HERITABILITY ESTIMATES AND GENETIC, PHENOTYPIC, AND ENVIRONMENTAL CORRELATIONS BETWEEN WEIGHT, GRADE, AND CONDITION OF ANGUS COWS

by

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TABLE OF CONTENTS

LIST OF TABLES

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INTRODUCTION

Compensation from a commercial beef herd depends for the most part on weights and grades of feeder and slaughter cattle. For this reason, most previous research in animal breeding has been directed toward quantitative traits that are measured prior to maturity. The results of these studies have provided considerable information.

However, profits from a beef enterprise are not wholly dependent on gross income; production costs also influence net returns. Economic studies have shown that the cost of feed is one of the primary determinants of a successful beef cow-calf operation. Also, animal scientists have found that feed requirements of beef cows approximate a direct relationship to their mature weight. Other research indicates that the over-all productive life of a cow may be positively related to body size. In view of these findings it appears that cow weight has important economic implications.

Type in beef cattle depends on grade and flesh condition as well as body size. These traits are highly variable and differences associated with age, year, and season suggest that environmental effects are important.

Further observation of differences among breeds and among herds within breeds indicate that genetic differences also exist.

In view of the above it appeared that further research directed toward obtaining a better understanding of the genetic and environmental nature of cow weight, grade, and condition was needed. The present study was undertaken to fulfill that need. The major objectives of this study were:

1. To estimate the effects of certain non-genetic sources of variation in weight, grade, and condition of beef cows;

2. To estimate the heritability of weight, grade, and condition of beef cows; and

3. To estimate the genetic, phenotypic, and environmental correlations between weight, grade, and condition of beef cows.

LITERATURE REVIEW

A. Environmental factors which affect cow weight and grade.

Researchers from various areas of the United States have reported that year, breed, season, age, previous parity, condition, and nursing status are important non-genetic sources of variation in cow weights (Marlowe, 1962; Maddox, 1964; Brown and Franks, 1964; Fitzhugh, 1965). With the exceptions of breed and age, it is possible that these factors affect flesh condition rather than skeletal growth. Breed may well have a binary influence, i.e. if condition and skeletal growth are both genetically and environmentally controlled. With regard to age, several workers have reported that beef cows reach maturity between five and seven years (Knox and Koger, 1945; Brinks et al., 1962; Marlowe, 1962; Fitzhugh, 1965). It appears that skeletal growth is nearly complete at three years of age and that additional increase in weight is due primarily to increases in muscle and fat development (Brown et al. 1956a, b).

Marlowe (1962), at the Virginia Agricultural Experiment Station, studied the effects of season, age, flesh condition and nursing status on body weight of Hereford and Angus cows. Two analytical models were used; one included all of the above effects, and a second included all except condition. In the first analysis, condition and age were of major importance and accounted for roughly 21 and 15 per cent of the total variation in weight of Angus and Hereford cows, respectively. Nursing status and season, collectively, accounted for not more than three per cent in either breed. In the second analysis, nursing status and season were significant sources of variation in weights of both Angus and Hereford cows. This finding indicated that adjusting cow weights for condition simultaneously removed most of the effects of the other temporary environmental factors.

Brinks et al. (1962) studied factors that affected spring and fall weights of Hereford cows which were raised under range conditions at Miles City, Montana. Year differences were significant. Younger cows gained more weight during winter months than older cows, which was probably due to additional skeletal growth in the younger animals. Cows five years and under gained weight from spring to fall, whereas those from six to ten years lost weight during this period. Since the spring weight contained the weight of nearly a full-term calf, it appears that all cows added weight to their own bodies during the summer grazing season, with the younger cows gaining substantially more than older cows.

Maddox (1964), using data from the Texas Agricultural Experiment Station, reported that breed, sex of calf, previous parity, year, month calved, age, and weight of calf significantly affected cow weight. In his study, cow weight was determined from an average of twelve monthly weights. Even though all of the above factors were significant, the mean squares for breed, year, previous parity, and age indicated that these factors were of greatest importance.

