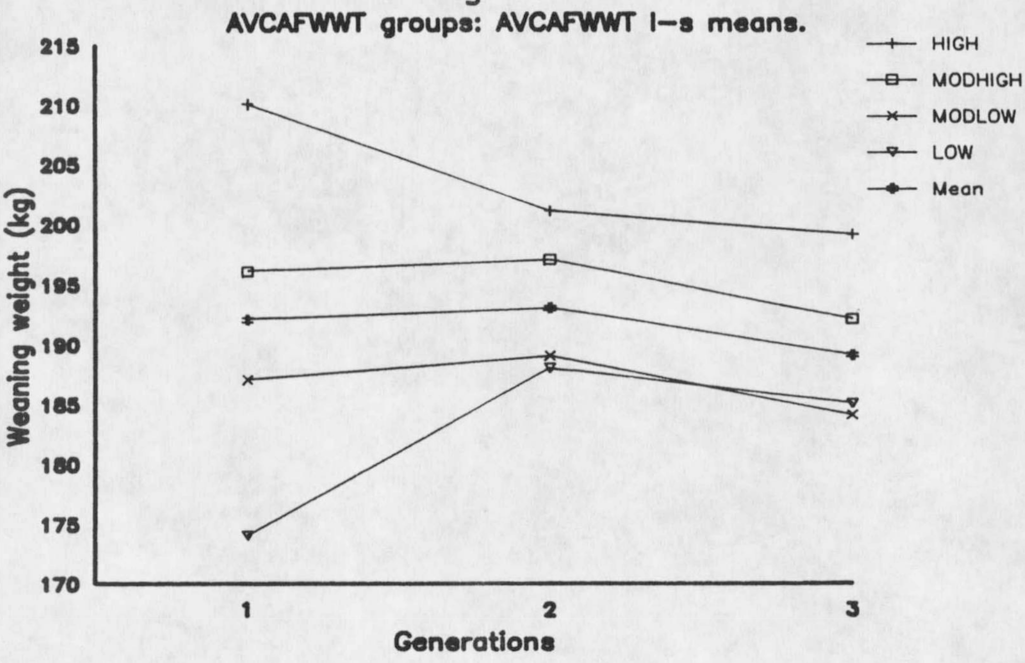


Table 14. Least-squares means for AVMP (kg) and AVCAFWWT (kg) compared among generations and among groups when generation 1 cows were grouped based on AVMP. (plotted in figures 9 and 10)

	AVMP			AVCAFWWT		
	Generation			Generation		
Group	1	2	3	1	2	3
HIGH	9.1^{aw}	6.9^{bw}	6.6^{bwx}	202^{aw}	193^{awx}	190^{aw}
MODHIGH	7.2^{ax}	8.1^{ax}	7.1^{ay}	194^{awx}	202^{aw}	194^{ax}
MODLOW	6.3^{axy}	6.9^{ax}	7.3^{by}	185^{ax}	191^{ax}	187^{ax}
LOW	5.4^{ay}	6.3^{ax}	6.0^{aw}	187^{ax}	190^{ax}	189^{awx}
Mean	7.0^{ax}	6.8^{ax}	6.8^{axy}	192^{awx}	193^{ax}	189^{awx}

a,b: significant difference ($P<.05$) within row, between columns.
w,x,y: significant difference ($P<.05$) within column, between rows.
see page 63 for glossary of variables

the least-squares means of AVMP2 of the MODHIGH group demonstrated the alternate generation trends (figure 6). This group in generation 1 was nearly at the mean, rose to 2.7 kg above the mean in generation 2 and dropped to 0.8 kg below the mean in generation 3. The HIGH group in generation 2 and the MODLOW group in generation 3 did not produce milk as was predicted by their dams milk production. The LOW group demonstrated no significant trends from generation to generation.

AVCAFWWT means were generally not significantly different between groups or between generations when grouped by AVMP2 (table 12). The MODHIGH group as a whole seemed to contain the best producers of weaning weight while the LOW group contained the worst producers.

