

GENETIC, ENVIRONMENTAL AND RESIDUAL MATERNAL
INFLUENCES ON COW PRODUCTIVITY
AND GROWTH OF CALVES

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TABLE OF CONTENTS

	Page
INTRODUCTION	1
REVIEW OF LITERATURE	6
The Heritability Concept.	6
The Notion of Permanent Environmental Effects	8
Sex as an Environmental Factor.	12
Age of Dam as an Environmental Factor	14
Season of Birth as an Environmental Factor.	18
Age at First Calving as an Environmental Factor	20
Effect of Previous Years' Calving History as an Environmental Factor.	21
Compensatory Growth and Relation of Various Growth Phases.	21
METHODS, MANAGEMENT AND DATA DESCRIPTION	29
ANALYTICAL METHODS	34
Contemporary Environmental Effects.	34
Contemporary Environmental Effects with Age of Granddam Adjusted (Model B)	46
RESULTS AND DISCUSSION	50
Contemporary Environmental Effects (Model A ₁)	50
Influence of Years	50
Influence of Age of Dam.	51
Influence of a Cow's Having Raised or Not Raised a Calf in the Previous Year.	55
Influence of Age of Dam at First Calving	56
Influence of Season of Birth	58
Influence of Plane of Nutrition.	58
Compensatory Growth Relationships.	60
Effectiveness of the Regression Models	62
Contemporary Environmental Effects with Age of Granddam Effects Adjusted (Model B ₁)	63
Repeatability Estimates of Growth Phases of Calves.	66
Estimates in Models A ₂ and A ₃	66
Estimates in Models B ₂ and B ₃	73
GENERAL DISCUSSION	75
SUMMARY AND CONCLUSIONS.	84
BIBLIOGRAPHY	88

LIST OF TABLES

Table		Page
1	Designations and Compositions of Individual Data of Growth Phases	32
2	Analyses of Variance and Least Squares Estimates of Certain Contemporary Environmental Effects on Growth Phases of Steers (Model A ₁)	39
3	Analyses of Variance and Least Squares Estimates of Certain Contemporary Environmental Effects on Growth Phases of Heifers (Model A ₁).	40
4	Analysis of Variance Model for all Traits in Sub-Model 3 of Primary Models A and B	45
5	Analysis of Variance Model for all Traits in Sub-Model 2 of Primary Models A and B	45
6	Analyses of Variance and Least Squares Estimates of Certain Contemporary Environmental Effects on Growth Phases of Steers with Age of Granddam Adjusted (Model B ₁)	47
7	Analyses of Variance and Least Squares Estimates of Certain Contemporary Environmental Effects on Growth Phases of Heifers with Age of Granddam Adjusted (Model B ₁).	48
8	Analyses of Variance for Growth Phases of Calves (Model A)	67
9	Components of Variance and Repeatability Estimates of Growth Phases From the Analyses of Variance in Table 8.	67
10	Analyses of Variance for Growth Phases of Calves (Model B)	72
11	Components of Variance and Repeatability Estimates of Growth Phases from the Analyses of Variance in Table 10	72

GENETIC, ENVIRONMENTAL AND RESIDUAL MATERNAL INFLUENCES ON COW PRODUCTIVITY AND GROWTH OF CALVES

INTRODUCTION

In the assessment of genotypes in animal breeding programs, the greatest obstacles are the identification or minimization of environmental influences affecting the phenotypes. Influences such as the effects of year, age of dam, size of litter and season of birth which in themselves express quantitative variations are adjustable by proper statistical methodology. These adjustments should be effective and reasonable within the assumptions on which they are based. They serve to remove phenotypic differences which occurred because the environmental conditions were not uniformly those recognized as standard. The logic on which correction factors are based must, however, be accompanied by sound experimental substantiation. Estimates of environmental influences are largely measures of postulated comparative advantage or disadvantage to which animals have been subjected. The values are indicative of effects, often obtained without a fundamental knowledge of their causation nor of the interaction which may have been endured between the genotype and the environment. The importance cannot be overemphasized of making adjustment for those effects which are environmental and in doing so in a manner which will not remove the genetic advantage which some animals have for withstanding these rigors.

In establishing criteria for selection and in establishing culling, feeding and marketing policies, a knowledge of the genetic and environmental relationships of various growth phases to total and marginal revenue and to aggregate genotype is forthcoming. The enterprising steer producer would use environmental relationships among growth phases to obtain the greatest advantage in utilizing feed supplies in a short-term enterprise and would utilize knowledge of genetic potential in procuring his animals and in making long-term decisions. The enterprising breeder would utilize genetic interrelations among traits in establishing accurate selection criteria. Thus, establishment of relative values of effects of known or assumed environmental factors, the lasting effect which they exert, their interrelated effects on growth, and their interrelation -- genetically and environmentally -- should give a more definite basis for distinguishing among animals when establishing any livestock program.

Differences in production from cows or in growth of calves which arise among years result grossly from variation in management practices, from differences in climatic and climatically influenced conditions including temperatures, humidities and forage supplies, and from variations in the stress impositions inherent in each of these causes. Similarly, among the probable factors which may occasion comparative differences among animals born in different seasons of the same year are variations in temperature, humidity, length of day, forage supply and the resultant climatic-nutritional-endocrine interrelations therein associated. Dissimilarities among otherwise similarly affected animals

of various litter sizes in multiparous groups are again, in part, due to comparative advantages, resulting from abundance or limitation in pre- and post-natal nutrient supply.

The effect of physiological immaturity, maturity, or senescence, on livestock production is outwardly expressed as an age of dam effect. Those differences in production which have been observed to occur among cows of varying ages are undoubtedly due to differences in ability to react to the interdependence of procuring, assimilating and adequately allocating nutrients to the various needs. Whereas a mature animal needs only to allocate nutrients toward milk production and maintenance during lactation, the young animal must allocate her nutrient resources toward maintenance, toward her own incomplete growth and toward the growth of her offspring. The decline in production with ensuing age subsequent to having reached a peak-age of production is associated with expression of accumulated effects such as loss of teeth, decrease in ability to procure forage, and in general deterioration in metabolic efficiency. The progressive senescence expressed by decreased production of livestock is the concession of ensuing victory of the environment over genetic potential.

The probability of similarity among related individuals compared to unrelated individuals forms the basis for the study of inheritance. The portions of differences in quantitative characters which are due to inheritance are determined by various methods on the basis of resemblance among related individuals and are cumulatively called the

heritable portion. Phenotype consists of a certain portion of variation due to environment and a certain portion due to heredity. The hereditary portion is further composed of additive effects, and of dominant and epistatic or less specifically non-linear hereditary effects. The environmental variance is recognized to consist of that part of environment which is random and common to all animals within that environment, and that portion which is particular to individuals within families or of the same maternal source. The latter would correspond to permanent environmental effects of a rather contemporary nature. Another portion of environmental variance is acknowledged, which if existent would exert itself in such a manner that it might be interpreted as hereditary variation; that is, the permanent environmental effect of having been subjected to environmental rigors which so limit the organism's ability to perform that the effect might be imposed upon the producing ability of its own young.

It is probable that drastic environmental physiological limitations such as the environmental effect associated with age of dam, when imposed upon an organism might result in a residual effect identifiable in the subsequent generation. If this were the case, it affords another logical source of error in the evaluation of genotypes particularly in those locations where environment is minimal rather than optimal. Apparent response, thus, in the extreme case would be for selection to favor the choice of an environmental reaction to environment rather than the response of a genotype to the environment. The permanent environmental portion of maternal effects which are of this

nature, as well of those of a mechanical nature which are often acknowledged, may well be surmised to exist among the influences which cause heritability estimates to differ when calculated by comparison of paternal relatives from those calculated from maternal relatives.

Through this study it will be proposed to ascertain whether a residual effect is realized in offspring whose female parents were subjected to various environmental rigors as a result of having been born to dams of various ages. It is acknowledged that the complexity of this phenomenon might exist such that the permanent effects could be expressed from dam to daughter, ad infinitum, and be modified progressively in the various generations. The ultrarefinement of the measurements thus are impractical under most points of view, other than theoretical, and in the long run the predictions of these residual effects might be no more consistent than practical. Moreover, the probability of this type of effect being expressed would be greatest under extremely rigorous environments such as those of many range areas and deserts. The effect might be negligible in those environments where a rapid compensatory growth can be made after weaning to replace any deficiency suffered prior to weaning.

In this study an attempt will be made to determine the extent to which the repeatability estimates vary as a result of ignoring or of removing various probable sources of permanent environmental effects.

REVIEW OF LITERATURE

Selection has the power to create new phenotypic variation by bringing together combinations of hereditary material. It can accomplish changes in the mean value of a population by change in the gene frequency or it can shift the original range of expression of traits by accumulation of the new genetic combinations. Lerner (42, p. 163) indicates that the rate of genetic change (ΔG) or gain achieved by mass selection is dependent on the heritability (h^2) or accuracy of genotypic identification, the intensity of selection (i) or population size, and time (t) or generation length such that $\Delta G = ih^2/t$. Changes in i , h^2 or t will therefore occasion changes in ΔG , thus measurement of their magnitude in a given population should lend predictive value in planning the breeding program.

The Heritability Concept

Lush (43, p. 90) states that phenotypic variance is expressed as $\sigma_P^2 = \sigma_G^2 + \sigma_E^2$, where σ_P^2 , σ_G^2 and σ_E^2 are phenotypic, genetic and environmental variances, respectively, if heredity and environment are uncorrelated; that is, where $2 \text{Cov}_{GE} = 0$. The genetic portion (σ_G^2) in the broad sense includes all the genetic differences while in the narrow or most useful sense (under random mating) it contains the additive effect of heredity. This additive fraction of phenotypic variance is called heritability, and it serves as a measure of identifying genotype from phenotype such that $\sigma_G^2 = h^2 \sigma_P^2$. Another way

of looking at heritability is that it is square of the correlation coefficient between phenotype and genotype. Thus it is consistent that if h^2 is the fraction "determined" by heredity, the remaining portion of variation is due to environment and to nonadditive effects of heredity which in a random breeding population are considered negligible (42, p. 112).

According to Koch and Clark (32, p. 778), by simple Mendelian theory under random mating, the genic values of half-sibs are correlated by one-fourth, dominance deviations are uncorrelated, and epistatic deviations are correlated by an undetermined but small amount. With proper discounting of environmental effects among half-sibs and with negligible maternal, permanent environmental, or epistatic effects, the expected value of the parental component of variance would be $\sigma_{S_r}^2 = \sigma_D^2 = 1/4\sigma_G^2$ under random mating, where S_r and D are sire and dam designations, respectively; and the expected mean square among offspring from the same parent $(\sigma_e^2) = 3/4\sigma_G^2 + \sigma_E^2$. Thus an estimate of heritability would be

$$h^2 = 4\sigma_{S_r}^2 / \sigma_{S_r}^2 + \sigma_e^2 = 4\sigma_D^2 / \sigma_D^2 + \sigma_e^2.$$
 However, with mammals and in our case with beef cattle this system is valid with sires but does not hold for estimating heritability from the dam component since the relationship among maternal half-sibs differs from paternal half-sibs because of maternal environmental influences both pre- and post-natally until weaning.

According to Koch and Clark (35, p. 979-996) the expectation for a given trait (i) among paternal half-sibs is $\sigma_{S_r}^2 = 1/4\sigma_G^2$ but the expectation for the same trait among maternal half-sibs

$$\sigma_D^2 = 1/4\sigma_{G_i}^2 + m_i^2 g_m^2 + m_i^2 p_m^2 + G_i m_i r_{G_i g_m}$$

where G_i is the heritability of the ith trait, m_i^2 is the direct determination by maternal environment, g_m^2 is the heritability of the maternal environment, p_m^2 is the direct determination of maternal environment by permanent environmental factors, and $r_{G_i g_m}$ is the genetic correlation between the ith trait and maternal environment. It is corollary that $m_i^2 g_m^2 + m_i^2 p_m^2 = m_i^2$ since $g_m^2 + p_m^2 = 1$. It is reasonable to presume that the maternal effects might become diminished with ensuing age of the calves, or that negative effects might be shown at certain of the growth phases. However, a lasting effect of maternal influence is not improbable, for in spite of the negative relationship of gains among growth periods, the final weights of the various growth phases are usually positively associated (37, p. 18), (4, p. 1018).

The Notion of Permanent Environmental Effects

McMeekan (47, part 4, p. 22) has aptly inferred that "recognition of the controlling influence of environment in the development of the animal body and of the permanent nature of its effects upon the mature form invites consideration of its relationship to the hereditary

* $\sigma_{S_r}^2$ indicates sire variance. Koch and Clark designated it σ_S^2 .
 In this study S refers to season of birth (p. 37).

factors believed to set the limit to the expression of all characters".

A given growth phase is measurable only once and in one environmental regime during the lifetime of the animal, and the hereditary effect on that growth phase is measurable through comparing it to the similar growth phase of related individuals in contrast to unrelated ones. Thus the average heritability of a trait is measured. Comparison, however, of the probable producing abilities among cows, based on successive records, reveals what Sidwell and Grandstaff (60, p. 373-380) quoting Lush called repeatability, which contains the additive genetic effect and permanent environmental influences. Lush (43, p. 300) states that "repeatability is useful in setting an upper limit to heritability". Botkin and Whatley (3, p. 552) asserted that repeatability includes all influences due to permanent differences among cows and therefore measures the accuracy of past production in predicting future production of the same herd of cows. They inferred that some of the permanent differences among cows may be nontransmissible, thus repeatability is an overestimate of probable gains through selection.

Permanent environmental effects are acknowledged (31, p. 768-755) to be the results of such factors as stunting when young, permanent injury to the udder, crippling, etc. Effects such as these would certainly be classified as random permanent environmental effects and perhaps would be evaluated more evidently as genic maternal influence

due to their contemporary occurrence and to lack of their reliable discernment in assessing a population. Lush (43, p. 300) stated "if the kinds of feeding to which calves and young heifers are subjected do affect their production all throughout the rest of their lives, whatever differences in their later production in feeding caused would appear again and again in subsequent lactations. Such differences would be included in the repeatability but they would not be heritable". McMeekan (47, part 4, p. 20) asked "Does a continued low level of nutrition or a permanently inadequate level stunt the mature size of the individual and alter its proportions?" "Further, ..., should environmental influences produce a permanent effect, what are the repercussions on subsequent generations?" He asserted (p. 23) that general evidence from the field of animal husbandry is in support of a permanency in effect. His evidence is clearly indicative of genetic-environmental interaction on body form, but it scarcely warrants adopting an environmentalist approach to the inheritance problem. The extent to which his "physiology of today is the developmental history of tomorrow" is, however, implicit in the probable residual effects of environment.

On the basis of these speculations it is reasonable to acknowledge probable existence of residual effects of environment in successive generations. It is reasonable, moreover, to infer that the permanent effects might be of both random and fixed source. The effect associated, for example, with age of granddam would be considered a

fixed source of variation, while residual variation among cows from given granddams would be demonstrable as random variations.

Repeatability sets an upper limit to the probable expectation of a cow's performance, and provides a reliable tool for setting up culling programs. It does not, however, necessarily enlighten one on the genetic usefulness, say, of heifer calves from two-year-old dams since the environmental inhibition endured by the calf might affect or be reflected in the calf's own eventual production.