Fitzhugh (1965) reported correction factors for fixed environmental effects on cow weights taken approximately at the time of calving (PCW) and at weaning (WCW). Data from seven southern states were represented in his study. When the data from each state were analyzed separately, the within breed within sire subclass mean squares for year, age, previous parity and birth month were generally significant for both weights. When the data from all states were combined and analyzed within location-year-breed-sire subclass, age and previous parity remained significant but birth month did not. Least squares constants from the combined analysis for PCW indicated that cows consistently gained weight from two to nine years of age. Two, three, and four year-old cows were 294, 126, and 49 pounds lighter, and nine year-old's were 79 pounds heavier than five year-old cows. Non-parous females, i.e. all heifers or cows not calving the previous year, were 60 pounds heavier than parous females. Constants obtained for age for WCW revealed the same general trend as those for PCW but the differences between WCW's of the younger and older cows were not as great. Aging alone is a possible explanation for these differences.

Brown and Franks (1964) studied the effects of date of measurement, breed, age, and reproductive status on weight and body measurements of young Angus and Hereford cows at the Arkansas Experiment Station. Weights and measurements, consisting of length of body, height at withers and hips, width at shoulders and hips, depth of chest and flank, and heart girth, were taken semi-annually. Those taken nearest the third birthday were used in their study. Least-squares analysis indicated that no definite trend was associated with date of measurement and that differences between breeds were small. Dry cows were about 100 pounds heavier than nursing cows, along with greater dimensions in those areas influenced by fatness.

Limited information is available on factors that affect the grade of beef cows; however, it is recognized that condition is of primary importance. Kildee (1956) cited flesh condition as the primary cause for variation in show-ring winners. Gifford et al. (1951) and Brown et al. (1953) reported that season and age, along with flesh condition, significantly affected the grade of beef cows. In contrast, Ray and Gifford (1949) suggested that the relatively high repeatability of grade of individual cows, when estimated from grades taken over a long period of time, indicated that age and seasonal differences have little influence on conformation score.

Marlowe (1962) concluded that flesh condition is the major environmental factor influencing the grade of beef cows. When analyzing Hereford and Angus data separately, it accounted for roughly 20 and 23 percent of the total variation in grade, respectively. The difference between very thin and fat animals was approximately one standard grade. Age, season, and nursing status were of minor importance when adjustments were made for differences in condition; however, they were a much greater source of variation when condition was not considered. This indicates that these effects were confounded with condition score and thereby influence grade through the effect that they have on the flesh condition of the animal.

B. Heritability of cow weight.

Heritability is the ratio of the additive to the phenotypic variance. Warwick (1958) presented a comprehensive summary of the range and general magnitude of heritability estimates for economically important traits in beef cattle, which had been reported up to that time. Average estimates for birth weight, weaning weight, post-weaning gain, weaning grade and slaughter grade varied between 0.26 and 0.45.

Several workers have published heritability estimates for weight of beef females taken prior to maturity. Wagnon and Rollins (1959), using data from the California Agricultural Experiment Station, obtained an estimate of 0.44 for 18 month-old heifers. Marchello et al. (1960) reported a comparable estimate of 0.36 computed from paternal half-sib analysis of 481, 18-month-old Hereford heifers at the Northern Montana Branch Station. By like procedure, Swiger et al. (1963), using data from the Fort Robinson Beef Cattle Research Station, Nebraska, published estimates on weights of heifers taken at 200, 396, and 550 days of age to be 0.42, 0.47, and 0.55, respectively. Pahnish et al. (1964) estimated the heritability of fall yearling weight in Hereford heifers at the Arizona Experiment Station to be 0.40.

Relatively high heritability estimates have been reported for mature cow weights. Lickley et al. (1960) and Brinks et al. (1962) published estimates derived from paternal half-sib analyses to be 0.72 and 0.75, respectively. Later, Brinks et al. (1964) reported somewhat lower estimates of 0.52 and 0.57 for average spring and fall weights. Brown and Franks (1964) obtained an estimate of 0.44 for three year old cows by intra-sire dam-offspring regression analysis. Similar estimates obtained by like procedure were reported by Fitzhugh (1965). He also presented estimates, computed by paternal half-sib analysis, for cow weight measured at the time of calving and at weaning of 0.96 and 0.74, respectively. The estimate taken at the time of parturition is unreasonably high; however, the author suggested that a sire by year interaction may have existed which would have over-estimated the sire component of variance.