A grouping of the first generation was made based on AVCAFWWT. Significant differences between generation means for AVCAFWWT occurred

Figure 9.

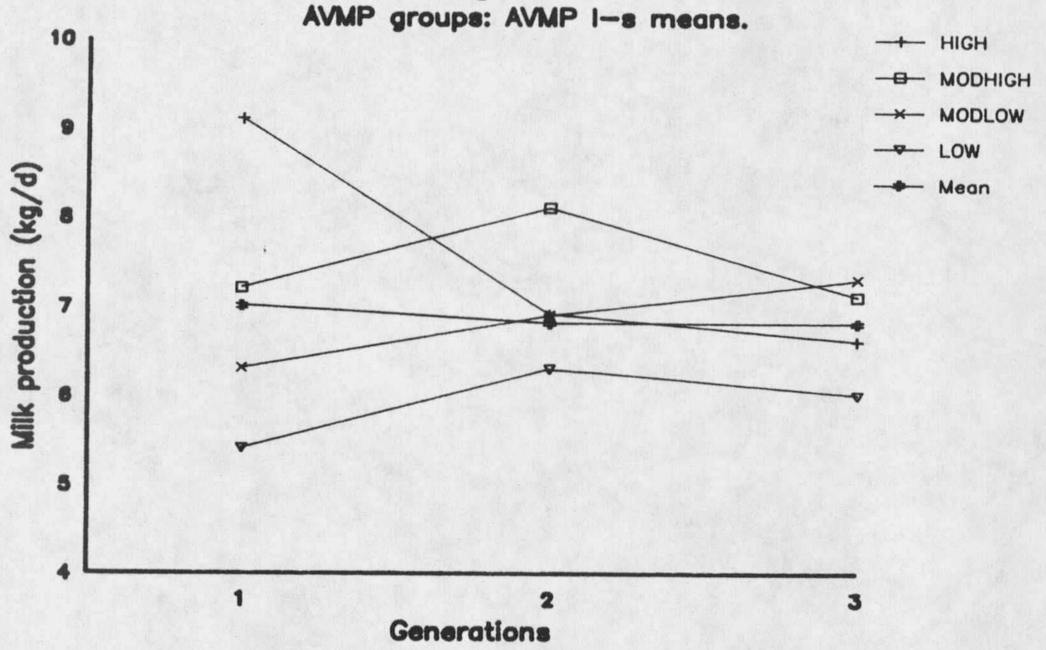
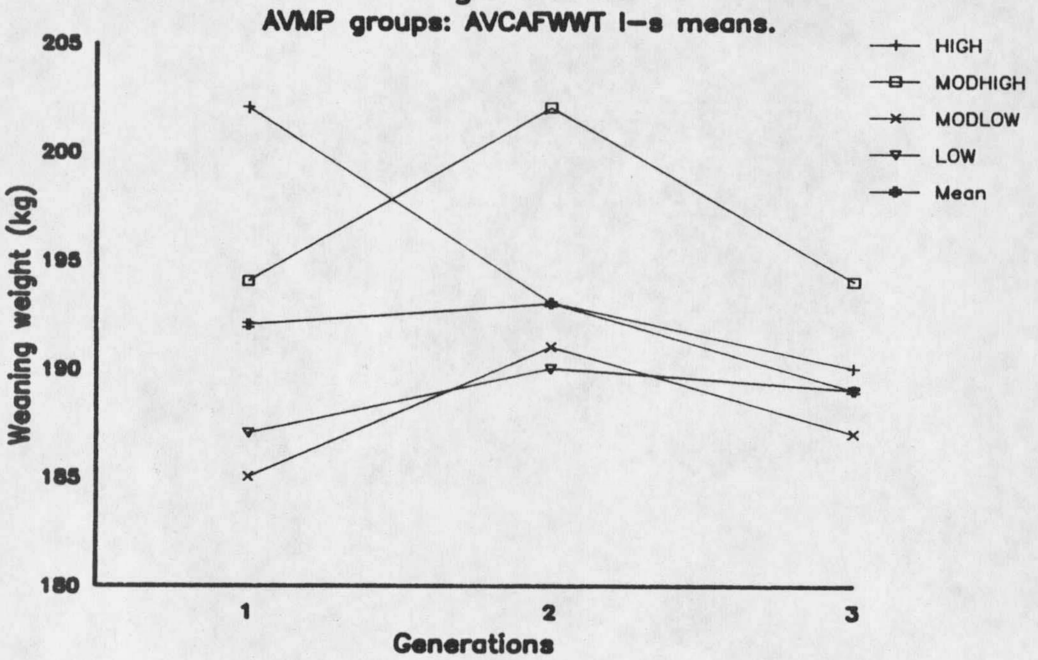