Gifford (16, p. 32) pointed out the effect of daily milk production of beef cows on the growth of beef calves. Significant differences between cows existed in 8-month calf weights. The within-cow correlation between milk records and 8-month calf weights was .47. Growth of heifers up to 36 months of age indicated that the level of milk production of the dams was rather highly positively correlated with the growth of heifers during the post-weaning period and up to three years of age.

Illustrative of the difference between heritability and repeatability estimates are those presented by Koch and Clark (32, p. 785). Heritability and repeatability estimates, respectively, were .35 and .26 for birth weight, .24 and .34 for weaning weight, .21 and .34 for suckling gains, .47 and .20 for fall yearling weight, and .39 and .09 for gain from weaning to fall yearling date. The relative effects of maternal environment and the inherent growth potential of the calf are evident in the differences among the estimates.

Koger and Knox (38, p. 461-466) obtained a repeatability estimate of .51 for weaning weight and stated that "a heifer that weaned a decidedly substandard calf barring accidents, etc, ..., was never a heavy producer in later years". Chambers, et al (11, p. 43) found the repeatability of cow performance (.30) to be similar when measured by calf growth at 112 and 210 days. Estimates of repeatability were obtained by various methods by Botkin and Whatley (3, p. 552) ranging from .33 to .66 for weaning weight, .14 to .25 for birth weight and .38 to .69 for suckling gain.

Sex as an Environmental Factor

Mason, et al. (46, 6 p.) and Koch et al. (36, p. 738) have shown that the means and variances of growth traits of bull and heifer calves differ, and that in such cases an additive correction to a similar sex basis is not valid. Mason, et al. (loc. cit.) asserted that to evaluate a cow's production, the adjustment of a heifer's growth characteristic to a male basis where the coefficients of variation of bulls and heifers are the same requires multiplication by R, which is a constant ratio (\bar{B}/\bar{A}), where \bar{B} is the mean of the bull growth characteristic and \bar{A} is the mean of the heifer growth characteristic. If the coefficients of variation are not equal, the correction of a heifer's trait (A_1) to a bull basis (\hat{B}_1) takes the form of: $\hat{B}_1 = [\bar{B} - (\bar{B} \frac{s_B}{s_A})] + \frac{s_B}{s_A} \times A_1$ where $\frac{s_B}{s_A}$ is the ratio of the standard deviations of bulls to heifers. Guilbert and Gregory (19, p. 3) attested that at 1 month the weight of heifers is 97 percent that of bulls, at 4 months 89 percent, at 12 months 77

percent, and at maturity 65 percent. Differences reported in the literature are greater between bulls and heifers than between steers and heifers. Carter and Kincaid (8, p. 331) found different heritability estimates for six-month weight of heifers and bulls which they indicate are the first such heritability estimate differences reported in the literature. Their estimates were 0.08 for steers which is in line with the findings of Blackwell, et al. (4, p. 1018) and 0.69 for heifers which is the highest of all estimates reported for this trait.

Whereas more information is handily available about birth and weaning phenomena than for other growth phases, indications are that sex differences are established at birth and become magnified with time. Koch and Clark (32, p. 397) found bulls to be heavier at birth than heifers, and differences are reported ranging from 4.2 to 5.8 pounds bull advantage by Burris and Blunn (6, p. 41), Dawson, Phillips and Black (13, p. 247) and Gregory, Blunn and Baker (17, p. 338). Dahmen and Bogart (12, 23 p.) found feedlot-daily-gains of bulls and heifers to be 2.0 and 2.3 pounds, respectively, and that 18 percent of the variations were due to birth weight differences. The sex differences were further borne out by the data of Koch (31, p. 768), Chambers, et al. (10, p. 10) and Rollins and Guilbert (53, p. 517), respectively, found bulls to be 44, 21 and 68 pounds heavier than heifers at 176, 210 and 240 days. Koger and Knox (37, p. 19) attested that steers at 205 days were 32 pounds heavier than heifers under semiarid range conditions. Hitchcock, et al. (24, 22 p.) showed a 43

pound difference in yearling weights of steers and heifers, again steers being heavier,

Age of Dam as an Environmental Factor

Sabin (57, 58 p.) has shown that the effect of the age of a cow on her producing ability is expressed as a quadratic function, that the effect on pre-weaning growth is largely due to differences in maternal effects associated with both weight and age, and that the reciprocal of this function is apparent in the post-weaning performance. Lush and Shrode (44, p. 338) state that "milk production increases with age at an ever decreasing rate until maximum production is reached at 6 to 8 years. Production then declines with advancing age. This makes the regression of production on age distinctly curvilinear but the nature and amount of the curvature does not appear deductible from any general physiological principles." Sawyer, et al. (59, 7 p.), assert that beef cattle might be expected to improve in milk yield as they reach maturity and that increased yield should reflect itself in heavier calves at weaning.

Koger and Knox (38, p. 466) found that weight of cows and weaning weights of their calves increased each year until cows were 7 years of age and that subsequently both weights decreased yearly. Cows of 3, 4, 5, 9, and 10 years of age average 67, 49, 25, 18 and 32 pounds, respectively, less calf weaned than 7-year-old cows. Sawyer, et al. (58, p. 514) found that weaning weights of calves increased with increasing age of dam through eight years of age and then declined.

Eight-year-old cows at the Squaw-Butte Harney Station produced calves which were 83 pounds and 59 pounds heavier at weaning than those from 2- and 3-year-old cows. Four-year-old cows were approaching producing ability of mature animals. Hitchcock, et al. (24, 22 p.) found no evidence to indicate that age of dam needs consideration when selection is based on yearling weights. Correction factors developed by Koch and Clark (32, p. 379) for converting birth, weaning, and fall yearling weights of calves from young cows to a mature basis were: 4, 41 and 24 pounds for 3-year-olds; 2, 18 and 13 pounds for 4-year-olds; 0, 6 and 3 pounds for 5-year-olds; 0, 12 and 7 pounds for 9-year-olds; and 2, 24 and 14 pounds for 10-year-olds. Rollins and Guilbert (53, p. 517) published data indicating the same magnitude of effects, however they emphasized the need for different correction factors for bulls and heifers with greater apparent variability among bulls. This need, moreover, was borne out by Kincaid and Carter (28, p. 683).

Gifford (16, 34 p.) reported that beef cows between the ages of two and three years produced less milk than cows of any other age studied. The quantity of milk produced had a tendency to increase with age of cow up to six years. Lasley and Bogart (41, p. 56) found that fertility (services per conception) follows the same age pattern as that reported for calf production. Pahnish (50, 108 p.) established the necessity of adjusting 270-day weaning weights to a common age of dam basis by adding 50 pounds to bull calves from 3-year-old cows, 25 pounds to those from 4- and 9-year-old cows and 0 pounds to calves

from 5- through 8-year-old cows, and 24, 12 and 0 to heifer calves from cows of the same age. Evans, et al. (14, p. 1181) estimated that the addition of 106, 54, 20, 14 and 43 pound weaning-weight-corrections to calves from 2, 3, 4, 9 and 10 year old cows, respectively would adjust for age-of-dam effects. Botkin and Whatley (3, p. 552) removed 82 percent of age of dam variation in weaning weight by addition of 35 and 15 pounds to weaning weights of calves from 3- and 4-year-old cows. Similarly, they removed 62 percent of the age-of-dam effect on birth weights by addition of 4 and 2 pounds to birth weights of calves from cows of the same ages. They asserted that older cows produced heavier calves than expected as a result of biases due to concurrent selection and to probable genetic time trend as explained by Lush and Shrode (44, p. 338).

Blackwell, Knox and Hurt (4, p. 1018) reported that yearling weights of calves from 3-year-old cows, 4- and 5-year-old cows, and 6- and 7-year-old cows were 33, 14 and 8 pounds less than those from 8- and 9-year-old dams. Yearling gains, however, showed the inverse relationship particularly in that yearling gains of calves from 3-year-old cows and from cows 10 years old and older were greater than those of 8- and 9-year-olds. They stated that "calves that were subjected to better than average or less than average environment prior to weaning because of the age of their dam will tend to exhibit compensating responses in post-weaning growth when nutritional environment becomes more nearly uniform". The effect of compensatory growth

was such that it reduced the effect of age of dam on yearling weight but some age-of-dam effect remained at approximately 18 months of age.

If in a herd some cows with low producing ability are culled at each age, then at each succeeding age the group would contain a larger share of high producing cows and a smaller share of low producing cows than would exist at younger ages. Bias, therefore, is introduced by concurrent selection and consequently correction factors may be biased from the true age effect, according to Lush and Shrode (loc. cit.). One bias is due to the effect of culling for low production at early ages causing survivors to contain effects of both selection and age. The other bias is due to genetic time trend which would be related to age. Accordingly, the true age change would be $\frac{k}{N} (K' - K) + \frac{c}{N} (C' - C)$ where N is the number of cows with records at a given age; K is the number of cows kept to make a record at the next age; C is the mean production of c cows at the first age; and C' is the mean production which c cows would have made at the next lactation had they been kept.

Method A presented by Lush and Shrode for calculating correction factors for age of dam compares averages of all records made at each age such that the apparent change is $K' - \frac{kK + cC}{N}$ which contains bias to the extent of $\frac{c}{N} (C' - K')$. Their Method B attempts to avoid effects of selection by comparing records of the same cow at successive ages such that the apparent change between two ages is $(K' - K)$ and the inherent bias is $\frac{c}{N} [(C' - K') - (C - K)]$. By Method A, correction factors would be biased upward from the true effect since correction

factors are derived from comparison of selected older cows with less intensively selected younger cows. Conversely, the factors computed by Method B would under-correct due to imperfect repeatability of records by the same cow. These methods were adapted for evaluation of milk production in dairy cattle, but are logically applicable to growth phenomena affected by maternal effects.

Season of Birth as an Environmental Factor

Under most managerial conditions, all calves in a beef operation are weaned on the same date. When birth dates and weights are known, actual daily gains can be computed and an accurate corrected weight can be obtained if the assumption of linearity of growth is valid to that age. If birth weight is not known, a linear regression equation can be fitted to obtain an average increase in weight per unit increase in age. The former system is inaccurate in so much as the birth weight and the post-natal environment may have been influenced by seasonal differences in forage conditions as a result of varying birth dates. The latter is inaccurate due to the same reason as well as the fact that all calves are put on an equal birth weight basis.

Koch and Clark (32, p. 397) found the regression of birth weight on weaning age to be $-.08$ pound per day, indicating that calves born later in the calving season were heavier at birth. The regression of gain from birth to weaning age was $-.04$ pound per day

(not significant) indicating a trend for calves born later in the season to grow more rapidly than those born earlier. The regression of weaning score on weaning age was .01 unit per day indicating that earlier calves tend to score a little higher than later calves.

Rollins and Gregory (53, p. 517) adapted correction factors of -39, 0 and -16 pounds to be added to calves born from August to November 15, November 16 to February, and March to May, respectively.

Nelms and Bogart (49, p. 662) indicated that calves born early in the year gain more rapidly during the suckling period than those born later. They contended that time of birth had an equal or greater effect on rate of suckling gains than did age of dam. Granting that selection for suckling gains had been applied to the younger cows, consideration must be given to the fact that 1) these cattle enjoy quasi-optimum environment, and that 2) a portion of differences among ages might have been removed by adjustment for birth weight, while the seasonal effects on gains is affected by seasonal effect on post-natal maternal conditions.

Marlow and Gaines (45, p. 1018) found that the mean suckling gains of calves born between December 16 and March 15, March 16 and May 31, June 1 and August 31, and September 1 and December 15 were 1.65, 1.69, 1.56 and 1.53, respectively the advantage being enjoyed by earlier calves.

Gifford (16, 34 p.) found that maximum milk and butterfat production on the average was attained during the first month of lactation and subsequently decreased at a decreasing rate. Gifford (15, p. 605)

also attested that the maximum milk production attained during these first weeks of lactation is affected by the capacity of the young calves to consume the milk. This ability of the calf to consume the cow's potential milk supply interrelated with seasonal effect on forage production is of deductive importance to the interpretation of seasonal phenomena.

Age at First Calving as an Environmental Factor

Sawyer, et al. (58, 7 p.) indicated that breeding heifers as yearlings had a much greater influence on size of cows as three-year-olds and on weaning weights of calves when cows were three years old than did feeding during development of heifers. Three-year-old cows weighed 643 pounds and raised 275 pounds of calf when bred first as yearlings, while they weighed 712 pounds and produced 320 pounds of calf if bred first as 2-year-olds.

Webb (64, p. 1190) of Illinois, asserted that approximately one additional calf is produced by breeding heifers to calve first as 2-year-olds. Zimmerman, et al. (68, p. 42) found that, in Oklahoma, cow-costs per calf weaned were less for cows that calved first at 2 years of age. Cows calving first at two years of age weaned 6.4 calves with an average weight of 477 pounds while those that calved first at three years of age produced 5.3 calves with an average of 487 pounds. More calving difficulties (dystocia) were encountered by calving first at 2 years of age. Pope, et al. (51, p. 42), converse to the data of Sawyer, et al. (59, 7p.), indicated a lack of

difference in calf production of 3-year-old cows having calved first as 2-year-olds and those calving first at 3 years of age. It is evident from the 400 pound weaning weights of calves from 2-year-olds that the Oklahoma environment is a quasi-optimum one at least during the suckling phase of the year. Nevertheless, Pope, *et al.* (*loc. cit.*) stated that early breeding retards body development of the female and increases time required to reach mature size.

No apparent literature is available on cows calving first at 4 years of age nor on the physiological significance of effect of age at first calf on subsequent production in terms of an effect imparted to the individual subsequent calf.

Effect of Previous Years' Calving History as an Environmental Factor

No apparent data exist to infer a relationship between the weight of a calf at a given growth phase and whether or not the dam raised a calf in the previous year. Lasley and Bogart (41, 56 p.) reported that dry cows were harder to settle than lactating cows. They required more services per conception and returned smaller calving percentages than lactating cows. They admitted the possibility of inherent infertility as well as immediate barrenness being the cause of these effects.

Compensatory Growth and Relation of Various Growth Phases

A knowledge of the relationship of growth made by animals in various periods of their lives is implicit in sound planning and

management of the livestock enterprise and in the selection of livestock or in estimation of future growth. Koger and Knox (39, p. 760) and Koger, et al. (40, p. 1018) reported that in range beef calves, weights at various periods in life were positively associated while growth rates or gains in adjacent periods were negatively associated or uncorrelated. Koger and Knox (loc. cit.) asserted that a positive relationship between growth rates in different periods would exist where environment to which the animals were subjected, in the various periods, was held uniform. Conversely, they inferred that a negative relationship between growth rates at different periods would be expected when environmental variations are experienced during one period and later removed allowing a compensation for over or under growth which occurred in the previous period.

McMeekan (47, part 4, p. 23) insists that the animal body possesses two outstanding characters -- plasticity and resiliency. On the one hand, its form and its tissues can be molded and shaped to a remarkable degree by the influence of its nutritional environment. Moreover, it possesses an amazing recuperative capacity; its tissues are capable, in certain cases and circumstances, not only of tolerating extreme environments, but under specific conditions, can largely recover from the limiting effects of unfavorable environment. The animal is not an isolate in a neutral environment but a living organism dependent upon and responsive to the environment in which it finds itself for expression of its inherent capacities.