Touchberry (1951), Tyler et al. (1958) and Johnson (1959), reported that heritability estimates for measurements of mature body size in dairy cattle varied between 0.28 and 0.73. These are in close agreement with those reported for beef cattle by Franks and Brown (1964).

C. Heritability of conformation scores.

Published heritability estimates for post-weaning conformation scores of females have been quite variable: 0.17 for yearling grade, estimated by sire component analysis (Roberson *et al*., 1963); 0.27 for 18-month score, estimated by sire component analysis (Brinks *et al*., 1964); 0.17, 0.32 and 0.002 for yearling grade, estimated by sire component analysis, intra-sire dam-offspring regression, and regression of progeny average on sire, in that order (Carter and Kincaid, 1959). It would appear that the environment under which the above estimates were computed varied, thereby permitting the genotypes involved to express themselves in different proportions. Also, the statistical procedures used would account for some of the differences in the magnitude of these estimates. This was demonstrated to some extent by Carter and Kincaid (1959).

D. Heritability of condition scores.

Few heritability estimates of condition in live animals have been published. Roberson *et al*. (1963) reported estimates calculated by sire component analysis, in heifers at 230, 347, and 594 days of age to be 0.32 ± 0.16, 0.16 ± 0.12, and 0.11 ± 0.11, respectively.

Hazel and Terrill (1946) reported heritability of condition score in Rambouillet lambs, to be 0.03 ± 0.03 from half-sib analysis and 0.14 ± 0.06 from intra-sire regression of offspring on dam. Both procedures were adjusted for inbreeding.

E. Phenotypic, Genotypic and Environmental Correlations.

No information is available in the literature which refers directly to phenotypic, genetic and environmental correlations between the weight and grade of beef cows. Several reports have been published, estimating the relationship between the mature and pre-weaning or post-weaning performance traits when all characters were measured in the same animal.

Koger and Knox (1951) reported a phenotypic correlation between 205-day weight of range heifers and gains from long yearling to three years of age to be 0.35. The estimated correlation between long yearling weight and gain from that point to three years of age was 0.24. However, correlations between weaning, post-weaning, or three year-old performance traits and subsequent gain from three years of age to maturity were 0.13 or less. The authors concluded that these small relationships probably were due to the fact that growth after age three is slight and what does occur most likely represents variation in fleshing rather than skeletal development.

Roberson _et al_. (1963) reported high (0.92 to 0.96) genetic correlations between grade and condition of beef females at each of the ages of 230, 347, and 594 days. Koch and Clark (1955) reported genetic (G), phenotypic (P) and environmental (E) correlations between weaning weight, weaning score, yearling weight and yearling score of heifers as summarized below:

		Weaning score	Yearling weight	Yearling score
Weaning weight	G	0.47	0.54	0.23
	P	0.68	0.46	0.27
	E	0.64	0.47	0.26
Weaning score	G		0.31	0.45
	P		0.25	0.26
	E		0.25	0.29
Yearling weight	G			0.49
	P			0.61
	E			0.56

Cobb _et al_. (1961) reported phenotypic correlations among weights and scores taken at 8, 12 and 20 months of age. Positive phenotypic correlations of 0.50 or higher were obtained for weights and grades taken at the same age. Correlations were slightly lower but positive for weights and grades taken at different ages. Phenotypic and genetic correlations among 200, 396, and 550 day weights and scores of heifers, steers and bulls were reported by Swiger et al. (1963). All phenotypic correlations were positive and were generally larger for bulls with heifers being intermediate. Genetic correlations between weights of heifers at various ages averaged above 0.80, but they were generally low or negative between scores. Similarly, Blackwell et al. (1962) reported negative genetic, as well as negative phenotypic correlations, between weaning weight and weaning grade of the order of -.28 and -.05, respectively.