Figure 10.



only for the HIGH and LOW groups from generation 1 to generation 2 (table 10).

The among generation analyses when the first generation was grouped by the average of AVMP1 and AVMP2 (AVMP) demonstrated some alternating generation trends (figures 9 and 10 and table 11). In addition, the plots of AVCAFWWT by group (figure 10) closely parallel the plots of AVMP (figure 9) which was not the case for groups by AVMP1 or AVMP2.

The results for analyses including average weaning weight produced (AVCAFWWT) did not strongly support the finding of Mangus and Brinks (1971). Small numbers in each group could have been the cause. Mangus and Brinks (1971) had 100 animals in each generation and divided the generation into three groups with a total of 33 cows per group. Also, correlations between AVMP1 and AVCAFWWT, and AVMP2 and AVCAFWWT were lower (0.54 and 0.35, respectively) for these data than the average value in the literature (0.55) reported by Kress and Anderson (1974).

Milk Production and Weaning Weight Correlations

All correlations were significant and positive among AJCAFWWT, MPAJ1 and MPAJ2 when the full data set (including multiple records on individual cows) of 880 records was included (table 15). Correlations between AJCAFWWT and MPAJ1 or MPAJ2 were 0.43 and 0.36, respectively. The correlation between MPAJ1 and MPAJ2 was a relatively low 0.17. Kress and Anderson (1974) found a correlation of 0.5 between milk production tests taken approximately 34 d apart. Persistence of lactation does vary between individual cows which would result in a low

Table 15. Correlations (r) of AJCAFWWT, MPAJ1, MPAJ2, AVCAFWWT, AVMP1 AVMP2 and AVMP.

Trait		MPAJ1	MPAJ2	AVMP1	AVMP2	AVMP
AJCAFWWT	r	.43	.36			
	P[a]	<.01	<.01			
	N[a]	316	362			
MPAJ1	r		.17			
	P		<.01			
	N		352			
AVCAFWWT	r			.54	.35	.56
	P			<.01	<.01	<.01
	N			206	209	201
AVMP1	r				.15	.76
	P				.03	<.01
	N				202	202
AVMP2	r					.76
	P					<.01
	N					202

[a] P=the significance probability and N=number of observations.
see page 63 for a glossary of variables.

correlation for this comparison. Lactation curves plotted by Swanson (1960) indicated that heifers fattened early in life had lower but more persistent milk production over 35 wk milkings. That trend was consistent over two lactations. Notter's (1976) study of biological types of beef cattle also found higher persistence in cattle with decreased average daily milk production. Observations by Nielsen et al. (1983) and Casebolt (1984) contradict those findings. They found that cows with higher average milk yield had more persistent production.

Two Generation Data Set

The regression analyses of daughter traits on dam traits using linear, quadratic and cubic models yielded few statistically significant relationships at a test level of $P<.05$. Two were worthy of further examination.

The linear regression of average calf weaning weight production by the daughter (DTCAFWWT) on average calf weaning weight production of the dam approached significance ($P<.10$) (table 16). The slope was significant and positive (0.18) indicating a trend for dams with high average calf weaning weight to produce daughters with higher average calf weaning weight. The implication from these data was that selection of a heifer calf as a replacement based on her dam's past performance for weaning weight produced has some merit. However, much of the daughter's weaning weight production in this herd was determined by other factors (not including year, age of cow, sex of calf and age of calf whose effects were adjusted out of these data) as indicated by the low R^2 value.