The profound influence of nutrition upon the development of the animal is fundamentally dependent on the fact of differential growth. McMeekan (1940) in his monumental study of the pig has shown the relationship between the influence of nutrition and the differences in body form and composition. Wide differences in quantitative control of the nutrient energy available and in the qualitative plane of nutrition, even to variations far greater than normally met with in the field in the ratio of protein to carbohydrate, are covered in principle by his results. The imposition of extreme differences in quantitative plane of nutrition upon pigs over the same age period occasioned tremendous differences in body development, over the same age period, to the extent that though the animals on various nutritional regimes were of similar chronological age, they were widely different in physiological age. The animals on continuous high plane nutrition attained a state of development of body proportions, organs, and tissues which was superior, that is, more greatly advanced than normally occurs at their age. The low plane resulted in developmental retardation, not in the sense that those retarded were miniatures of those on high nutritional level, but to the extent of characteristic inhibition of growth in "late developing" parts of the body.

Environmental effects, such as those imposed on young cattle because of being born to dams of certain weights and ages in certain seasons of given years, for example, exert influences of comparative advantage on the individual calves such that their environments

(nutritional planes) vary at different phases of their life and are classifiable into all permutations of the thesis of McMeekan (47, part 1, p. 278-282). Hammond (20, p. 401-411) presents material indicating that the effects of underfeeding only to the extent that live-weight growth is arrested does not arrest skeletal growth, thus a recuperative expression after a period of underfeeding results in prolongation of the growth period. It was noticed that an animal which was underfed -- but not to the extent of detriment -- during early life will continue to grow after a normally fed animal has ceased to grow. McMeekan (41, p. 276) found that animals changed from a high to a low plane of nutrition improve in the overall efficiency of feed conversion while transfer from low to high plane decreased efficiency. Hammond (20, p. 401) learned that long term retardation of growth depresses efficiency of food conversion because of high maintenance costs and also that if the retardation is extreme the animals may never reach normal size. Stunting may be permanent if the retardation of growth is sufficiently severe, occurring early in life, and over a sufficient length of time. Short-term retardation at the appropriate stage, however, may improve the overall efficiency of food conversion. Compensatory growth occurs at a rate appropriate to physiological age rather than chronological, yet cheaper feed can be used to obtain physiological maturity on retarded animals. Physiological age is inversely related to the rapidity of growth and development (20, p. 395).

Sabin (57, 58 p.) and Blackwell, et al. (5, 6 p.), showed that the environmental effect on post weaning gains associated with age of dam resulted in a quadratic function reciprocal to that generally associated with preweaning gains. Blackwell, et al. (loc. cit.), found that compensating effects were still evident at 18 months for rigors endured during the suckling period. They found that after adjusting contemporary effects of environment the weights and gains from weaning through final weight were generally positively associated, genetically and phenotypically. Differences in magnitudes of the correlations indicated that compensatory actions must have been operative on yearling gains and weights. Similarly, Romo and Blackwell (54, 5 p.) found positive genetic correlations between weights and gains at various periods. They inferred that "since size attained at a particular age is dependent on growth rate, it is reasonable to expect positive genetic correlations between size and gains at different periods."

The work of Kidwell (27, p. 54) established that correlations between gains of adjacent periods (winter, summer, fall and second winter) subsequent to weaning were negative and significant. Correlations involving weaning weight were not significant. There was a positive significant correlation between the gains of the two winter periods. He clarified that nutritional and other environmental factors vary widely among the growth periods and concluded that "environmental influences exert the greatest effect on the relation between gains at different periods

but that heredity is also effective." Ruby, et al. (56, p. 280) found generally similar phenotypic relationships as those found by Kidwell. Urick, et al. (67, p. 1026), found positive genetic correlations among first winter, second summer and second winter gains.

Koger, et al. (40, p. 1018), stated that negative phenotypic relationships exist between growth made during adjoining periods, but that in general, growth during one period is basically positively related to growth at other periods. They report that the within-breed and within-year correlations between: birth weight and weaning weight was 0.47; birth weight and suckling gain was 0.31; birth weight and gain from 6 to 12 months was 0.00; and birth weight and 24-month weight was 0.43.

Wagnon and Rollins (62, p. 1026) demonstrated the relative role of genetic and environmental interactions and asserted that identification of genotypes would be most accurate under optimum nutritional regimes. The correlations of the weaning and long-yearling weight of a cow with the weaning weight of her calf were 0.16 and 0.36, respectively, for those under optimum conditions and -0.06 and 0.01, respectively, for those on sub-optimal regime.

Sabin (57, 58 p.) found the partial regressions of total gain in the feedlot and final weight, respectively, to be 2.10 and 2.19 pounds, per pound increase in birth weight, and 0.23 and 0.92 pounds per pound increase in weaning weight, in the same order. Dahmen and Bogart (12, 23 p.) found that 0.1 pound per day increase

in daily gain in the feed lot resulted from each 10 pounds increase in birth weight and that 10 days difference in age-put-on-test was accompanied by 0.05 pounds daily gain difference. Suckling gain played no important role in determining rate of feedlot gain. The magnitudes of the findings of Pierce, et al. (52, 32 p.) were similar to those of Dahmen and Bogart.

Ross, et al. (55, p. 49), Pope, et al. (51, p. 42) and Zimmerman, et al. (68, p. 42) found no difference in life time production of cows being calved first as 2-year-olds or 3-year-olds and wintered on low, medium or high level of nutrition. Woodward, et al. (65, 14 p.) indicated that calves from full-fed three year old cows were significantly heavier at birth and made greater daily gains than those from limited-fed cows. After this age the influence of the ration was not apparent on any factor of the cow's production. The indication was that the effect of low plane of nutrition was not permanent. (Winchester and Howe (66, 34 p.) subjected monozygotic twins to 75 percent, 62 percent and 50 percent rations while their co-twins were allowed a full ration.) They found that in cases of growth arrested between 6 and 12 months efficiency in feed utilization, quality of meat and quantity of lean meat were not adversely affected. The time required to reach 1,000 pounds by identical twins subjected to growth-arresting nutrition varied from 2 to 4-1/2 months more than the co-twins on high plane. After the period of reduced intake ended, the retarded animals gained weight rapidly and economically,

and although they required 10 to 20 weeks more to reach 1,000 pounds they did so on a similar energy intake. The increase in efficiency of feed utilization in the restricted group compensated for the delay in time, and ultimately the efficiency of producing a unit of beef was not different between the restricted and ~~unrestricted~~ groups. These data are somewhat in contradiction to the work of Guilbert, et al. (1944) in which lowered efficiency was attested to be associated with gains subsequent to interrupted growth. From Winchester's data it might be inferred that the animals which were retarded at a given physiological age, since they were on a "balanced" maintenance ration rather than on depletion diets, were actually undergoing a physiological aging in the "priority" portions of the body at the expense of the "low priority" regions. When restored to a growth diet they were actually physiologically more mature than it was outwardly apparent. Thus these animals were able to grow at the level characteristic of physiologically older individuals than they themselves appeared to be.

Bohman (2, p. 249) reported a trial in which he fed early-cut and late-cut hay, reflecting stage of maturity and nutritive value, to beef calves during a winter such that they, on the respective rations, gained 0.92 and 0.29 pound per day during the winter. The gains on subsequent summer pasture were 1.29 and 1.54 pounds, in the same order. The group restricted by inferior hay quality gained significantly more during the summer following feeding of

the different quality hay. Yet, in spite of the compensation in growth, the non-restricted (early-cut hay) group were heavier at the end of the trial. These concepts on compensatory growth are consistent with the reasoning of Taylor (60, p. 291) who describes the linear growth process on a basis of the broad fact that with respect to rate of maturing in liberally fed animals, each linear body measurement occupies a fixed position relative to every other throughout life.

METHODS, MANAGEMENT AND DATA DESCRIPTION

The data used in this study were from the grade Hereford herd maintained at the Squaw-Butte Harney Experiment Station under the auspices of the Agricultural Research Service, United States Department of Agriculture, and the Oregon Agricultural Experiment Station. The data involved calves born during the 10-year period from 1947 through 1956, inclusive. The study integrated data on birth through long-yearling weights of 390 steers and 417 heifers which are progeny of 250 dams and 165 granddams. The ages of the dams and the granddams are from 2 to 10 years.

Management of the herd is in general accordance with that of other cattle operations in the same sagebrush-bunchgrass region of the Northern Great Basin. The management cycle for the calves and yearlings is similar to that for the cow herd. The summer grazing area is a sagebrush (Artemesia tridentata) -bunchgrass (Agropyron, Festuca spp.) range at an elevation of 4,600 to 5,000

reet, in a rainfall belt of 8 to 12 inches per year. The highest plane of nutrition is achieved during May and June with a progressive decline to 3 percent in grass protein content in the fall.

The overall condition of the environment has improved markedly in the past few years as a result of sagebrush control, reseeding to crested wheat grass and re-establishment of the bunch grasses by reduction of competition from sagebrush. This, however, is accounted for by measurements of year differences.

The cattle are trucked to summer range in late spring subsequent to calving and trucked to fall pasture in early fall. Prior to 1951, the cattle were trail-driven to summer range over a three-day period and returned to fall pastures over another three-day period (25, p. 279). Fall pastures consist of meadow stubble and scattered hay left during the haying operations on the station near Burns, Oregon, at an elevation of approximately 4,000 feet. The meadows are of the wet-land type with 80 percent of the forage consisting of rush (Juncus spp.) and sedge (Carex spp.). The rather low-quality native meadow hay consisting of rush, sedges and native grasses is fed beginning in early December and continuing through April. Basically, the plane of nutrition is low in this entire area, however, as previously stated, great strides in technology within the past few years have resulted in marked increases in forage and beef production.

Purebred Hereford sires were used during restricted breeding seasons on summer range so that calves were born mainly in March,

April and May. Breeding was done in multiple sire groups, thus no data were available for sire classification and mating must be assumed random.

Birth weights were taken to the nearest pound as soon after birth as possible. All other weights represent "overnight shrink" weights. For purpose of analyses, weaning weights were adjusted to 225 days, yearling weights to 385 days and long-yearling to 505 days by the methods presented in Table 1 and the gains in the periods were derived by the various differences. The ages to which the weights are corrected are the average ages at which the weights were taken.

The birth weight of an individual calf is dependent on the genetic constitution of the calf itself, that is the egogenotype, /1 and on the prenatal maternal effects imparted by the dam. Weaning weight is likewise a result of egogenotype of the calf, as well as prenatal and preweaning maternal influences which in turn are influenced environmentally and by the egogenotype of the cow. Yearling weight includes the effects peculiar to weaning weight and either positive or inverse relationship between pre-weaning growth and post-weaning growth. Maternal influences on growth should be progressively diminished or might exert a negative effect with ensuing age of calves as a result of the probable action of compensatory relationships. Long yearling weight would be affected

/1 The term "egogenotype" will be used to designate the calf's own genetic constitution in regard to a given trait in contrast to the contribution of genetically influenced maternal effects to the expression of the trait.

Table 1. Designations and Compositions of Individual Data of Growth Phases.

Variable	Designations ^{/1}	Composition of Age-adjusted Data
Birth Weight	Y_1 and BW	Actual Birth Weight
Weaning Weight	Y_2 and WW	$\left(\frac{\text{Observed WW} - \text{BW}}{\text{Actual age in days}} \right) 225 + \text{BW}$
Yearling Weight	Y_3 and YW	$\left(\frac{\text{Observed YW} - \text{BW}}{\text{Actual age in days}} \right) 385 + \text{BW}$
Long-yearling weight	Y_4 and LYW	$\left(\frac{\text{Observed LYW} - \text{BW}}{\text{Actual age in days}} \right) 505 + \text{BW}$
Suckling Gain	Y_5 and SG	WW - BW
Yearling Gain	Y_6 and YG	YW - BW
Long-yearling Gain	Y_7 and LYG	LYW - BW
Weaning-to-yearling-Gain	Y_8 and W-YG	YW - WW
Weaning-to-long-yearling-Gain	y_9 and W-LYG	LYW - WW
Yearling-to-long-yearling-Gain	Y_{10} and Y-LYG	LYW - YW

^{/1} Designations herein used will be used in all subsequent tabular presentation for brevity sake.

therefore by the factors affecting yearling weight and by the relationships between weaning-to-yearling gains and yearling-to-long-yearling gains. Actual gains such as birth to weaning, i.e., suckling gains are indicative of genetic ability of the calf to grow and of maternal environment. Suckling gains are exclusive of birth weight other than through causative effects, if they are correlated through maternal environment or through genetic interrelation. Weaning-to-yearling gains, weaning-to-long-yearling gains and yearling-to-long-yearling gains are exclusive of birth weight and suckling gains, however they represent the egogenic ^{/2} ability of a calf to grow and the environmental effect of changing environments. The changing environments to which these animals are subjected during these phases does not lead one to expect uniform direction and magnitude of gains in all phases. Maternal influences affect these gains only through residual means or perhaps in a negative way due to the alteration of environmental regimes. Long-yearling gain is the gain from birth to long-yearling age exclusive of birth weight and is a composite of egogenic potential, maternal effects to weaning, and compensatory interrelations through the wintering and subsequent summer phases.

^{/2} An "egogenic" effect will refer to an expression of the egogenotype.

ANALYTICAL METHODS

Acknowledging the general difference in variances as well as the difference in mean values of growth traits between sexes, heifer and steer data were combined for this study after appropriate corrections were made for mean differences in growth traits and for the differences in variances. The correction for sex is explained in greater detail subsequently. A discussion of methods of sex adjustment is presented in the literature review in the section on sex effects.

The traits or growth phases which are dependent on the genetic and environmental forces operating in this herd are designated Y_w where Y is the dependent trait and w = trait number as given in Table 1. The analysis of the data was conducted by the least squares method of estimation (1, p. 153-337). Simultaneous equations associated with two primary models, each composed of 2 sub-models, were solved to obtain estimates of the contemporary environmental effects, and the presumed residual permanent effects. The equations associated with the primary models were solved separately for heifers and steers so that any interaction between sex and environment would not enter into the analysis.

Contemporary Environmental Effects (Model A)

For purposes of estimating the effect of contemporary environment (ignoring permanent environmental effects and among-cow variation),

each observation on trait Y_w is assumed to be the sum of the influences or effect of the identifiable variables as follows: Model A_1 describes

$$Y_{hlmok} = \mu + J_h + A_1 + C_m + N_o + b_F F + b_S S + e_{hlmok} \quad \text{where}$$

Y_{hlmok} = trait Y_w of the k^{th} calf

μ = a constant, common to all calves, analagous to the intercept on the ordinate when the effects of $J_h = A_1 = C_m = N_o = F = S =$ Zero

J_h = a constant for the h^{th} year; $h = 1947, \dots, 1956$.

A_1 = a constant for the l^{th} age of dam; $m = 2, \dots, 10$.

C_m = a constant for the effect of a cow's having raised a calf or not having raised a calf in the previous year; $m = 1$ or 0 , respectively.

N_o = a constant for the o^{th} plane of nutrition; $o = 0, 1$ and 2 , for "herd plane", "low plane", and "high plane", respectively.

The effects are estimated only in the heifer group since all steers were subjected only to the "herd plane".

b_F = the partial regression coefficient of trait Y_w on age of dam at first calving.

F = age of cow at first calving; $F = 2, 3$ or 4 .

b_S = the partial regression coefficient of trait Y_w on season of birth.

S = season of birth; S = days from January 1 to birth.

e_{hlmok} = error or failure of the above to estimate trait Y_w for the k^{th} calf.