Carter and Kincaid (1959b) reported phenotypic and genetic correlations among 182 day weight, feeder grade and yearling grade in beef heifers. They were as follows with the genetic correlation listed first: 182 day weight and feeder grade, 0.31 and 0.37; 182 day weight and yearling grade, 0.50 and 0.28; feeder grade and yearling grade, 0.63 and 0.56. Marlowe and Vogt (1965) reported a breed difference between the genetic correlations of preweaning gain and grade of heifer calves. Their estimates were 0.49±0.07 for Hereford and 0.23±0.08 for Angus, respectively. Their corresponding phenotypic correlations were 0.28±0.02 and 0.24±0.01.

Brinks *et al*. (1964) reported genetic, phenotypic and environmental correlations between mature spring and fall weights, which were adjusted for age of cow, and weights and scores at various stages from birth to maturity. Approximately 5200 observations were involved. The genetic correlations are summarized below:

Trait	Mature spring weight	Mature fall weight
Birth weight	0.61	0.68
Weaning weight	0.59	0.51
Weaning score	0.10	0.09
10-mo. weight	0.66	0.62
18-mo. weight	0.84	0.74
18-mo. score	0.28	0.20
Mature spring weight		0.93

These genetic relationships indicate that genes or gene combinations which affect body weight at one stage of growth also affect weight at other stages. On the other hand, it seems that the genes which control body weight and conformation score are relatively independent.

EXPERIMENTAL MATERIAL

The data for this study consisted of observations on 1371 Angus cows by 365 sires in 13 purebred herds. These were considered a random sample of purebred Angus cows in Virginia. Observations on weight, grade, condition and nursing status were obtained during the years 1958, 1959, 1960, 1964 and 1965.

Generally, all cows within a herd were weighed within the same year, therefore year effects were not considered since they were, for the most part, confounded with differences among herds.

At the time of weighing, cows were graded by one or more individuals using grading standards described by Marlowe et al. (1958). These standards are essentially the same as those adopted by the Southern Regional Beef Cattle Breeding Project, S-10. Grading classifications consisted of high, middle and low thirds of standard grades which included fancy, choice, good, medium and common. In order to calculate average grades among various sub-groups, a numerical value was assigned to each third of a grade. In this study the grades ranged between low fancy (15) to low medium (6). Throughout this dissertation a grade-point will be considered as one-third of a standard grade.

The distribution of cows by season, age, condition score and nursing status is given in Table 1. Seasonal classifications were made by coding each cow according to the period of the year in which she was weighed as follows: (1) January 1 - March 31; (2) April 1 - June 30; (3) July 1 - September 30; (4) October 1 - December 31. In the interest of ease and clarity of presentation, the above seasons shall henceforth be referred to as winter, spring, summer and fall. Most of the cows were weighed in the winter and fall. During these intervals the cattle were more accessible since they were on winter feed or pasture and the farmers' workload was such that they could relinquish their time.

Cows ranged in age from two to 18 years. Age groups were coded according to their actual age in years from (2) through (9). Ten and 11 year-old's were grouped and coded (10) and all cows 12 years and older were coded (11).

Classifications and code numbers used for scoring on flesh condition were described by Marlowe _et_ _al_. (1962). They were as follows: (1) = very thin; (2) = thin; (3) = average or breeding condition; (4) = good or above average; (5) = fat or in show condition. In this study, the numbers of cows classified as (5) were not considered

Table 1. Cow numbers within season, age, condition and nursing status subclasses.