The cubic fit of the regression of DTAVMP2 (daughter average milk production during period 2) on AVMP2 (dam average milk production during period 2) had a $P=.16$ for the entire model (table 17). The coefficients of the quadratic and cubic terms were both significant and the linear coefficient approached significance. The linear and cubic coefficients were negative and the quadratic positive. Predicted peak DTAVMP2 resulted from AVMP2 values near 1 kg/d (the low end of the data) and again at approximately 10 kg/d. It was suggested that milk

Table 16. Regression of DTCAFWWT on AVCAFWWT

Source	DF	SS	MS	F	P	R^2
Model	1	1019.9	1019.9	3.07	.08	.02
Error	168	55744.2	331.8			
Total	169	56764.1				

Parameter	Estimate	T	P	SE
Intercept	155.89	7.73	<.01	20.1
AVCAFWWT	.18	1.75	.08	.1

see page 63 for a glossary of variables.

production levels over 10 kg/d were not conducive to higher daughter milk production (figure 11).

None of the analyses involving AVMP1 had P-values less than 0.85. This suggests that high peak milk intake is less important than sustained high levels of milk intake when considering deleterious effects on subsequent maternal ability. Or, perhaps high rate of gain at approximately 4 mo of age was the critical period. This is speculation and based on nonsignificant statistical trends. However, Hill (1965) reported positive covariances between maternal and direct effects at 90 and 120 d of age and increasingly larger negative covariances at 150, 180 and 210 d. More evidence of a change of sign of the covariance between maternal and direct effects comes from research done with crossfostered swine by Ahlschwede and Robison (1971a). Covariances were positive for the first 4 wk postpartum and then changed to negative at week 5 based on weight gain.

Table 17. Regression of DTAVMP2 on AVMP2; cubic fit.

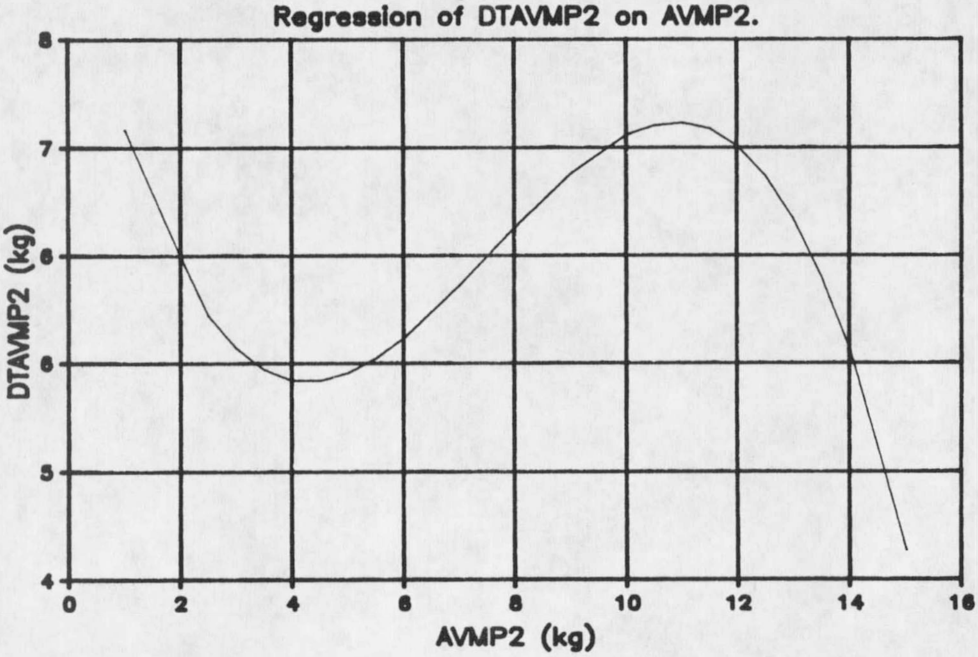
Source	DF	SS	MS	F	P	R^2
Model	3	25.5	8.5	1.77	.16	.06
AVMP2	1	15.7	15.7	3.25	.07	
$AVMP2^2$	1	19.6	19.6	4.07	.05	
$AVMP2^3$	1	22.2	22.2	4.62	.03	
Error	91	438.2	4.8			
Total	94	463.7				