This linear combination of effects serves to measure the relative sources of contemporary environmental variation affecting any one of the w traits. The common effect, μ in this mathematical model includes the basic similarity of the observations due to the animals being of the same species and having been subjected to similar general environmental conditions. Year effects, J_h represent dissimilarities explicable in terms of differences among years in weather and its effects on forage and foraging conditions. Changes in management practices are reflected in the year effects. The effects of age of dam, A_1 , are imparted as a result of differences among dams in physiological maturity associated with age and in consequential differences in their ability to procure, assimilate and allocate their nutrient resources to maintenance, to lactation, to their own and to their calf's growth, under existing environmental regimes. The effect of the dam having calved in a previous year, C_m , represents the probable advantage or disadvantage imposed upon a calf whose dam raised a calf or failed to raise a calf in the previous year. Under these rigorous environmental conditions, calving "skips" are quite frequent and the reproductive rest might impart an advantage to a calf whose dam "rested" by having failed to calve in the previous year.

During the years, 1951 through 1956 inclusive, a group of heifers was allotted to each of two levels (high and low) of post-weaning winter nutrition for purposes of another experiment and the balance

of the heifers was fed in the usual manner with the steers under the managemental conditions previously described. The "high plane" group was fed to gain from one to one and one-half pounds per day during the winter period while those on the "low plane" were fed to gain from one-half to three-fourths pound per day. The conditions, to which the "low plane" group was subjected, reasonably simulated those under which the cow- and steer-herd are managed. In order to utilize these animals in these analyses, equations were included in the models to estimate the effect of plane of nutrition, N_0 , during the first winter. Obviously, the effects are estimable only in the heifer group since the steers were subjected only to the herd plane.

Age of dam at the time of first calf, F , represents the probable effect, on the trait of the calf, of differences in physiological maturity of the cow, at the time she first calved, as a consequence of age differences. All cows in this herd calved either at 2, 3 or 4 years of age or were eliminated. The economics of the age to first breed heifers is argumentative although it would hardly seem logical to retain a cow other than under experimental conditions that did not raise a calf by her third year. Nevertheless, the phenotypic effect on a calf resulting from different numbers of barren years might be considerable and may not be accountable by correction for age of dam alone. Season of birth, S , has been shown to impart an effect on growth in given periods and on compensatory relations of gains in other periods. In these analyses the effect of season is expressed as the rate of change in the trait Y_w resulting from progressive lapse of

time expressed as days from January 1 of each year. The availability of forage relative to the time a calf was born may have been perhaps expressed both prenatally and postnatally. Therefore, the variation associated with season effect might account for deviations from linearity associated with correcting weaning weights for age by regression methods. The effects peculiar to the individual animal, error, depending on the model, include additive and non-additive effects of heredity, the probable sex-linkage effects, environmental effects and failure of the mathematical model to accurately estimate trait Y_w .

The constants, regression coefficients, analyses of variance, coefficients of variation and coefficients of determination for model A_1 are presented in Tables 2 and 3 for steers and heifers, respectively. The error mean squares in the analyses of variance estimate the variance in trait Y_w among calves with the expectation $\sigma_e^2 = \sigma_G^2 + \sigma_E^2$ where, with random mating, the σ_G^2 should have the Mendelian expectation of $1/4 \sigma_G^2$ due to sires, $1/2 \sigma_G^2$ due to chance at meiotic segregation and $1/4 \sigma_G^2$ due to dams. The expectation of the relationship among maternal half-sibs is such, however, that the variance among dams (σ_D^2) would include $1/4 \sigma_G^2 + \sigma_{Gm}^2 + \sigma_{Pm'}^2 + \sigma_{Pm''}^2 + \sigma_{Pm'''}^2$ and the probable covariances, where σ_G^2 , σ_{Gm}^2 and σ_{Pm}^2 are the genetic, genetic maternal and permanent maternal variances according to Koch and Clark (35, p. 979); and p_m' is the contemporary permanent environmental effect indistinguishable from the genetic-maternal effect, p_m'' is the random permanent

Table 2. Analyses of Variance and Least Squares Estimates of Certain Contemporary Environmental Effects on Growth Phases of Steers (Model A₁).

Effects studied	Symbol	Estimates of the Effects in the Various Growth Phases									
		BW	WW	YW	LYW	SG	YG	LYG	W-YG	W-LYG	Y-LYG
Common effect	μ	67.5*	348.1*	466.3*	613.1*	280.7*	398.9*	545.6*	118.2*	265.0*	146.8*
Years	1947	-11.5*	-50.0*	-21.7	-14.0	-38.4*	-10.2	-2.5	28.3*	35.9*	7.7
	1948	-7.9*	-53.0*	-2.7	-6.0	-45.1*	5.2	1.9	50.3*	47.0*	-3.3
	1949	-5.8*	-66.8*	-27.6	-18.4	-61.0*	-21.8	-12.5	39.2*	48.4*	9.2
	1950	-4.4	-8.8	37.3	16.1	-4.4	41.7*	20.5	46.1*	24.9*	-21.2*
	1951	-1.3	-6.5	19.0	30.8	-5.2	20.3	32.1*	25.5*	37.3*	11.8
	1952	-6.4*	-46.2*	9.8	27.7	-39.8*	16.1	34.1	55.9*	73.9*	18.0*
	1953	-1.5	92.8*	73.5	90.2*	94.2*	75.0*	91.6*	-19.2	-2.6	16.6*
	1954	-2.8	44.2*	117.5*	83.1*	47.0*	120.3*	85.9*	73.3*	38.9*	-34.4*
	1955	-4.9	31.9*	100.7*	70.0*	36.9*	105.7*	74.9*	68.8*	38.0*	-38.0*
	1956	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Age of dam	2	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
	3	5.4*	14.8	2.5	37.7	9.5	-2.9	32.4*	-12.4	22.9	35.3*
	4	5.8*	34.2*	13.4	34.9	28.4*	7.6	29.1	-20.8*	.7	21.5*
	5	7.6*	39.2*	10.2	34.4	21.6	2.6	26.8	-19.0	5.2	24.2*
	6	7.2*	23.3	-.2	35.5	16.1	-7.4	28.2	-23.5*	12.2	35.7*
	7	5.6*	19.1	-12.9	15.6	13.2	-18.8	9.7	-32.0*	-3.5	28.5*
	8	8.2*	28.7	4.6	34.9	20.5	-3.6	26.7	-24.2*	6.2	30.4*
	9	7.3*	18.2	-1.4	28.5	10.9	-8.8	21.1	-19.6	10.3	29.9*
	10	8.0*	10.2	-4.5	24.4	2.2	-12.5	16.5	-14.7	14.3	28.9*
Dam calved last year	1	-1.9	-1.6	10.0	5.0	.4	11.9	6.9	11.6	6.6	-5.0
Dam not calved last year	0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Age of dam at first calf	b _F	.27	.79	-1.79	-7.01	1.06	-1.52	-6.74	-2.59	-7.81	-5.22
Season of birth	b _S	.076*	.063	.417*	.329*	.138	.492*	.405*	.354*	.267*	.088
Analyses of Variance											
Source	d/f	Sums of Squares									
Total	389	29,175	1,791,447	1,933,803	1,845,170	1,610,379	1,777,767	1,659,313	740,179	752,043	410,784
Regression	20	5,393	1,029,597	959,259	683,472	956,800	931,804	639,033	335,756	181,767	157,583
Residual	369	23,782	761,850	974,544	1,161,698	653,579	845,963	1,020,280	404,423	570,276	253,201
R ² **		.185	.575	.496	.370	.594	.524	.385	.454	.242	.384
Coefficient of Variation		.107	.127	.112	.090	.148	.124	.096	.327	.150	.159
Standard Deviation		8.0	45.4	51.3	56.0	42.0	47.8	52.5	33.1	39.3	26.2

* Significant at P<.05

** R² infers percentage of variation accounted for by regression due to effects studied. All significant at P<.05.

Table 3. Analyses of Variance and Least Squares Estimates of Certain Contemporary Environmental Effects on Growth Phases of Heifers (Model A₁).

		Estimates of the Effects in the Various Growth Phases									
Effects studied	Symbol	BW	WW	YW	LYW	SG	YG	LYG	W-YG	W-LYG	Y-LYG
Common effect	μ	61.3*	344.9*	456.9*	584.1*	299.3*	395.6*	522.8*	116.1*	243.3*	127.2*
Years	1947	- 8.6*	-10.4	-12.0	23.0	- 3.4	- 4.1	31.6*	- 2.8	33.0*	35.8*
	1948	- 4.5	-10.1	-13.4	24.5	- 6.0	- 8.9	29.0	- 3.3	34.6*	37.9*
	1949	- 3.3	-44.5*	-50.4*	- 8.5	-40.6*	-47.1*	- 5.1	- 5.7	36.2*	41.9*
	1950	- 1.5	3.9	3.7	31.1*	4.8	5.2	32.6*	- .3	27.1*	27.4*
	1951	- 1.2	-14.0	-41.3*	1.9	-11.9	-40.2*	3.1	27.1*	16.2	43.3*
	1952	- 4.8	-39.2*	-12.5	29.0	-27.9*	- 7.7	33.8*	28.4*	69.8*	41.5*
	1953	- 1.0	61.3*	15.9	58.2*	63.9*	16.9	59.2*	-44.9*	2.7	42.3*
	1954	- .4	37.4*	77.8*	96.7*	39.7*	78.2*	97.1*	40.8*	59.7*	18.9*
	1955	- .5	44.6*	77.2*	72.6*	46.9*	77.7*	73.1*	33.1*	28.5	- 4.6
	1956	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Age of dam	2	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
	3	5.2*	9.0	7.0	9.2	5.3	1.9	4.0	- 1.6	.6	2.2
	4	7.2*	34.0*	31.0*	34.3*	26.5*	23.7	27.1	- 3.1	.2	3.4
	5	7.4*	28.7*	26.1	24.5	23.2	18.7	17.0	- 2.1	- 3.8	- 1.7
	6	7.2*	28.8*	24.4	18.4	20.0	17.2	11.2	- 4.9	-10.8	- 6.0
	7	7.0*	30.1*	21.3	20.8	20.9	14.2	13.8	- 9.3	- 9.8	- .4
	8	6.8*	34.1*	26.2	22.4	24.5*	19.4	15.6	- 8.5	-12.4	- 3.8
	9	6.4*	30.5*	34.3*	29.2	21.0	28.0	22.8	3.0	- 2.2	- 5.2
	10	7.9*	19.7	32.1	29.6	9.2	24.2	21.7	11.7	9.2	- 2.5
	1	- 2.0	-10.3	-14.2*	-17.5*	- 7.3	-12.2	-15.5*	- 3.6	- 6.9	- 3.3
Dam not calved last year	0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Herd plane of nutrition	0	- 2.9*	-50.2*	-50.9*	-44.5*	-44.7*	-48.0*	-41.6*	0.0	6.4	6.4
Low plane of nutrition	1	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
High plane of nutrition	2	- .4	1.43	48.7*	37.4*	2.0	49.1*	37.9*	47.3*	36.0*	-11.3*
Age of dam at first calf	b _F	.32	6.42	8.26	6.82	2.52	7.94	6.50	.90	- .54	- 1.44
Season of birth	b _S	.082*	- .038	- .193	- .152	- .211*	- .275*	- .234*	- .178*	- .138	.041
Analyses of Variance											
Source	d/f	Sums of Squares									
Total	416	29,740	1,634,220	2,738,594	2,349,857	1,430,788	2,564,102	2,156,935	1,083,109	1,048,845	412,245
Regression	22	5,429	957,994	1,790,515	1,143,125	877,780	1,709,429	1,079,910	456,453	215,132	131,011
Residual	394	24,311	676,226	948,079	1,206,732	553,008	854,673	1,077,025	626,656	833,713	281,234
R ² **		.182	.586	.654	.486	.613	.667	.500	.421	.205	.318
Coefficient of Variation		.111	.122	.111	.092	.138	.125	.099	.391	.177	.169
Standard Deviation		7.85	41.42	49.05	55.33	37.46	46.57	52.28	39.87	45.99	26.71

* Significant at $P < .05$

** R² infers percentage of variation accounted for by regression due to effects studied. All significant at $P < .05$.

environmental effect residual from granddams and p_m''' is the fixed permanent environmental effect residual from granddams such that

$$p_m' + p_m'' + p_m''' = p_m .$$

The observations of trait Y_w (where w was limited to 1, ..., 7) were adjusted within-sex, by virtue of the separate analyses, for the effects estimated by the constants and regression coefficients for subsequent use in obtaining variances. The data on traits Y_8 , Y_9 , and Y_{10} , which are weaning-to-yearling gains, weaning-to-long-yearling gains and yearling-to-long-yearling gains, respectively, were not treated in the analyses of sub-models 2 and 3, which are yet to be discussed, because of limitations in computer facilities. The age-adjusted traits 1, ..., 7 of each individual calf were adjusted for the estimated environmental influences such that the adjusted value (Y_{wc}) for the trait w is; $Y_{wc} = Y_{wa} - \sum b_i X_i$ where Y_{wa} refers to the age-adjusted value of trait w as described in Table 1; b_i refers to the constants and regression coefficients which estimate the environmental influences; and $i = 1, \dots, n$, where n is the number of independent variables (X_i), of which there were 21 for steers and 23 for heifers in model A, and 29 for steers and 31 for heifers in model B.

When the solutions to the equations estimating the effects affecting heifers, were obtained it became apparent that the heifers allotted to the "high plane" and "low plane" groups were not randomly allotted to these groups, rather they were selected from the "top end"

of the heifer groups. This was further apparent by there being significant differences between the birth weights, weaning weights, yearling weights and long-yearling weights, suckling gains, yearling gains and long-yearling gains of the "herd plane" group and the "low plane" group but not so between those of the "low plane" and "high plane" groups. Conversely, significant differences existed between the traits of the "low plane" and "high plane" groups which were affected by plane of winter nutrition; namely weaning-to-yearling gain, weaning-to-long-yearling gain, yearling-to-long-yearling gain, yearling weight, long yearling weight, yearling gain and long yearling gain. Since, however, the weaning-to-yearling gains, weaning-to-long-yearling gains and yearling-to-long-yearling gains were not significantly different between the "low plane" and "herd plane" groups it was inferred that the significant differences which existed in the several traits between these two groups must be largely due to productive differences in the dams of these animals or to their own genetic differences. The only adjustments made for plane of nutrition were in traits Y_3 , Y_4 , Y_6 , Y_7 , where the differences between the "low plane" and "high plane" groups were subtracted from each individual in the "high plane" group. Had traits Y_8 , Y_9 and Y_{10} been studied in sub-models 2 and 3, the difference between the "low plane" and "high plane" would have been subtracted from the high plane, too.

As becomes evident from examining Tables 2 and 3 (pp. 39 and 40), the coefficients of variation of the two sexes were similar after

removal of the regression associated with both Models A_1 and B_1 , for all traits (Y_w) except weaning-to-yearling gain (Y_8) and of weaning-to-long-yearling gain (Y_9). With the coefficients of variation between sexes being similar in traits 1, ..., 7, adjustment of heifer data to a steer basis simply required multiplicative adjustment according to the method of Mason et al. (45, 6 p.). Each observation of a heifer's trait (Y_{wc}) was multiplied by the ratio \bar{S}/\bar{H} where \bar{S} and \bar{H} are the means of the trait being considered for steers and heifers, respectively. The factors by which the phenotypic value (Y_{wc}) of each trait of a heifer was multiplied for adjustment to a steer basis were: birth weight, 1.06; weaning weight, 1.05; yearling weight, 1.04; long yearling weight, 1.04; suckling gain, 1.05; yearling gain, 1.03; and long yearling gain, 1.04.