	Grand Total	Seasons				Age										Condition				N.S.	
		1	2	3	4	2	3	4	5	6	7	8	9	10	11	1	2	3	4	2	3
Total	1371	407	206	203	555	64	144	224	177	151	169	105	87	155	95	79	315	708	269	687	684
Season 1		407	0	0	0	19	50	48	44	42	48	32	32	61	31	62	147	150	48	126	281
Season 2			206	0	0	9	20	24	26	24	35	22	12	16	18	7	46	127	26	183	23
Season 3				203	0	12	21	45	22	11	14	23	7	27	21	4	36	110	53	181	22
Season 4					555	24	53	107	85	74	72	28	36	51	25	6	86	321	142	197	358
Age Groups 2						64	0	0	0	0	0	0	0	0	0	3	17	34	10	31	33
Age Groups 3							144	0	0	0	0	0	0	0	0	6	36	72	30	65	79
Age Groups 4								224	0	0	0	0	0	0	0	13	57	114	40	109	115
Age Groups 5									177	0	0	0	0	0	0	8	34	100	35	73	104
Age Groups 6										151	0	0	0	0	0	11	33	82	25	58	93
Age Groups 7											169	0	0	0	0	11	35	86	37	85	84
Age Groups 8												105	0	0	0	3	23	55	24	62	43
Age Groups 9													87	0	0	3	23	44	17	52	35
Age Groups 10														155	0	7	29	74	45	92	63
Age Groups 11															95	14	28	47	6	60	35
Condition 1																79	0	0	0	24	55
Condition 2																	315	0	0	167	148
Condition 3																		708	0	384	324
Condition 4																			269	112	157
N.S. 2																				687	0
N.S. 3																					684

adequate to obtain a reasonable estimate of their effect and therefore were removed from the sample.

Information on nursing status was obtained from the breeder at the time of weighing. Generally, cows in all herds were bred to calve for the first time at two years of age. All females that were mothering a calf were coded (2), and dry cows were coded (3). The number of wet and dry cows under study were about equal.

Within the larger sample of cows there were 198 dam-daughter pairs, representing 63 sire groups. These were used to estimate parameters from a regression analysis.

STATISTICAL PROCEDURE

Advancements in theory and methodology pertaining to the analysis of nonorthogonal data have come about by the general availability of high speed computing equipment. These advancements have made possible more accurate estimation of genetical and environmental phenomena considered in animal breeding research.

Statistical models, which have been developed to account for sources of variation in the dependent variable, are generally classified as fixed, random, or mixed. These are analogous to Eisenhart's (1947) Model I, Model II, and Mixed model. Generally the models which describe animal breeding problems are of the mixed type in that they include both random and fixed variables.

The method of "fitting constants", similar to least-squares analysis, was described by Yates (1934) for a model involving only fixed independent variates. Henderson (1953) described the analysis of a random model, which is generally referred to as Henderson's Method I. The mixed model requires special analytical procedures. Henderson (1953) and Searle and Henderson (1961) applied the method of least-squares for analyzing mixed models with unequal subclass numbers and estimating variance and covariance components. This method, which is Henderson's Method II, adjusts for fixed effects and thus gives unbiased estimates of the components of variance and covariance. Also, Henderson (1953) described a short cut procedure, which involves equation absorption, when the number of least-squares equations are large. Least-squares analyses with unequal subclass frequencies were discussed in detail by Harvey (1960).

A. Estimating adjustment factors and variance and Covariance components.

In any statistical analysis it is of primary importance that the mathematical model underlying the analysis be laid out completely and accurately. All sources of variation under consideration must be included if unbiased estimates of individual effects are to be obtained. In addition, the general assumptions of homogeneity of variance and normality of error should be realized.

The following models were fitted in this study.

Model A

$$Y_{ijklmn} = \mu + H_i + S_{ij} + W_k + A_l + C_m + N_n + AC_{lm} + CN_{mn} + AN_{ln} + e_{ijklmn}$$