Parameter	Estimate	T	P	SE
Intercept	8.89	4.2	<.01	2.12
AVMP2	-1.85	-1.8	.07	1.03
$AVMP2^2$	.30	2.0	.05	.18
$AVMP2^3$	- .01	-2.2	.03	.01

see page 63 for a glossary of variables

Figure 11.

Regression of DTAVMP2 on AVMP2.



Pearson correlation coefficients were calculated for all pairs of AVMP1, MPAJ2, AVCAFWWT, AJCAFWWT, DTAVMP1, DTAVMP2 and DTCAFWWT (table 18). Most within generation correlations were significant. The correlation between MPAJ2 and MPAJ1 was significant ($P<.05$) but low (0.20). Within the second generation, the correlation between DTAVMP1 and DTAVMP2 was not significant. These two results underscore the weak relationship between MP1 and MP2. Even when repeated records on individuals in the first generation were used (AVMP1 with AVMP2), the correlation was only 0.17. Also, the correlation between a daughter's own weaning weight (AJCAFWWT) and her weaning weight production (DTCAFWWT) was not significant.

To understand the direct relationship between dam and daughter maternal phenotype (f_m), it was helpful to study the correlations of dam milk production with daughter milk production. For these data, none of these correlations was significant. However, MPAJ2 with DTCAFWWT did approach significance and was negative (-.17). This evidence suggested that a negative relationship existed between the maternal phenotype of a dam and the individual phenotype (weaning weight) of the granddaughter. According to Koch's (1972) path diagram (see figure 1, page 13), that negative relationship could occur if the correlation between dam maternal genotype and dam individual genotype for growth was negative. This agrees with the literature on beef cattle (Christian et al.,1967; Deese and Koger, 1967; Ellicott et al., 1970; Vesely and Robison, 1971; Hohenboken and Brinks, 1971a and 1971b; Mangus and Brinks, 1971; Koch, 1972; Willham, 1972a and 1972b; Kress and Burfening, 1972; Kress et al., 1979; Robison. 1981; Chenette and

Table 18. Correlations (r) in 2-generation data set.

Trait		MPAJ1	AVMP2	MPAJ2	AVCAF WWT	AJCAF WWT	DT AVMP1	DT AVMP2	DT CAFWWT
AVMP1	r	.78	.17	.29	.49	.45	−.01	.02	−.05
	P[a]	<.01	.04	<.01	<.01	<.01	.95	.81	.53
	N[a]	123	153	118	155	155	93	96	154
MPAJ1	r		.28	.20	.34	.29	−.05	−.15	−.18
	P		<.01	.03	<.01	<.01	.68	.18	.05
	N		121	117	123	123	76	76	122
AVMP2	r			.87	.45	.42	−.02	.00	−.03
	P			<.01	<.01	<.01	.85	.99	.72
	N			119	155	155	92	95	154
MPAJ2	r				.47	.52	−.07	−.07	−.17
	P				<.01	<.01	.53	.56	.07
	N				119	119	76	76	118
AVCAFWWT	r					.77	.09	.16	.13
	P					<.01	.37	.10	.08
	N					171	100	103	170
AJCAFWWT	r						.04	.13	.13
	P						.68	.19	.08
	N						100	103	170
DTAVMP1	r							.05	.49
	P							.60	<.01
	N							97	99
DTAVMP2	r								.26
	P								<.01
	N								102

[a] P=the significance probability and N=number of observations.