After adjusting for the environmental effects and for the differences between sexes, model A_1 takes the form $Y_k = \mu + \epsilon_k$ for each trait, where Y_k is the individual calf and ϵ_k is the error with the expectation described on page 38.

Model A_2 redefines the value of each trait of the individual calf such that $Y_{jk} = \mu + d_j + \epsilon_{jk}$, where d_j is the effect of a calf being from the j^{th} cow; $j = 1, \dots, 250$. The main differences among cows includes the repeatability of cow performance, and those permanent environmental effects such as birth year of dam, injuries and permanent effects of indistinguishable source. Thus the variance of the effect of a calf being from cow d_j can be partitioned from total variance, and repeatability of cow performance can be estimated by the

intra-class correlation. Repeatability is estimated by the ratio $\frac{\sigma_D^2}{\sigma_D^2 + \sigma_e^2}$ from the analyses of variance as defined by Kempthorne (26, p. 231).

The expectations of the mean squares of trait Y_w ($w = 1, \dots, 7$) among-dam subclasses in model A_2 were obtained by the method described by Kempthorne (26, p. 236-243) and are shown in Table 5 (p. 45). In order to compare the results of the analyses of sub-model 2 and sub-model 3, which is yet to be described and which is an hierarchical classification which includes the among-dam classification, the among-dam expectations are derived by pooling the among-granddam and the among-dam-in-granddam variances in sub-model 3 both variances being shown in Table 4 (p. 45). The among-dam variance (σ_D^2) in the model A_2 should have the expectation $1/4 \sigma_G^2 + \sigma_{Gm}^2 + \sigma_{Pm1}^2 + \sigma_{Pm11}^2 + \sigma_{Pm111}^2$. The error mean square, that is, the variance among offspring within dams should have the expectation $\sigma_e^2 = 3/4 \sigma_G^2 + \sigma_E^2$ as previously indicated (p. 7).

To measure the combined genetic effects and random permanent effects peculiar to granddam, g_i , an equation was further included in model A_2 giving model A_3 . Thus account is taken of the variance among granddams (σ_{g1}^2) where g_i is the genic and maternal difference reflected in trait Y_w of calves from the i th granddam; $i = 1, \dots, 165$. The change causes σ_D^2 of sub-model 2 to be reflected as σ_{Dg}^2 , the variation among cows-within-granddams, and σ_{g1}^2 , the variation among granddams. Therefore model A_3 is expressed as $Y_{ijk} = \mu + g_i + d_{ij} + e_{ijk}$.

Table 4. Analysis of Variance Model For All Traits in Sub-Model 3 of Primary Models A and B.

Source of Variance	d/f	Expected Mean Square
Among Granddams	$g' = 164$	$\sigma_e^2 + K_1 \sigma_{D_g}^2 + K_2 \sigma_g^2$
Among Dams in Granddams	$d' = 85$	$\sigma_e^2 + K_1' \sigma_{D_g}^2$
Among calves in Dams in Granddams	557	σ_e^2

$$K_1 = \frac{1}{g'} \left[\sum_{ij} \frac{n_{ij}^2}{n_i} - \frac{1}{N} \sum_{ij} n_{ij}^2 \right] = 3.18$$

$$K_2 = \frac{1}{g'} \left[N - \frac{1}{N} \sum_i n_i^2 \right] = 4.87$$

$$K_1' = \frac{1}{d'} \left[N - \sum_{ij} \frac{n_{ij}^2}{n_i} \right] = 3.30$$

Table 5. Analysis of Variance Model for All Traits in Sub-Model 2 of Primary Models A and B.

Source of Variance	d/f	Expected Mean Square
Among Dams	249	$\sigma_e^2 + K \sigma_D^2$
Among Calves within Dams	557	σ_e^2

$$K = \frac{g'K_1 + d'K_1'}{g' + d'} + \frac{g'K_2}{g' + d'} = 3.21$$

$$\sigma_D^2 = \frac{1}{K} \left[\frac{g'K_1 + d'K_1'}{g' + d'} \sigma_{D_g}^2 + \frac{g'K_2}{g' + d'} \sigma_g^2 \right]$$

where the values are obtained from Table 4 and have the same meaning as in Table 4. The degrees of freedom in Table 4 are designated g' and d' for among-granddams and for among-dams-in-granddams, respectively.

This regression model describes the expectation of the mean squares for sub-model A_3 where Y_{ijk} is the observation of trait Y_w on the k^{th} calf from the j^{th} dam whose dam in turn was granddam i . The expectations of the sums of squares among granddam subclasses were obtained as indicated in Table 4 (p. 45). The variances and repeatability estimates obtained from this model should differ from those in model A_2 to the extent of the effect of $1/16 \sigma_G^2 + \sigma_{Pm}^2$, since the variance of dams-within-granddams (σ_{Dg}^2) should be $3/16 \sigma_G^2 + \sigma_{Gm}^2 + \sigma_{Pm}^2 + \sigma_{Pm}^2$.

Contemporary Environmental Effects with Age of Granddam Adjusted (Model B)

Considering the logic involved in model A_1 , it may be surmised that through inclusion of suitable equations it may be ascertained whether age of granddam -- a fixed effect (σ_{Pm}^2) of permanent environmental nature -- might exert a residual effect on calves through the effect it may have had on their dams. This fixed portion of presumed variance was measured by adding the equation R_q where R is the residual permanent effect associated with the q^{th} age of granddam and $q = 2, \dots, 10$. The presumable effect is the expression of a residual effect of environment which is shown in calves as a result of their dams having been subjected to different environmental rigors by having been born to dams of various ages. Thus model B_1 is obtained which differs from model A_1 by the removal of σ_{Pm}^2 . Model B_1 describes $Y_{hlmoqk} = \mu + R_q + J_h + A_l + C_m + N_o + b_{FF} + b_{SS} + e_{hlmoqk}$, where R_q is the effect described above and all other effects are described for model A_1 .

Table 6. Analyses of Variance and Least Squares Estimates of Certain Contemporary Environmental Effects on Growth Phases of Steers with Age of Granddam Adjusted (Model B₁).

Estimates of the Effects in the Various Growth Phases											
Effects studied	Symbol	BW	WW	YW	LYW	SG	YG	LYG	W-YG	W-LYG	Y-LYG
Common effect	μ	67.0*	326.2*	421.8*	569.1*	259.3*	354.9*	502.2*	95.6*	242.9*	147.3*
Years	1947	-11.5*	-50.0*	-21.1	-11.6	-38.5*	- 9.7	- .1	28.9*	38.4*	9.6
	1948	- 8.2*	-51.8*	2.0	.1	-43.6*	10.2	8.3	53.8*	51.9*	- 1.9
	1949	- 5.7	-68.6*	-25.7	-14.8	-62.9*	-20.1	- 9.2	42.8*	53.7*	10.9
	1950	- 4.5	- 8.2	40.2*	21.4	- 3.7	44.7*	25.9	48.4*	29.6*	-18.8*
	1951	- 1.6	- 7.3	21.1	36.6*	- 5.7	22.7	38.2*	28.4*	43.9*	15.5
	1952	- 6.9*	-48.9	8.3	29.5	-42.0*	15.2	36.5*	57.2*	78.4*	21.2*
	1953	- 1.8	91.6*	73.2*	92.7*	93.4*	75.0*	94.5*	-18.4	1.1	19.5*
	1954	- 3.3	43.6*	116.8*	86.2*	46.9*	20.2	89.5*	73.3*	42.6*	-30.7*
	1955	- 6.0*	30.0	95.3*	68.5*	36.0*	101.3*	74.5*	65.3*	38.5*	-26.8*
	1956	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Age of dam	2	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
	3	5.5*	15.0	4.1	39.5	9.6	- 1.3	34.1*	-10.9	24.5*	35.4*
	4	6.2*	34.4*	14.8	35.4	28.3*	8.7	29.2	-19.6	1.0	20.6*
	5	8.0*	30.9*	14.7	38.1	22.9*	6.7	30.1	-16.3	7.2	23.4*
	6	7.4*	24.0	2.0	36.7	16.6	- 5.4	29.3	-22.1*	12.7	34.8*
	7	6.7*	21.0	- 8.4	17.1	14.3	-15.1	10.4	-29.4*	- 3.9	25.5*
	8	8.9*	31.1*	12.2	41.0	22.2	3.3	32.1	-18.9	9.9	28.9*
	9	8.2*	18.9	2.9	29.2	10.8	5.2	21.1	-16.0	10.3	26.3*
	10	9.1*	11.2	1.6	27.3	2.1	7.6	18.2	- 9.7	16.1	25.8*
	2	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Age of granddam	3	- 1.1	37.5*	41.0*	38.9*	38.5*	42.1*	40.0*	3.6	1.4	- 2.1
	4	- .2	15.8	32.0*	27.7	16.0	32.2*	27.9	16.2	11.9	- 4.3
	5	.9	17.3	5.5	15.3	16.4	24.6	14.4	8.3	- 2.0	-10.2
	6	- 1.2	13.3	35.2*	36.3*	14.5	36.3*	37.5*	21.9*	23.0*	1.2
	7	1.0	23.5	34.4*	29.7	22.5	33.4*	28.7	11.0	6.2	- 4.7
	8	.8	18.2	37.4*	39.0*	17.4	36.6*	38.2*	19.2	20.8	1.7
	9	2.9	26.3	51.3*	41.0*	23.5	48.4*	38.1*	24.9*	14.6	-10.3
	10	0.0	28.8	37.9*	40.3*	28.8*	37.9*	40.3*	9.1	11.5	2.4
Dam calved last year	1	- 2.0	- 2.2	8.6	4.0	- .2	10.6	6.0	10.8*	6.2	- 4.6
Dam not calved last year	0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Age of dam at first calf	b _F	.05	1.63	1.52	- 3.90	1.68	1.57	- 3.85	- .11	- 5.53	- 5.4*
Season of birth	b _S	.071*	- .066	- .440*	- .336*	- .137	- .513*	- .407*	- .376*	- .270*	.105
Analyses of Variance											
Source	d/f	Sums of Squares									
Total	389	29,175	1,791,447	1,933,803	1,845,170	1,610,379	1,777,767	1,659,313	740,179	752,043	410,784
Regression	28	5,897	1,054,526	1,028,830	717,956	978,161	960,345	674,367	352,961	207,548	164,394
Residual	361	23,316	736,921	904,973	1,127,214	632,218	817,422	984,946	387,218	544,495	246,390
R ² **		.202	.589	.532	.389	.607	.540	.406	.477	.276	.400
Coefficient of Variation		.107	.126	.109	.090	.148	.124	.095	.324	.146	.159
Standard Deviation		8.04	45.18	50.07	55.90	41.85	47.59	52.23	32.75	38.85	26.12

* Significant at P<.05

** R² infers percentage of variation accounted for by regression due to effects studied. All significant at P<.05.

Table 7. Analyses of Variance and Least Squares Estimates of Certain Contemporary Environmental Effects on Growth Phases of Heifers with Age of Granddam Adjusted (Model B₁).

Estimates of the Effects in the Various Growth Phases											
Effects studied	Symbol	BW	WW	YW	LYW	SG	YG	LYG	W-YG	W-LYG	Y-LYG
Common effect	μ	61.8*	351.3*	456.1*	571.6*	304.7*	394.3*	509.9*	108.8*	224.3*	115.5
Years	1947	- 8.7*	- 8.6	- 9.1	29.9	- .2	- .5	38.6*	- .6	38.4*	39.0*
	1948	- 4.2	- 8.8	- 9.9	32.1	- 3.6	- 5.6	36.3*	- .9	41.1*	41.9*
	1949	- 3.2	-42.4*	-47.9*	2.6	-37.2*	-44.7*	.6	- 5.0	40.3*	45.3*
	1950	- 1.4	4.4	6.0	36.0*	6.4	7.4	37.4*	1.7	31.7*	30.0*
	1951	- 1.1	-10.1	-38.2*	8.3	- 6.9	-37.1*	9.4	-27.5*	19.0	46.5*
	1952	- 4.8	-35.3*	- 9.4	35.3*	-22.6	- 4.7	40.1*	28.0*	72.7*	44.8*
	1953	- .7	67.1*	20.9	66.8*	70.7*	21.5	67.5*	-45.4*	.5	46.5*
	1954	- .4	40.2*	79.7*	100.9*	43.4*	80.1*	101.2*	40.3*	61.5*	21.1*
	1955	- .5	50.4*	82.5*	80.0*	53.8*	83.0*	80.5*	32.8*	30.4*	- 2.4
	1956	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Age of dam	2	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
	3	5.3*	6.2	8.0	9.5	2.2	2.6	4.2	2.1	3.6	1.6
	4	7.3*	31.2*	32.3	35.4*	23.5*	25.0	28.1	.9	4.0	3.1
	5	7.4*	23.3	24.4	21.4	17.3	17.1	14.0	1.6	- 1.5	- 3.1
	6	7.2*	24.9	24.0	18.2	16.1	17.0	11.0	- 1.2	- 7.2	- 6.0
	7	7.0*	24.5	19.1	17.9	14.9	12.1	10.9	- 6.1	- 7.2	- 1.2
	8	6.7*	25.0	22.5	17.5	15.0	15.8	10.8	- 3.4	- 8.3	- 5.0
	9	6.6*	23.8	32.7	28.3	13.9	26.1	21.7	8.1	3.7	- 4.4
	10	7.9*	13.6	30.7	28.7	2.8	22.8	20.8	16.4	14.4	- 2.0
	2	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Age of granddam	3	- .1	17.5	1.4	13.4	16.9	1.5	13.5	-16.4	- 4.4	12.0
	4	- 1.4	- 6.7	0.0	3.5	- 6.6	1.4	4.8	6.4	9.8	3.5
	5	.9	4.1	5.3	16.4	3.1	4.4	15.5	1.2	12.3	11.1
	6	- .9	-12.9	-11.5	- 5.2	-13.6	-10.7	- 4.3	1.0	7.3	6.3
	7	.7	-13.0	- 6.3	2.4	-15.1	- 6.9	1.8	6.4	15.1	8.7
	8	- .4	- 1.6	.3	5.9	- 2.3	.7	6.3	1.6	7.2	5.6
	9	.1	- 1.4	7.0	23.8	1.7	6.8	23.7	9.2	26.0	16.8
	10	1.2	11.5	21.9	33.9	9.1	20.8	32.8	10.1	22.1	12.0
	1	- 2.0*	- 8.0	-12.4	-15.7*	- 4.9	-10.4	-13.7	- 4.1	- 7.4	- 3.3
	0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Dam not calved last year	0	- 2.9*	-46.8*	-49.3*	42.1*	-41.1*	-46.4*	-39.2*	- 1.7	5.5	7.2
Herd plane of nutrition	1	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Low plane of nutrition	2	.3	5.8	51.3*	-40.7*	6.3	51.6*	41.0*	45.6*	35.1*	-10.5*
High plane of nutrition	b_F	.24	5.01	7.09	6.40	1.32	6.85	6.16	1.19	.50	- .69
Age of dam at first calf	b_S	.078*	- .066	- .199	- .178	- .237*	- .277*	- .256*	- .158	- .136	.021
Season of birth											

Analyses of Variance											
Source	d/f	Sums of Squares									
Total	416	29,740	1,634,220	2,738,594	2,349,857	1,430,788	2,564,102	2,156,935	1,083,109	1,048,845	412,245
Regression	30	5,671	998,208	1,816,141	1,186,561	919,458	1,732,844	1,119,694	476,980	239,768	137,071
Residual	386	24,069	636,012	922,453	1,163,296	511,440	831,258	1,037,241	606,129	809,077	275,174
R ² **		.191	.611	.663	.504	.643	.676	.519	.440	.228	.332
Coefficient of Variation		.112	.119	.110	.093	.134	.125	.098	.389	.176	.169
Standard Deviation		7.89	40.58	48.88	55.69	36.38	46.39	51.82	39.61	45.77	26.69

* Significant at $P \leq .05$

** R² infers percentage of variation accounted for by regression due to effects studied. All significant at $P \leq .05$.