where

Y_{ijklmn} = $ijklmn^{th}$ cow weight or grade

μ = effect common to all observations

H_i = effect of the i^{th} herd

S_{ij} = effect of the j^{th} sire within the i^{th} herd

W_k = effect of the k^{th} season

A_l = effect of the l^{th} age

C_m = effect of the m^{th} condition score

N_n = effect of the n^{th} nursing status

AC_{lm} = effect of the lm^{th} AC interaction

CN_{mn} = effect of the mn^{th} CN interaction

AN_{lm} = effect of the ln^{th} AN interaction

e_{ijklmn} = random error; assumed $NID(0, \sigma_e^2)$

Model B

$$Y_{ijklm} = \mu + H_i + S_{ij} + W_k + A_l + N_m + AN_{lm} + e_{ijklm}$$

where

Y_{ijklm} = $ijklm^{th}$ cow weight, grade, or condition score

μ = effect common to all observations

H_i = effect of the i^{th} herd

S_{ij} = effect of the j^{th} sire within the i^{th} herd

W_k = effect of the k^{th} season

A_l = effect of the l^{th} age

N_m = effect of the m^{th} nursing status

AN_{lm} = effect of the lm^{th} AN interaction

e_{ijklm} = random error; assumed $NID(0, \sigma_e^2)$

<u>Model C</u>

$$Y_{ij} = \mu + H_i + S_{ij} + e_{ij}$$

where

Y_{ij} = ij^{th} cow weight or grade

μ = effect common to all observations

H_i = effect of the i^{th} herd

S_{ij} = effect of the j^{th} sire within the i^{th} herd

e_{ij} = random error; assumed NID(0, σe^2)

Model D

$Y_{ij} = \mu + S_i + bX_{ij} + e_{ij}$

where

Y_{ij} = ij^{th} daughter weight or grade

μ = population mean when $X_{ij} = 0$

S_i = effect of the i^{th} sire of the j^{th} daughter

b = partial regression of Y_{ij} on X_{ij}

X_{ij} = effect of the j^{th} dam weight or grade within the i^{th} sire subclass, calculated as deviation from the arithmetic mean

e_{ij} = random error; assumed NID(0, σe^2)

Models A and B are mixed models with unequal subclass numbers, where the (Y) is the dependent variate, (μ), (H), (S) and (e) are random, and all other factors are fixed independent variates. Models A and B are the same except that condition score and its respective interactions were considered fixed independent variables in Model A; whereas in Model B, condition score was regarded as a dependent variable and its respective interactions were eliminated from the model. Flesh condition may be genetically as well as environmentally controlled and an objective appraisal of the adjustment factors in Model A and the variance components in Model B for condition score will reveal the heritable as well as the environmental nature of this trait.

Model C involves only random variables. The data were adjusted for fixed effects, including interactions, using the constants obtained from the analysis of Model A. The primary difference between the analyses of Models A and C is the computation of the coefficients (k values) for the within sire (σ_W^2) component of variance included in the among sire and herd adjusted expected mean squares (EMS). The EMS for Models A, B, and C are

	df	EMS
Herds'	H-1	$k_2\sigma_W^2 + k_3\sigma_{S:H}^2 + k_4\sigma_H^2$
Sires':Herds'	S-H	$k_0\sigma_W^2 + k_1\sigma_{S:H}^2$
Within Sires'	N-S-R	σ_W^2

Where (R) is the number of degrees of freedom corresponding to the fixed effects fitted by least-squares analysis.

Generally the coefficients k_0 and k_2 are considered unity, i.e. it is assumed that the adjustments are made without error. However, least-squares constants are merely estimates, therefore a certain amount of error can be expected when adjusting for fixed effects. With this in mind, all coefficients including k_0 and k_2 were computed for Model A using procedures described by Harvey (1960). In Model C, k_0 and k_2 were considered unity and k_1, k_3 and k_4 were calculated as in Model A.

The sire components of variance (σ_S^2) and covariance (cov S) were calculated as follows:

$$\sigma_S^2 = \frac{\sigma_{S.H}^2 - k_0 \, \sigma_W^2}{k_1}$$

$$\text{cov } S = \frac{\text{Cov } S{:}H - k_0 \text{ COV } W}{k_1}$$

where $\sigma_{S:H}^2$, σ_W^2, Cov S:H, and Cov W are equal to their respective adjusted mean squares and mean products. The coefficient k_0 is a measure of the degree of confounding between random sires and the fixed effects which were fitted. If the data were balanced, this value would be unity. The coefficient k_1 is equal to the weighted average number of offspring per sire.

Model D is a regression analysis and was analyzed by least-squares procedure according to Harvey (1960). The constant (b) was obtained on a within sire subclass basis. If a dam had more than one daughter her record was repeated with each progeny record. The data used were adjusted for temporary environmental effects using correction factors from the analysis of Model A.