Frahm, 1981; Cantet et al., 1988) and other species (Falconer, 1955: Ahlschwede and Robison, 1971a and 1971b; Revelle and Robison, 1973; Ahlschwede and Robison, 1971a and 1971b; Revelle and Robison, 1973; Tanida and Hohenboken, 1987).

The correlations also suggested that there was no relationship between maternal phenotype of the dam and maternal phenotype of the daughter. However, from work with dairy cattle it is known that the heritability of milk production is in the range of 0.23 to 0.51 (Lush et al., 1941; Van Vleck and Bradford, 1966; Thompson and Loganathan, 1968), and is a positive relationship by definition. Therefore, a counterbalancing negative environmental relationship must also be affecting the phenotypic relationship. The relationships are depicted in figure 1, page 13. P_m, the maternal phenotype of the daughter and P'_m, the maternal phenotype of the dam, are related by two pathways so that the composition of the correlation of P_m with P'_m is

$$r_{P_mP'_m} = 0.5\ g_m^2 + f_m$$

where g_m, the standard partial regression coefficient of the phenotype for maternal ability on the additive genetic component of maternal ability, is the square root of heritability (h_m^2). For $r_{P_mP'_m}$ to be negative, f_m must be negative and of a magnitude of at least $0.5h_m^2$. The range of values, then, for f_m given $r_{P_mP'_m} = 0$ that would be consistent with dairy data for heritability of milk production is $-.11$ to $-.25$.

The results of the analyses involving the three generations support this conclusion. The practice of artificial rearing in dairy cattle where there are no maternal environmental effects after birth (although rate of gain differences and cytoplasmic factors would still be present) makes a good comparison for evaluation of postnatal maternal effects. If there was no negative influence of dam milk production on daughter milk production, the groups would not have been expected to change their relative order from generation to generation in a cyclic pattern.

The reason for the effect remains unexplained. Behavioral, hormonal, anatomic, genetic and/or metabolic factors could be involved. These results from direct measurement of milk production support the hypothesis that milk production is a component of maternal ability that contributes to the alternating generation effect for calf weaning weight and the negative environmental effect of female weaning weight on her subsequent calf weaning weights (Mangus and Brinks, 1971; Kress and Burfening, 1972).

SUMMARY

The detrimental effect of high preweaning gain in heifers on their subsequent maternal ability as measured by amount of calf weaned has been well established using artificial rearing and preweaning supplementation as well as pedigree analysis. Also, the high importance of milk production as a component of maternal ability has been researched and generally agreed upon. There is additional evidence that high preweaning gain from high concentrate rations has a negative effect on milk production. However, the direct effect of high dam milk production on daughter milk production has not been elucidated. Using data gathered on a single breed of beef cow (Hereford) in a relatively consistent environment (the plains and foothills near Havre, Montana) over a period of 17 yr, this thesis attempted to make that connection.

Weigh-suckle-weigh milk production estimates, weaning weights of cows and their offspring, weights of cows and calves at the time milk production was measured, condition scores for cows and calves at weaning, and sires and dams of each individual are among the data collected.

Analyses performed on individual cow/calf pairs confirmed the positive correlation between milk production of the dam and weaning weight of the offspring. Analyses of milk production during early and mid-lactation of maternal lines through three generations demonstrated that high dam milk production can be detrimental to daughter milk production. More surprising was the evidence that low milk production in one generation can lead to high milk production in the next generation. The third generation more reflected the milk production of the grandam than the dam.

Regression and correlation analyses of dam traits and daughter traits generally indicated relationships near zero. The relationship between a dam's average weaning weight produced and her daughter's weaning weight produced was positive and significant but the correlation between the daughter's adjusted weaning weight and her weaning weight produced was not. There was a negative correlation between dam milk production approximately 131 d postpartum and daughter weaning weight produced that approached significance. The correlation between dam milk production approximately 39 d postpartum and daughter weaning weight produced was near zero and not significant. These findings indicate that dam milk production later in lactation is more critical to the development of daughter maternal ability than is dam milk production earlier in lactation.