In Tables 6 and 7 the resulting constants, regression coefficients, analyses of variance, coefficients of determination and coefficients of variation are presented for steers and heifers, respectively. Herein again the data were handled separately for heifers and steers as in model A_1 , and adjustment of individual data in traits 1, ... 7, for the effects in model B and for sex was described for model A.

Incorporation of equations into model B_1 to determine 1) the effects of the j^{th} dam (σ_D^2), and 2) the effect of the i^{th} granddam ($\sigma_{g_1}^2$) and thus the effect of the ij^{th} dam-within-granddam ($\sigma_{D_g}^2$) modifies model B_1 such that model B_2 and model B_3 , respectively, result. Model B_2 defines $Y_{jk} = \mu + d_j + \epsilon_{jk}$ as does model A_2 .

The expectation of the estimated mean squares among dam subclasses in model B_2 are the same as in model A_2 (Table 5) except that the expectation of the variance among cows (σ_D^2) for model B_2 should be $1/4 \sigma_G^2 + \sigma_{Gm}^2 + \sigma_{Pm}^2 + \sigma_{Pm'}^2$, since $\sigma_{Pm''}^2$ has been removed in the estimation of the effects of age of granddam.

Model B_3 has the value $Y_{ijk} = \mu + g_i + d_{ij} + \epsilon_{ijk}$ and has the expectation of the mean squares among-granddam subclasses similar to model A_3 , but the variance among-dams-within-granddams ($\sigma_{D_g}^2$) should have the expectation $3/16 \sigma_g^2 + \sigma_{Gm}^2 + \sigma_{Pm}^2$. Again the variance among granddams ($\sigma_{g_1}^2$) should be $1/8 \sigma_G^2 + \sigma_{Pm}^2$ (p. 46).

RESULTS AND DISCUSSION

Contemporary Environmental Effects (Model A₁)

The effects of contemporary environment on various traits of heifers and steers were measured and are presented in Tables 2 and 3. They are presented in the portion on analytical methods since part of the justification for treatment of the data in sub-models 2 and 3 was dependent on the results presented in these tables.

Influence of Years

The influence of years needs to be considered only grossly since they were estimated only to compare the growth phases of cattle on a within-year basis by adjustment to a common year. Generally speaking selection of replacement livestock is done on a within-year basis. The effects of years followed a pattern of progressive improvement in all traits -- with individual yearly variations which characterize the uncertain nature of desert ranching. Birth weights, for example, were 11.5 pounds greater among steers and 8.6 pounds greater in heifers in 1956 than in 1947. Weaning weights were 50 pounds greater in steers and 10 pounds greater in heifers in 1956 than in 1947. In the same year comparisons, steers were 14 pounds heavier and heifers were 23 pounds lighter as long-yearlings in 1956. The years 1952, 1953, 1954 and 1955 were superior, however, to 1956 in weaning, yearling, and long-yearling weights, re-emphasizing the yearly variation and

uncertainty. The improvement in the later years over the earlier ones is consistent with the improvement in management practices which have been initiated on the experimental range. These yearly differences bore similar magnitudes relative to each other among heifers as they did among steers. Certain growth traits varied more markedly with respect to years than did others as a result of compensation or decompensation for growth in preceding growth phases.

Compensation describes the phenomenon in which an animal grows at an accelerated rate in an improved environmental regime to make up for deprivation in a previous growth phase during which the environment was less adequate. Decompensation, conversely, describes a deceleration in growth rate in a growth phase subsequent to one in which rapid growth had been enjoyed by the individual. This problem is discussed subsequently in greater detail.

Influence of Age of Dam

Age of dam differences which reflect the physiological maturity or immaturity of the producing abilities of cows are directly expressed in birth weights and in suckling gains of their calves. Any other expression of age of dam influences of necessity bears relation to these two phases. The effects (Tables 2 and 3) of age of dam on birth weights of both heifers and steers indicate that once a cow has attained three years of age she is fully able to provide a gestational environment equal to fully mature cows. Calves from

two-year-old cows were 5.2 and 5.4 pounds lighter at birth than those in the age group with the next lightest birth weights of calves. In meeting their own maintenance and growth requirements, two-year-old cows are less able to simultaneously promote the prenatal growth of their calves to the same extent as mature cows. On the other hand, the calves from ten-year-old cows were the heaviest at birth (7.9 and 8.0 pounds heavier than two-year-olds) of all the age groups except eight-year-olds though the weights were not significantly greater than those of any group except the two-year-olds. Presumably, genetic time-trends and selection practices are expressed in the ten-year-old cows.

The influence of progressive maturity and senescence are more clearly exemplified in the suckling gains of calves from cows of various ages. The calves from two-year-old cows averaged approximately 20 pounds less in suckling gain than those from the cows in the mature age groups. Three-year-old cows produced heifer calves which had 9.5 pounds greater and steer calves which had 5.3 pounds greater suckling gains than did those from two-year-old cows. These greater gains in calves from three-year-old cows, incidentally, were not significantly different from those of the calves from two-year-old cows. The difference in both analyses does suggest a definite trend, however, the full extent of which is obscured perhaps by the fact that not all cows calved as two-year-olds and perhaps the genetically superior or those endowed with a superior environment

up to the age of puberty are those being compared as two-year-olds with the less productive cows calving first as three-year-olds. The suckling gains of calves from four-year-old cows were significantly different from those from two-year-olds in both the heifer and steer analyses (26.5 and 28.4 pounds, respectively). Heifer calves from eight-year-old cows were also significantly different (24.5 pounds) from those two-year-old cows. The values for the other mature age groups compared to two-year-olds were only slightly below those for significance at $P < .05$. In the steer analysis, calves from nine-year-old cows showed a decline in suckling gain in comparison to that shown by the heifers. In both analyses, the suckling gains of calves from ten-year-old cows were decidedly below those of the other mature groups. Heifers from ten-year-old cows gained only 9 pounds more and steers gained only 2 pounds more, on the average, than those from two-year-old cows.

In digressing to enlarge on these differences, it was apparent that the greatest suckling gains in both heifers and steers were achieved by calves from four-year-old cows. There is no apparent logic upon which to explain this effect since an attempt was made to remove the influence on production of cows having calved or not calved in the previous year. The data from this station (24, 22 p.) show that cows which calve first as two-year-olds tend to calve later in the season of their third year or to skip a year in production, then calve again in their fourth year. Also, they show that those cows which calve as two-year-olds

are those which were heaviest at that age. If the cows which calve as two-year-olds are those with the greatest genetic potential producing ability, and if an advantage did exist in skipping a year in production, then when these cows do produce as four-year-olds, they might express both their genetic ability and the response of skipping a year in production. It may be due to this interrelation of effects that a superiority is reflected for this age group. It is noteworthy, though no explanation is apparent, that the data (unpublished) indicate that five-year-old cows are represented to a lesser extent as dams and decidedly less as granddams than are three-, four-, six-, seven-, and eight-year-old cows.

Finally, age of dam effects which were expressed were most apparent in suckling gains of calves. These data do not substantiate the bulk of the literature with respect to an increase in producing ability of cows from two to eight years of age with a subsequent decline. Rather it can be inferred that the cows attained mature producing ability at four years of age and maintained a plateau of production until nine years of age, after which a decline became apparent. The advantage enjoyed at birth by calves born to ten-year-old cows was reduced by weaning time by virtue of their suckling gains being less than those of calves from the four-through nine-year-old groups. The performance of old cows in providing a superior gestational environment and then providing a less abundant post-natal environment bears out the contention

that lactation is a more drastic burden than pregnancy. It lends to inference that ensuing senescence is initially characterized by decrease in milking ability. The influence of age of dam was still apparent in yearling and in long-yearling weights and gains of heifers from two- and three-year-old cows and in long-yearling weights and gains in steers from two-year-old cows. It is felt, however, that the estimates for age of dam in heifers might reflect certain errors in post-weaning traits due to separate estimation of the influence of "low plane" and "herd plane" nutrition groups which was discussed in the methods section, and which is yet to be discussed in greater detail. The effect of age of dam on gains in the post-weaning periods are more effectively discussed in the subsequent section on compensatory growth.

Influence of a Cow's Having Raised or Not Raised a Calf in the Previous Year

The effect of cow's having calved or not calved in the previous year presents an interesting feature (Tables 2 and 3). The influence on birth weight was consistent in the steer and heifer analyses in that calves born to cows which raised a calf in the previous year were 2 pounds lighter at birth than those from cows which did not raise a calf. In both cases, the estimates were only slightly below the value at which they would have been significant at $P < .05$. The effects on suckling gain were not significant in either sex group. The average steer

whose dam raised a calf in the previous year was 0.4 pound heavier than the one whose dam did not raise a calf. That is, the cow was able to provide a post-natal environment which together with the calf's inherent growth potential allowed compensation in growth during the suckling period for environmental retardation which occurred prenatally. Among heifers, however, the calves from cows which raised a calf in the previous year were 7.3 pounds lighter than their contrast group indicating that either 1) heifers do not possess the recuperative mechanism inherent in steers or 2) that the effect in heifers is obscured in the adjustment for plane of nutrition effects. This negative effect in heifers, whose dams raised a calf in the previous year, is continuous through all weights and gains. Conversely, in the weaning-to-yearling phase in the steer group the gains were 11.6 pounds greater among those whose dams had raised a calf, whereas in the succeeding period -- yearling-to-long-yearling -- their gains were 5 pounds less than the contrasting group indicating a decompensation in gain following the periods in which the environmental retardation in birth weights were compensated.

Influence of Age of Dam at First Calving

The age of the dam at the time in which she first calved did not impart a significant nor meaningful influence on any of the growth phases studied. In the steer analysis, the estimates --

none of which were significant -- of the influence of this source of variation indicated that cows that first-calved later in life would have calves which were lighter at birth ($-.27$ pound per year of age of dam), gained slightly more during the suckling period (1.60 pounds per year of age of dam), gained less in the post-weaning period and ultimately attained lighter final weights (-7.01 pounds per year of age of dam). Consistently opposite results were obtained in the heifer analysis, in that calves from cows that first-calved later in life gave birth to calves of slightly heavier birth weight ($.32$ pound per year of age of dam), slightly heavier suckling gain (2.52 pounds per year of age of dam), and larger long-yearling weights (6.82 pounds per year of age of dam) than those from cows that first-calved earlier. The estimates are presented in Tables 2 and 3 and their lack of significance precludes inference as to their meaning. If, however, the estimates in the steer analyses are to be regarded meaningful, it may be that the different effect in heifers arises from heifers that were from older cows being in the "herd plane" of nutrition group and that the influence of age at first calf is obscured by another variable. If the efficiency complex were in reality a uni-directional entity, then one would expect cows which first-calve later in life to be genetically less productive in growth, lactation and fertility and to transmit this lower productive potential to the offspring.

Influence of Season of Birth

Season of birth was expressed in this analysis as the number of days which lapsed from January 1 to the birth date of the calf. With the passage of each additional day from the base date, there was associated an average of .08 pound increase in birth weight, in both steers and heifers (Tables 2 and 3). These same steers and heifers experienced a diminution in suckling gains of .14 and .21 pound, respectively, for each day which elapsed from January 1 to the date of their birth. In the weaning-to-yearling phase steers gained .35 pound less and heifers gained .18 pound less per day for each day they were later in birth. In the yearling-to-long-yearling phase the gains were .09 pound greater in steers and .04 pound greater in heifers for each later day of birth. In the post-weaning period the estimates for heifers were almost exactly half the magnitude of those for steers. To infer whether this is due to differences in the compensatory mechanisms in the two sexes or to the effect of the plane of nutrition, would be conjecture.

Influence of Plane of Nutrition

The influences of planes of nutrition from the weaning-to-yearling phase were measured in heifers only, since all steers were managed under the "herd plane", as has been discussed earlier. The estimates are presented in Table 3. The model estimating the environmental effects for heifers has been ill-defined as it was pointed out earlier. The model was designated with the

impression that heifers had been randomly chosen for the "high and low" plane groups from the available animals, and that the effects might be sufficient to categorize the individuals into a "high plane" group, a "low plane" group, and the residual "herd plane" group. The solution to the equations in the model (Tables 2 and 3) revealed, however, that 1) the heifers allotted to the "high" and "low" plane groups were those heaviest at weaning and that 2) there was no difference in the post weaning gain phases (weaning-to-yearling, weaning-to-long-yearling and yearling-to-long-yearling) in the "herd plane" and "low plane" groups. The significant differences between the "herd plane" and "low plane" groups in weights and total gains (suckling gains, yearling gain and long-yearling gain) are thought to be due to productivity differences of the dams, to differential environmental impositions on the animals in the two groups, and to differences in inherent growth capabilities of these animals. However, the differences in post-weaning weights and gains between the "high" and "low" plane groups are due to imposed nutritional differences and to the compensatory effect resulting from the impositions. The differences between the "low" and "high" plane groups in pre-weaning traits -- suckling gain and weaning weight -- were not greater than those due to chance. In the post-weaning phases, the "high plane" group exceeded the "low plane" group by 47.3 pounds in weaning-to-yearling gain, 49.1 pounds in yearling gain, 48.7 pounds in yearling weight, 36.0 pounds in weaning to long-yearling gain, -11.3 pounds in

yearling to long-yearling gain, 37.9 pounds in long-yearling gain, and ultimately, 37.4 pounds in long-yearling weight. The decompensation for the advantage enjoyed by the "high plane" group in the weaning-to-yearling phase is evident in the lessened gains in the yearling-to-long-yearling phase.

Compensatory Growth Relationships

One of the most important aspects which emerged from the solution to the equations in these models in the relationships of the estimates in adjacent and subsequent growth phases (suckling, weaning-to-yearling, and yearling-to-long-yearling), and the bearing which they reflect on the weights which result from these gains. The reports of Kidwell (27, p. 54), Koger and Knox (39, p. 760), Bohman (2, p. 249) and Winchester and Howe (66, 34 p.) well emphasize the negative relationships of gains in adjacent periods which arise from non-uniform environments in various growth phases. Their reports reflect the average reaction of a group of animals to non-uniform environmental treatment, but do not reflect what the compensating effects might be within the various environmental sources of variation. Blackwell, et al. (5, 6 p.) and Sabin (57, 58 p.) did show that the residual effects of the comparative effects of age of dam were still apparent in yearling cattle in an expression reciprocal to that at weaning. The data employed in the present study particularly show that in every category -- year, age of dam, past calving history, age of

dam at first calving, season of birth, and plane of nutrition -- there is a compensation or decompensation for the advantage or disadvantage enjoyed or imposed upon the animals within each category in the previous growth phase. Also the extent of compensation or decompensation is dependent largely on the relative advantage or disadvantage in the previous phase; for example, the greater the relative advantage enjoyed in one phase, the greater will be the decompensation in the subsequent phase, and vice versa. The most clear-cut example of this situation exists in a comparison of the suckling, weaning-to-yearling and yearling-to-long-yearling growth phases of steers (Table 2). Whereas the suckling gains in all of the age-of-dam groups estimated are positive in relation to those of calves from two-year-old cows, the weaning-to-yearling gains are all negative and bear the same relative negative difference during this phase as they did a positive effect in the previous phase. The animals in these age-of-dam groups do, however, recompensate in the yearling-to-long-yearling phase for the decompensation in the weaning-to-yearling period. Ultimately, the ranks in long-yearling weights are similar to those at weaning, whereas the yearling weights are less clearly defined with respect to calves from two-year-old cows. This same relative pattern occurred in the previous calving history measurements and in the age-at-first-calf influences.