B. Estimating genotypic, phenotypic and environmental correlations

Various procedures are available for estimating heritability and genetic, phenotypic, and environmental correlations for metric characters when all traits considered are measured in the same animal. These procedures and the underlying respective genetic and environmental contributions were summarized by Dickerson (1960) and Becker (1964).

In practice, the method of analysis used generally depends on the nature of the experimental data. The procedure used in this study for estimating heritability in Models A, B, and C was paternal half-sib analysis. Estimates derived by this method involve dividing the intraclass correlation among half-sibs by the expected genetic relationship among them. The expected value of the sire component of variance (σ_S^2) is 1/4 σ_G^2 since E (σ^2) =

$\sigma_W^2 + 3/4\,\sigma_G^2$. In algebraic terms

$$h^2 = 4\,\sigma_S^2 / (\sigma_S^2 + \sigma_W^2)$$

The above formula assumes random mating and appropriate corrections should be made if it is clearly apparent that the relationship among half-sibs is greater than .25. The obvious weakness of using this method for computing heritability is that any inaccuracies involved in calculating the half-sib correlation, which may be due to sampling and environmental correlation, will be quadrupled. The standard error of the heritability estimate was computed according to Falconer (1960).

The heritability estimate from the use of Model D was calculated by doubling the intra-sire regression coefficient of offspring on dam. An advantage of calculating a heritability estimate by this method is that it theoretically avoids the effects of assortative mating and genotype-environmental correlations, (Lush, 1948).

The genetic correlation between traits which are measured in the same animal, quantifies the tendency of any two traits to vary together, in the same or opposite directions, due to effects of the same genes or gene combinations. Similarly, environmental correlations measure the inclination for two traits to vary together, in the same or opposite direction, due to the same environmental influences. Phenotypic correlations measure the same tendency, due to a combination of similar genic and environmental effects. The formula for the part-whole relationship of the above correlations as presented by Hazel (1943) is

$$R_{X_iX_j} = g_i g_j R_{G_iG_j} + e_i e_j R_{E_iE_j}$$

where $R_{X_iX_j}$, $R_{G_iG_j}$ and $R_{E_iE_j}$ are the phenotypic, genotypic, and environmental correlations, respectively. The (g.) and (e.) represent the heritability estimate and one minus the heritability estimate, respectively.

Algebraic formulas used in this study to compute the correlations were:

$$R_{G_iG_j} = \frac{CovSij}{\sigma S_i^2 \cdot \sigma S_j^2}$$

$$R_{X_iX_j} = \frac{CovWij + CovSij}{(\sigma W_i^2 + \sigma S_i^2)(\sigma W_j^2 + \sigma S_j^2)}$$

$$R_{E_iE_j} = \frac{CovWij - 3\ CovSij}{(\sigma W_i^2 - 3\,\sigma S_i^2)(\sigma W_j^2 - 3\,\sigma S_j^2)}$$

The standard errors of the genetic correlations were computed according to Tallis (1959).

C. Computer procedures.

Analyses of the models were completed at the Biometrical Research Laboratory, United States Department of Agriculture, Beltsville, Maryland. The programs used were:

1. #110 - "Conventional Least-Squares Analysis of Variance." This program was used to determine relative importance of fixed environmental effects. Print out included an ANOVA table and F-test, least-squares constants, inverse elements, submatrix distribution, and submatrix sums of squares associated with each effect fitted in the model.

2. #101 - "Least-Squares Coding Program." From a deck of original data cards, this program was designed to punch cards correctly coded and in format acceptable as input to the ARS sums of squares and cross-products program (#306B).

3. #302 - "Computation of Estimates of Absorbed Effects in Least-Squares Analyses and Adjustment of Detail Data with Constants Fitted." Adjusted data cards were obtained from this program. Input cards were output of program #101.

4. #305 - "Total Reduction and Error Cross-Products." Using coded data (program #101) and degrees of freedom for error (program #110) as a parameter

card, total reduction in sums of squares and/or cross-products, error sums of squares and/or cross-products and error expected mean squares and/or cross-products were computed with this program.