Correlations between dam and daughter milk productions were not significant and were near zero. If the correlations are zero, f_m (direct influences of dam on daughter milk production) would range from −.11 to −.25 based on published milk production heritability estimates. More records are needed in order to quantify f_m using this technique. Measurement of milk production continues on the herd and re-analysis of the between generations correlations would be valuable when larger numbers of records are available.

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APPENDICES

APPENDIX A

GLOSSARY OF VARIABLES

GLOSSARY OF VARIABLES

E_m – environment other than that provided by the dam effecting an individual's maternal phenotype

E_w – environment other than that provided by the dam effecting an individual's weaning weight phenotype

G_m – genotype for maternal ability of an individual

G'_m – genotype for maternal ability of a dam

G''_m – genotype for maternal ability of a grandam

G_w – genotype for weaning weight of an individual

G'_w – genotype for weaning weight of a dam

G''_w – genotype for weaning weight of a grandam

P_m – phenotype for maternal ability of an individual

P'_m – phenotype for maternal ability of a dam

P''_m – phenotype for maternal ability of a grandam

P_w – phenotype for weaning weight of an individual

P'_w – phenotype for weaning weight of a dam

e_m – standard partial regression coefficient of P_m on E_m

e_w – standard partial regression coefficient of P_w on E_w

f_m – standard partial regression coefficient of offspring phenotype for maternal ability on dam phenotype for maternal ability

g_m – standard partial regression coefficient of an individual phenotype for maternal ability on the same individual's genotype for maternal ability

g_w – standard partial regression coefficient of an individual phenotype for weaning weight on the same individual's genotype for weaning weight

p_m – standard partial regression coefficient of a dam's phenotype for maternal ability on an offspring's phenotype for weaning weight

r_E – the environmental correlation between direct and maternal effects

r_G – the genetic correlation between direct and maternal effects

h^2 – heritability

AGEGRP – age group of a cow based on her age in years at the time the measurement was taken

MP1 – weight of milk in kg measured an average of 39 d postpartum

MP2 – weight of milk in kg measured an average of 129 d postpartum

SEPTIME – the period of time to the closest hour that the cow and calf were separated when taking milk production measurements

MP24HR1 – MP1 put on a 24 h basis

MP24HR2 – MP2 put on a 24 h basis

AGEMP1 – age of calf in days at the time MP1 was taken

AGEMP2 – age of calf in days at the time MP2 was taken

CAFAGE – age of the calf in days at weaning

CAFSEX – sex of the calf at weaning: bull, steer, or heifer

CAFWWT – actual weaning weight of the calf in kg

YRRECD – year in which a measurement was taken

AJCAFWWT – CAFWWT adjusted for YRRECD, AGEGRP, CAFSEX and CAFAGE

MPAJ1 – MP24HR1 adjusted for YRRECD, AGEGRP and AGEMP1

MPAJ2 – MP24HR2 adjusted for YRRECD and AGEGRP

AVMP – average of AVMP1 and AVMP2 for a given cow

AVMP1 – average across years of MPAJ1 for a given cow

AVMP2 – average across years of MPAJ2 for a given cow

DTAVMP1 – daughter's AVMP1

DTAVMP2 – daughter's AVMP2

DTCAFWWT – daughter's AVCAFWWT

GENRNO – generation number: 1 = dam, 2 = daughter, 3 = granddaughter

HIGH – highest of four groups of approximately equal numbers into which first generation cows of three generation data set was assigned

MODHIGH – second highest of four groups of approximately equal numbers into which first generation cows of three generation data set was assigned

MODLOW – third highest of four groups of approximately equal numbers into which first generation cows of three generation data set was assigned

LOW – lowest of four groups of approximately equal numbers into which first generation cows of three generation data set was assigned

GRPMP – groups of first generation cows by AVMP; either HIGH, MODHIGH, MODLOW or LOW

GRPMP1 – groups of first generation cows by AVMP1; either HIGH, MODHIGH, MODLOW or LOW

GRPMP2 – groups of first generation cows by AVMP2; either HIGH, MODHIGH, MODLOW or LOW

GRPWWT – groups of first generation cows by AVCAFWWT; either HIGH, MODHIGH, MODLOW or LOW

APPENDIX B

STATISTICAL TABLES RELATED TO ANALYSES OF THREE GENERATION DATA SET

Table 19. ANOVA: AVMP1 = generation + groups AVMP1 + interaction.