Calves which were born later in the season were apparently insufficiently mature to withstand the rigors of the weaning-to-yearling phase. They decompensated in the suckling period for an

advantage in birth weight and indeed had a further decrease in gain during the weaning-to-yearling phase. It would seem that as the general environment improved and became more uniform, the compensating relations become less drastic as is evidenced in the year effects and in the "high plane" group, although the compensating mechanism was still distinctly operative.

The general evidence (unless the effect of plane of nutrition is masking the true effect) indicates that heifers have a less sensitive compensatory mechanism than steers. This should be taken lightly at the present time, although the responses in all categories are less marked than in the steer analysis.

Effectiveness of the Regression Models

The coefficients of determination (R^2), which are measures of the percentage of total variation in trait Y_w which was accounted for by the regression model, are presented in Tables 2 and 3. In these tables are also the standard deviations and coefficients of variation.

The coefficients of determination in the preweaning traits are very similar. Whether this would have been the case with a different definition of the plane-of-nutrition effects remains questionable. In those growth phases in the heifer analyses, however, where the effects of the "high plane" imparted an effect, the percentage of variation accounted for by regression were somewhat higher. Only 18 percent of the variation in birth weights was described by the model,

whereas in suckling gains and in weaning weights the model accounted for 60 percent. In the post-weaning phases the weaning-to-yearling gains were more accurately measured (45 percent for steers and 45 percent for heifers) than were the yearling-to-long-yearling gains (38 percent for steers and 32 percent for heifers). Presumably the lessened accuracy in measuring the causes of yearling-to-long-yearling gains was due to the presumed sources of variation having been diminished through compensation for the effects in the previous phase. Those phases which were more intimately related to maternal influence were the most accurately measured. Nevertheless, the coefficients of variation, which express the standard deviation of a trait as a percentage of the mean of the trait, were similar for the two sexes except in the cases of weaning-to-yearling and weaning-to-long-yearling gains. The coefficients of variation ranged from 9 to 18 percent, except for weaning-to-yearling gain in which the standard deviation exceeded 30 percent of its mean. The standard deviations were slightly smaller in heifers than steers except in weaning-to-yearling gain and in yearling-to-long-yearling gain.

Contemporary Environmental Effects With Age of Granddam Effects
Adjusted (Model B₁)

The estimates of the contemporary effects adjusted for age of granddam are presented in Tables 6 and 7. They were not materially different from those estimated in Model A₁ in which age

of granddam influences were ignored. The coefficients of determination, coefficients of variation and standard deviations were practically the same in the two models. The estimation of the effects of age of granddam resulted in a reduction in the common effect, μ , rather than in reduction in variance. There was a redistribution of the variance rather than a reduction in variance due to adjusting age of granddam. The effects of age of granddam are quite marked in the steer analysis (Table 6) in all weight and gain phases other than birth weight and yearling-to-long-yearling gain. There is no particular pattern to these effects upon which one might establish a basis for trends or other inference. It might be implied from the steer data, that those calves whose dams were from two-year-old dams were subjected to an environmental disadvantage which was expressed throughout their growth. It is noteworthy that those calves, whose granddams were 5 years of age, show a smaller estimate indicating a comparative disadvantage. Mention was previously made that five-year-old granddams were represented to a lesser extent than those of other ages. The reason for the smaller number of granddams of this age, and for the disadvantage imposed on their grand-offspring, is not understood. The discrepancy in numbers of granddams in the various aged groups was similar in both the steer and heifer analysis.

In the heifer analysis, there is a tendency for the effect of age of granddam to follow the pattern of the steers. The values

measuring the influence are much smaller, however, and in no case significant. The influence of the five-year-old dams in heifer actually implies the opposite of that in the steer analysis.

Basically, little was accomplished by classifying the data in model B. It would appear that the effect of p_m' -- the permanent effect of age of granddam -- might impart an influence on the growth of grand-offspring. The evidence from this study does not warrant a definite statement in this regard, although a tendency for expression of permanent residual effect is apparent in the steer analysis. The fact that every cow was the same-aged granddam to every calf from each one of her daughters, tends to associate age of granddam effect with repeatability of the dams. To clarify this point, say that a given dam (ij) was born to a given granddam (i) when (i) was 3 years of age. Then, calf (ijk, where $k = 1, \dots, 5$) was born to dam (ij). The granddam was 3 years of age for all 5 calves from one cow, which would tend to make the effect (if an effect does exist) a permanent characteristic of dam (ij). This association shows up in discussion of sub-models B_2 and B_3 , in the next section.

Repeatability Estimates of Growth Phases of Calves

Estimates in Models A₂ and A₃

The analyses of variance for the hierarchical classification of the data in Model A are presented in Table 8. The variance components and repeatability estimates for the various growth phases are presented in Table 9. Models A₂ and A₃, in all traits, are both based on this hierarchical classification. In model A₃, the variances are partitioned into 1) that ascribed to differences among granddams (σ_g^2) which should have the expectation $1/8 \sigma_G^2 + \sigma_{pm}^2$, 2) that among dams-within-granddams (σ_{Dg}^2) with the expectation $3/16 \sigma_G^2 + \sigma_{gm}^2 + \sigma_{pm}^2 + \sigma_{pm}^2$, and 3) error variance which is assumed to include $3/4 \sigma_G^2 + \sigma_E^2$. Model A₂ is derived by pooling the variances due to granddams (σ_g^2) and to dams-within-granddams (σ_{Dg}^2). In this way the variance among dams-ignoring-granddams (σ_D^2) is obtained, which should have the expectation $1/4 \sigma_G^2 + \sigma_{gm}^2 + \sigma_{pm}^2 + \sigma_{pm}^2 + \sigma_{pm}^2$.

The differences among granddams were not significant in any trait, (Table 8) while the effect of dams was significant at $P < .01$ for all traits. The value for the granddam effect in birth weight approached the value for significance at $P < .05$. The components of variance of granddams in model A₃ (Table 9) were negative except in the cases of birth weight and yearling weight. The variance in birth weight which is ascribed to granddams would account for only 4 percent of the total variation in birth weight. The

Table 8. Analyses of Variance for Growth Phases of Calves (Model A)

Item	Among Granddams	Among dams within granddams	Error
		Mean Squares	
Birth Weight	138	118**	83
Weaning Weight	3943	4752**	1637
Yearling Weight	5747	5380**	2099
Long-yearling Weight	4767	6414**	3231
Suckling Gain	3445	3893**	1168
Yearling Gain	4535	5120**	2400
Long-yearling Gain	4136	5466**	2843
Degrees of Freedom	164	85	557

**Significant at $P < .01$

Table 9. Components of Variance and Repeatability Estimates of Growth Phases from the Analyses of Variance in Table 8.

Source of Variation	Error common to models A2 and A3	Model A2		Model A3		
	σ_e^2	σ_D^2	Repeatability (ignoring granddams)	σ_{Dg}^2	σ_g^2	Repeatability
Birth Weight	83	15	.15	11	4	.11
Weaning Weight	1643	800	.33	944	-143	.37
Yearling Weight	2099	953	.31	995	10	.32
Long-yearling Weight	3231	628	.16	965	-335	.23
Suckling Gain	1168	754	.39	828	-73	.41
Yearling Gain	2401	724	.23	825	-100	.26
Long-yearling Gain	2843	540	.16	795	-254	.22

granddam component for yearling weight accounted for only .3 percent of the yearling weight variations. The lack of significance in the granddam effects demands that the components of variance ascribed to granddams be considered equal to zero, although those with negative calculated value exert an upward bias on the estimates of repeatability obtained from Model A_3 . It was established in the discussion of Model B_1 that permanent residual effects of a fixed source p_m , -- age of granddam -- may possibly exist. From the analyses in Model A_3 , it may be inferred that the genetic effects imparted from granddams are of insufficient magnitude to be measured and that the random residual maternal effects -- p_m -- are not measureably expressed in grand-offspring. This is not to infer that permanent environmental effects do not exist, for the genetic effects and the permanent environmental effects might counteract one another. However, this study does not acknowledge the effects of granddams on any growth trait of calves.

The estimates of the repeatability of a cow's productivity expressed in the growth phases of the calves are presented in Table 9. Those derived from Model A_3 (dams-within-granddam) vary little from those in Model A_2 , (dams-ignoring-granddams) as would be expected with the effect of granddams effectively equal to zero. The estimates of repeatability obtained in model A_3 were: birth weight, .11; weaning weight, .37; yearling weight, .32; long-yearling weight, .23; suckling gain, .41; yearling weight, .26;

and long-yearling gain, .22. Similarly, the estimates obtained in Model A_2 were: birth weight, .15; weaning weight, .33; yearling weight, .31; long-yearling weight, .16; suckling gain, .39; yearling gain, .23; and long-yearling gain, .16. Those estimates which were most intimately associated with post-natal maternal influences were the highest. The estimates of the repeatability of birth weight (.11 and .15) were surprisingly low. This perhaps follows from the fact that the regression Model A_1 estimated only 18 percent of the variation to be due to contemporary environmental effects. It was previously acknowledged that the effects of birth year of dam had not been adjusted. With the changes in management, this could possibly have a sizeable effect on the ultimate weight of the cow and perhaps this might be expressed in the contemporary permanent environmental effects of dams -- p_m . Nevertheless, the estimates for birth weight are considerably below the estimates of Koch and Clark (35, p. 979), Burris and Blunn (6, p. 34) and Gregory, et al. (17, p. 338). They do correspond to values obtained by Dawson, et al. (13, p. 247) and Botkin and Whatley (3, p. 552).

The repeatability estimates for weaning weight were .33 and .37 in Models A_2 and A_3 , respectively, and those for suckling gain were .39 and .41 for the two models in the same order (Table 9). The estimates of suckling gain appear to express more fully the maternal capabilities of the cow -- g_m -- than do weaning weights which of necessity are a composite of the productive expression of

a cow in both birth weight and suckling gains. Weaning weight should be an expression of both the egogenotype of the calf and the inherent maternal characteristic of the dam, and it appears that the maternal influence is more measurably repeatable in suckling gains than in birth weights. The author feels that an important cause of the difference in the repeatability estimates for birth weight and suckling gains lies in the fact that those environmental conditions in which gestation occurs are less adequate than those in which the suckling gains are made. A breeding season is normally planned such that the suckling period will coincide with the period of greatest abundance of forage and consequently with a greater milk supply. The period of abundant forage is also the period in which nutritive value of the forage, in this area, is greatest.

The repeatability estimates for yearling weights and yearling gains (Table 9) are adequately high. The estimates for yearling weights in Model A_2 and A_3 , respectively, are .31 and .32. The estimates for yearling gain in the same order are .23 and .26. The only difference between yearling weight and yearling gain is that yearling weight is composed of weight at birth plus the gain from birth to yearling age, while yearling gain is only the gain from birth to yearling age. The difference in the repeatability estimates for these two traits must lie in the fact that a correlated genetic expression of birth weight is reflected in the yearling weight estimate to a greater extent than in gain. Despite

the aspects of compensatory growth, the productivity of the dam maintains its identity through the winter period after weaning.

The repeatability estimates obtained for long-yearling weights and long-yearling gains (Table 9) are lower than those for weaning weights, suckling gains, yearling weights and yearling gains. The estimates for long-yearling weights in Models A_2 and A_3 , respectively are .16 and .23. The difference between the two estimates is due to the negative component in the granddams in Model A_3 which results in the estimate (.23) being biased upward. It is felt that these low estimates for long-yearling weights and gains are environmentally realistic but genetically unrealistic. These traits are the summation of the effects of genetic potential -- egogenotype -- and the drastically non-uniform environmental conditions. While the yearling weights and gains were made subject to compensating and decompensating growth in the weaning-to-yearling phase, the long-yearling weights and gains were made subject to these same influences and subject to recompensation in the yearling-to-long-yearling phase as was previously described. It was inferred from Table 2 that recompensation is not as complete in the yearling-to-long-yearling phase as was apparent in the weaning-to-yearling phase. Therefore, it is conceivably deducible that under drastically non-uniform environments, the compensatory relationships tend to obscure the true growth potential. The estimates for long-yearling weight were similar to those obtained by Hitchcock, et al. (24, 22 p.) from data from this same station. The animals had been subjected to similar non-uniform environmental changes.

Table 10. Analyses of Variance For Growth Phases of Calves (Model B)

Item	Among granddams	Among dams within granddams	Error
		Mean Squares	
Birth Weight	10	289**	56
Weaning Weight	1517	4112**	1470
Yearling Weight	5204	5171**	2723
Long-yearling Weight	4911	5384**	3256
Suckling Gain	3634	3675**	1365
Yearling Gain	1729	4531**	2422
Long-yearling Gain	1570	4684**	2885
Degrees of Freedom	164	85	557

** Significant at $P < .01$

Table 11. Components of Variance and Repeatability Estimates of Growth Phases from the Analyses of Variance in Table 10.

Source of Variation	Error common to models B ₂ and B ₃	Model B ₂		Model B ₃		
	σ_e^2	σ_D^2	Repeatability (ignoring granddams)	σ_D^2	σ_g^2	Repeatability
Birth Weight	56	15	.21	71	- 55	.56
Weaning Weight	1471	296	.17	801	-502	.35
Yearling Weight	2723	770	.22	752	19	.22
Long-yearling Weight	3256	563	.15	645	- 81	.17
Suckling Gain	1365	709	.34	700	9	.34
Yearling Gain	2423	77	.03	639	-560	.21
Long-yearling Gain	2885	-267	.00	535	-626	.16

Estimates in Models B_2 and B_3

It would appear that by removing the regression ascribed to age of granddams and subsequently analyzing the data in an hierarchical classification, in which the variance among granddams is considered, the effect of granddams is removed twice. The situation was previously described in which it appears that age-of-granddam effects are quite intimately associated with repeatability. Also it is apparent that this type of classification would tend to inflate the effects of the birth year of the dam. The estimates obtained in this classification (Table 11) are less realistic than those from Model A.

In Models B_2 and B_3 (Table 10), the effects of granddam were not significant for any trait, whereas the effects of dams were highly significant in every case. The estimated repeatability of birth weight in Model B_3 was .56 which is biased upward by the negative component of granddams. The other estimates in Model B_3 are: weaning weight, .35; yearling weight, .22; long-yearling weight, .17; suckling gain, .34; yearling gain, .21; and long-yearling gain, .16. The fact that these estimates in Model B_3 , other than for birth weight, are of reasonably similar magnitude to those in Model A_2 is not fully understood. Those estimates of repeatability obtained from Model B_2 do not follow a logical pattern. The repeatability estimates obtained in Model B_2 were : birth weight, .21; weaning weight, .17; yearling weight, .22; long-yearling weight, .15; suckling gain, .34; yearling gain, .03; and long-yearling gain, 0.