Source	DF	SS	MS	F	P	R^2
Model	11	185.2	16.8	5.87	<.01	.31
GENRNO	2	18.3	9.2	3.19	.04	
GRPMP1	3	73.6	24.5	8.56	<.01	
GENRNO X GRPMP1	6	72.4	12.1	4.21	<.01	
Error	144	412.8	2.9			
Total	155	598.0				

see appendix A for definitions of variables

Table 20. ANOVA: AVCAFWWT = generation + groups AVMP1 + interaction.

Source	DF	SS	MS	F	P	R^2
Model	11	3947.5	358.9	1.47	.15	.08
GENRNO	2	371.1	185.6	.76	.47	
GRPMP1	3	2380.4	793.5	3.25	.02	
GENRNO X GRPMP1	6	1177.7	196.3	.80	.57	
Error	189	46149.3	244.2			
Total	200	50096.8				

see appendix A for definitions of variables

Table 21. ANOVA: AVMP2 = generation + groups AVMP2 + interaction.

Source	DF	SS	MS	F	P	R^2
Model	11	251.9	22.9	6.29	<.01	.32
GENRNO	2	3.5	1.8	.48	.62	
GRPMP2	3	83.0	27.7	7.60	<.01	
GENRNO X GRPMP2	6	151.8	25.3	6.95	<.01	
Error	149	542.8	3.6			
Total	160	794.7				

see appendix A for definitions of variables

Table 22. ANOVA: AVCAFWWT = generation + groups AVMP2 + interaction.

Source	DF	SS	MS	F	P	R^2
Model	11	3733.2	339.4	1.38	.18	.07
GENRNO	2	434.7	217.4	.89	.41	
GRPMP2	3	2748.8	916.3	3.74	.01	
GENRNO X GRPMP2	6	595.1	99.2	.40	.88	
Error	189	46363.6	245.3			
Total	200	50096.8				

see appendix A for definitions of variables

Table 23. ANOVA: AVCAFWWT = generation + groups AVCAFWWT + interaction.

Source	DF	SS	MS	F	P	R^2
Model	11	16066.3	1460.6	8.11	<.01	.32
GENRNO	2	379.3	189.7	1.05	.35	
GRPWWT	3	12955.1	4318.4	23.98	<.01	
GENRNO X GRPWWT	6	2721.9	453.7	2.52	.02	
Error	189	34030.5	180.2			
Total	200	50096.8				

see appendix A for definitions of variables

Table 24. ANOVA: AVMP = generation + groups AVMP + interaction.

Source	DF	SS	MS	F	P	R^2
Model	11	139.0	12.6	7.70	<.01	.38
GENRNO	2	3.0	1.5	.91	.41	
GRPMP	3	59.8	19.9	12.16	<.01	
GENRNO X GRPMP	6	67.5	11.3	6.85	<.01	
Error	141	231.4	1.6			
Total	152	370.5				

see appendix A for definitions of variables

Table 25. ANOVA: AVCAFWWT = generation + groups AVMP + interaction.

Source	DF	SS	MS	F	P	R^2
Model	11	5265.1	478.6	2.02	.03	.11
GENRNO	2	411.9	206.0	.87	.42	
GRPMP	3	2976.1	992.0	4.18	.01	
GENRNO X GRPMP	6	1899.7	316.6	1.33	.24	
Error	189	44831.7	237.3			
Total	200	50096.8				

see appendix A for definitions of variables