The disagreement in the estimates of weaning weight and suckling gain, yearling weight and yearling gain, and long-yearling weight and long-yearling gain in this model in contrast to their similarity in Models A_2 and A_3 , would seem to justify placing greater reliance on those estimates obtained from Model A.

GENERAL DISCUSSION

The phenotype of an individual at any one time is the result of the response of the genotype of that individual to the many environments in which it has existed. In beef cattle these environments are often many and varied, and they may occur separately or simultaneously. Success in a breeding program depends on the accuracy with which the genotype can be identified by observing the phenotype. These many environments and their effects must be identified in the many cattle-producing areas so that corrections can be made in all phases of management in order to derive greater revenue and to better identify animals with superior genotypes. Meanwhile, estimates must be made of these environmental effects so that the observed traits of individual animals might be adjusted to a reasonable standard of comparison. This study is an attempt to measure the variations in growth attributable to genetic, residual maternal, and environmental sources in calves from the Squaw-Butte Harney Experiment Station in the Northern Great Basin in Oregon.

The reasoning which led to the attempt to evaluate effects of a permanent environmental nature was based on the fact that heritability estimates are often derived from regression of a trait of the offspring on that of the female parent. If the true value of the trait in the dam were obscured by certain environmental factors and the effect of these factors imported a physiological effect on her productivity, then the regression would be due in part to permanent environmental

effects. The relationships among maternal half-sibs differ from those of paternal half-sibs because of the additional effect through maternal influence. There is no way to directly measure the influence of maternal and permanent environmental effects; however, the influence can only be inferred by comparing the relationships when the effect has been excluded with those where it is included (33, p. 775).

None of the methods employed in these analysis was effective in measuring residual maternal effects. There was an indication in the analysis of the steer data that a residual effect of the age of grand-dam might exert an influence on growth of calves. These proposed permanent influences must be intimately interrelated with the repeatability of the productivity of the dams. This does not dismiss the contention that permanent residual maternal effects do exist, for it remains that if a cow's productivity in terms of calf production is related to her body weight, then if environmental factors imposed on the cow by her dam result in failure to achieve full growth potential, these effects surely must be reflected in the offspring. Part of the failure of these analyses to acknowledge the residual maternal effects might be due to disposal, prior to reproductive age, of the majority of animals which endured the obvious limitations herein implied as probable permanent environmental sources. It must be emphasized, that in spite of the re-established contention, permanent environmental effects were not measured by these analyses.

Numerous estimates of the extent of genetic variability which characterizes beef cattle populations have been reported in the past

fifteen years. Also many estimates of the extent of environmental influences on growth of cattle have been reported in this same period of time. In general the estimates of heritability for most growth traits are high indicating that individual selection should be effective. The genetic correlations reported between weights at various times in growth by Blackwell et al. (4, p. 1018), Romo and Blackwell (54, 5 p.) and Koch and Clark (33, p. 775) have been mostly between .30 and .70. The genetic correlations between gains in certain periods reported by Blackwell et al. (loc. cit.), Kidwell (27, p. 54) and Koch and Clark (33, p. 775); however, have been negative or zero. Koch and Clark (34, p. 786) indeed proposed that negative correlations may exist between the genes affecting maternal environment and the genes directly affecting the growth response of some of the traits. Urick, et al. (67, p. 1026) on the contrary found positive genetic correlations among first winter, second summer and second winter gains. It is the opinion of this writer that the negative genetic correlations among gains in different periods are due to erroneous definition of the data in these phases, and to interpretation of the results based on these definitions. The discontinuity of previously reported genetic correlations appears from the data in the present study (as seen in discrepancies among repeatability estimates) to be due to compensations or decompensations in growth in various phases and to imperfect recompensation in subsequent phases. Therefore, it is not so much a contradiction in the reported estimates of the genetic parameters that

obscures genetic merit as it is the contradictory environments from which the estimates were obtained. This reasoning is substantiated in the results obtained by Carter and Kincaid (8, p. 331) and in their remarks relative to difference in their estimates and those from the Miles City data (34, p. 786). Carter and Kincaid (loc. cit.) found positive genetic correlations among gains in all periods. It is not conceivable from a physiological standpoint that separate inherent growth mechanisms exist in the overall efficiency complex to cope with different environments, but that these mechanisms might be accelerated or decelerated by environmental changes. That physiology which is genetic in one phase can scarcely be expected not to be genetic in another. Moreover, the pattern of compensatory growth does not appear to be genotype discriminating, but if such were not true, it is antagonistic to the superior genotypes.

In this study, those estimates of repeatability of traits which are most intimately related to maternal influence are the highest. The average estimates for suckling gain and weaning weights were .40 and .35, respectively. They are practically the same as those of Koch and Clark (33, p. 775) and those of Botkin and Whatley (3, p. 552) though somewhat lower than the estimates of Koger and Knox (38, p. 461) and Gregory et al. (17, p. 338). These estimates of performance reflect the effect of the highest nutritional plane to which the animals are subjected during the production year. The comparative similarity of the estimates of genetic variability (including and excluding maternal influences) in pre-weaning traits, the consistently positive

genetic relationships found among pre- and post-weaning weights and gains by Carter and Kincaid (8, p. 31) and Urick, et al. (67, p. 1026), and the consistently positive genetic correlations among pre- and post-weaning weights found by Blackwell, et al. (4, p. 1018) and Koch and Clark (33, p. 775) provide sufficient justification for selecting replacement animals at weaning time. Selection among progenies for heavier weaning weight should lead to improvement in subsequent growth rates. The low repeatability estimates obtained for birth weights in this study are attributed to an austere winter environment to which the dams are exposed and to random variations in the winter environments. The lowered estimates for long-yearling weights and gains are attributed to the multiplicity of environments and to periods of interrupted growth which an animal endures in reaching long-yearling weights and ages. The results from other stations (op. cit.) would lead to the belief that the estimates of repeatability of long-yearling weights and gains would be high under more uniform environmental conditions.

In range-cattle selection programs, greater emphasis is generally given in selection to weights at given times rather than to gains over a given period of time. The data in the present study indicate that much care must be taken in evaluating animals on the basis of gains in given periods. Also, cognizance must be taken of the differences in environmental conditions under which animals have been raised if these animals are to be taken from the range into "rate-of-gain" trials. The phenomenon of compensatory growth assumes sizable proportions particularly in the case of drastic changes in environment

from one growth phase to another. In this study it was found that compensation occurs in one phase to offset the advantages or disadvantages imposed in the previous phase by any of the environmental influences or minor environments -- year, age of dam, season of birth, etc. -- and that the compensation for one influence is measurably independent of that for another. To distinguish between compensation for an advantage and a disadvantage, the terms compensation and decompensation have been used. Compensation refers to growth rate being increased to offset a disadvantage in the previous phase. Decompensation refers to growth rate being decreased to offset an advantage in the previous phase. The extent of initial compensation or decompensation appears to be directly related to the magnitude of advantage or disadvantage in the initial phase. It would appear from the indications in these data that the compensatory mechanisms are less sensitive in heifers than in steers. To further complicate matters, the compensations and decompensations are further offset in the subsequent phase. This has been referred to as recompensation. The extent of recompensation does not appear to be quite as complete as the initial compensations and decompensations. This imperfection occasions a reduction in repeatability estimates of long-yearling weights and gains. It is felt that these phenomena are those which have been responsible for the negative genetic correlations in growth phases which have been reported from various stations (op. cit.) The effect of these compensatory relations must be carefully considered in any evaluation of growth in austere or sub-optimal environments.

Economic considerations preclude drastic changes in management practices which would rapidly minimize interruptions in growth and improve the identification of superior genotypes. The cost of major changes could easily exceed the gain derived from improved growth. It is evident, however, that improved management is being reflected in heavier weights of cattle at the Squaw-Butte Harney Station. Nevertheless, it was previously implied that an animal is subjected to many environments which tend to obscure the true growth potential. Selection is generally done within a year, so that year effects need to be considered, only from a long-range point of view with emphasis on ultimately achieving a continuous rate of growth in calves through long-yearling age.

Differences in season of birth are reflected in the birth weights. Compensatory influences due to season of birth are also expressed in post-weaning weights and gains. Season of birth, in effect, constitutes a minor environment, the effects of which should be lessened by shortening the breeding season to two or three heat periods. This practice would also tend to eliminate the cows which are shy-breeders if those cows are eliminated which do not calve.

The effects of age of dam, through differences in physiological maturity affecting cow productivity, impart a sizeable effect on growth and in final weights of calves. It is disclosed that under the environmental conditions herein experienced, two-year-old dams are incapable of providing either a pre-natal or a post-natal environment which approximates that of mature cows. Three-year-old cows were intermediate in producing ability to two-year-old cows and mature cows.

Nine- and ten-year-old cows were showing evidence of ensuing senescence which is initially expressed in lowered milk production. This evidence of senescence is not expressed in the birth weights of the calves.

In order to minimize the influences which ages of dam impart at weaning, the weaning weights of older and younger cows should be adjusted to a mature-dam equivalent. Approximate corrections for these analysis would infer addition of the following amounts to weaning weights of calves from young and old cows: 1) to steer calves from 2-, 3-, 9-, and 10-year-old cows; 25, 10, 7 and 15 pounds, respectively; and 2) to heifer calves from 2-, 3-, and 10-year-old cows; 30, 20, and 10 pounds, in that order. It is noteworthy to mention again that the compensatory relations were most clear-cut in the influences of age of dam on various growth traits. Those animals which were in the age groups which deprived their calves most during the suckling period were those which decompensated least in the weaning-to-yearling phase. Also their recompensation was least in the subsequent period. This compensatory mechanism cannot be overemphasized under these environmental conditions.

Multiplicative corrections were used in these data to correct all weights and gains of heifers to a steer equivalent. The performance of steers exceeded that of heifers in every trait. The percentage of variation accounted for by the regression models for steers and heifers was very similar in all traits. The literature reveals that in every instance (op. cit.) the growth of bull calves quite markedly exceeds

that of heifers and that growth in steers exceeds that of heifers, but to a lesser extent. In this study, steers exceeded heifers in the various traits, by the following amounts: birth weight, 4.4 pounds or 6.28 percent; weaning weight, 17.6 pounds or 5.16 percent; yearling weight, 16.5 pounds or 3.73 percent; long-yearling weight, 23.0 pounds or 3.83 percent; suckling gain, 12.9 pounds or 4.74 percent; yearling gain, 12.1 pounds or 3.25 percent; and long-yearling gain, 18.6 pounds or 3.51 percent. The differences between steers and heifers in weaning-to-yearling gain, yearling-to-long-yearling gain, and weaning-to-long-yearling gain by the method in which they were handled are not in reality sex differences since they reflect the impositions of different planes of winter nutrition to which some heifers were exposed.

This study well agrees in principle with the results of most other works reported (op. cit.) The interpretation, however, differs from some. The interpretation in this study is accomplished by evaluating these data and comparing the results with contentions of the many authors cited. The main difference in interpretation lies in acknowledging the lowered estimates in the latter growth stages to be due to growth compensation in non-uniform environments. The main contention is that the inherent physiological growth potential is not antagonistic to its own expression under various environments, but that the growth mechanism is accelerated or decelerated by environmental change.

SUMMARY AND CONCLUSIONS

A study was conducted on 417 heifers and 390 steers which were progeny of 250 dams and 165 granddams. The calves were born and raised in the years 1947 through 1956 on the Squaw-Butte Harney Experiment Station at Burns, Oregon.

Least squares analyses were employed to study the extent of genetic, environmental and residual maternal influences on growth from birth through long-yearling age. The growth traits studied were birth weight, weaning weight adjusted to 225 days, yearling weight adjusted to 385 days, long-yearling weight adjusted to 505 days, and all possible combinations of gains obtained by differences. Environmental effects considered in the analyses were: years, age of dam, whether a cow raised or did not raise a calf in the previous year, age of dam at first calving, season of birth, plane of winter nutrition and age of granddam. Separate analyses of environmental effects were conducted for heifers and steers. The data for seven traits were adjusted for the environmental effects and the sexes were combined by an appropriate multiplicative adjustment.

1. Estimates of repeatability of cow productivity were calculated for seven of the ten growth traits. The estimates were: birth weight, .15; weaning weight, .33; yearling weight, .31; long-yearling weight, .16; suckling gain, .34; yearling gain, .23; and long-yearling gain, .16.

2. There are some indications, in the steer analyses, of permanent environmental influences due to age of granddam; however, no pattern of

influence was established. It was ultimately concluded that the methods employed did not identify influences which can be definitely attributed to permanent residual maternal sources.

3. Animals which in one period endure a restriction in growth due to one or more of many environmental influences -- age of dam, season of birth, etc. -- tend to compensate for the restrictions in the next period. The compensations for the various influences are shown to be measurably independent, and are directly related to the extent of deprivation in the initial phase. Furthermore, the compensations are offset in subsequent phases through a reversed compensation. Compensations in later phases are less complete than the initial compensations.

4. The discrepancies among the repeatability estimates for the various traits are attributed to differences in the environments to which animals were subjected in various growth phases rather than to changes in genetic potential. Changes in growth rates due to compensatory growth relationships result in the lower repeatability estimates for long-yearling weights and gains.

5. Selections of calves with heavy weaning weights should lead to improvement in subsequent growth rates. Selections based on gains in given phases of post-weaning growth would contain inaccuracies due to compensatory growth.

6. Differences were noted between all growth traits of heifers and steers. Steers exceeded heifers in the various traits by the following amounts: birth weight, 6.28 percent; weaning weight, 5.16

percent; yearling weight, 3.73 percent; long-yearling weight, 3.83 percent; suckling gain, 4.74 percent; yearling gain, 3.25 percent; and long-yearling gain, 3.51 percent. The coefficients of variation were similar for animals of the two sexes. Adjustment of heifer data to a steer equivalent was accomplished in each trait by multiplicative correction to the extent of the difference between the sexes.

7. Effects of years were measured for the express purpose of adjusting the data to a constant-year basis. Improved management practices which have been initiated on the experimental range are being reflected in greater gains and weights in all growth phases.

8. Age-of-dam influences were apparent in all pre- and post-weaning growth phases. Two-year-old cows were unable to provide their calves with either pre- or post-natal environment approximating that of mature cows. This deprivation is still measurable in long-yearling weights. Birth weights of calves from cows of all ages except two-year-olds were similar. Cow productivity reflected in suckling gains of calves increased with increased age to four years, then maintained a plateau through eight years of age. After nine years of age there was a decline in productivity which was more marked in steer offspring than in heifers. Approximate additive correction factors developed to adjust weaning weights of calves to mature age-of-dam equivalent were: 25, 10, 7 and 15 pounds for steers from 2-, 3-, 9- and 10-year-old cows, respectively; and 30, 20 and 10 pounds for heifers from 2-, 3- and 10-year-old cows, in that order.

9. An influence of differences in season of birth was reflected in birth weights and in post-weaning gains. Each day lapse from January 1 to birth of the calf was associated with .08 pound increase in birth weight. This influence was compensated during the suckling period, but was again expressed in post-weaning gains. It was recommended that the breeding season be limited to two or three heat periods to minimize this effect and to eliminate cows which are hard to settle.

10. The influences of age of cow at first calving and whether or not a cow raised a calf in the previous year were not consistent. Opposing estimates of these effects were obtained in the separate analyses of steer and heifer data. No conclusions were drawn relative to the meaning of the results obtained.

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