5. #306B - "Sums of Squares and/or Cross-products and k-values for Henderson's Method 2 Analysis." This is an SPS 1620/1710 coded program which calculates the sum of squares and cross-products for absorbed classes (sires and herds in this study), and the coefficients (k_0 and k_2) for the error variance components, when the fixed effects were first estimated by least-squares.

6. #401 and #402 - "Nested Analysis of Variance and Covariance." This program will work with or without unequal subclass numbers. The program is written in two parts; output from Part I constitutes input for Part II. Part I calculates the coefficients of the variance components (k_1, k_3 and k_4) and the degrees of freedom for each subclass. Part II computes the sums of squares and cross-products according to the nested (hierarchial) analysis of variance and covariance.

7. #309 - "IBM Procedures for Estimating Heritabilities of Genetic Correlations with Adjustments

for Fixed Effects (Paternal half-sib)." Heritabilities, correlations (genetic, phenotypic and environmental), and standard errors of the heritabilities and genetic correlations were calculated with this program. Coefficients of variance components (k_0, k_1, k_2, k_3 and k_4 from programs #306B and #401) and error mean squares (program #305) were used in making these computations.

RESULTS AND DISCUSSION

Constants for fixed effects and their two-way interactions were fitted by least-squares procedures in the analyses of Models A and B. Throughout this discussion it should be kept in mind that condition score and its respective interactions were considered as independent variables in Model A; whereas, in Model B, flesh condition was considered a dependent variable along with cow weight and grade.

The F-ratio for each fixed effect was derived by dividing its respective mean square by the residual mean square. The effects of herd and sires within herd were not tested for significance in this study. The F-test for these effects would not be valid when using unbalanced data.

A. Factors that affect cow weight.

The least-squares analyses of variance for weight using Models A and B are given in Table 2. In Model A the effects of season, age, condition, and nursing status were significant sources of variation in cow weight ($P < .01$). The age by nursing status interaction was significant at the .05 level of probability. The relative magnitude of the mean squares for flesh condition indicates that it is by far the most important source of variation.

Table 2. Analysis of variance for cow weight.

Source of Variation	Degrees of Freedom	Model-A Mean Squares	Model-B Mean Squares
Total	1370		
Herd	12	300,535	593,411
Sires:Herd	364	11,021	13,998
Within Sires:Herd	994		
-- Season	3	30,391**	105,890**
-- Age	9	61,067**	140,538**
-- Condition	3	639,435**	---
-- Nursing Status	1	30,358**	234,706**
-- A x C	27	9,124	---
-- C x NS	3	12,398	---
-- A x NS	9	16,082*	11,961
-- Residual	939	7,497	10,484

* $P < .05$
** $P < .01$

All main effects were highly significant in Model B ($P < .01$). The size of the mean squares for season, age, and nursing status were considerably larger in Model B than in Model A, indicating that these factors influence cow weight through their effect on flesh condition.

The least-squares means and constants for cow weight by season, age, condition, and nursing status are shown in Table 3 for Model A and in Table 4 for these same effects with condition omitted (Model B). Constants for interactions for Models A and B are presented in appendix Tables 1A and 2A, respectively. The means of the subclasses for season (Model A) indicate that cow weights taken during the winter were approximately 36 pounds lighter than the average for all seasons or 67 pounds lighter than the average of those taken during the summer. This was probably due to winter rations being fed which were only sufficient for maintenance. Since many of the cows were in the later stages of gestation or were calving during this time (see Table 1), without additional feed a corresponding loss in weight would occur. During the spring season, when most of the cattle were put on pasture, they began to gain weight and continued to gain into the summer. Fall weights were slightly lower

Table 3. Least-squares means and constants for cow weight by season, age, condition, and nursing status subclasses: Model A.

Variable	Number of Cows	Weight(lbs.) Mean	Constant
Seasons			
Winter	407	905	-36
Spring	206	928	-13
Summer	203	972	31
Fall	555	959	18
Age			
2	64	819	-122
3	144	889	-52
4	224	892	-49
5	177	938	- 3
6	151	960	19
7	169	966	25
8	105	976	35
9	87	965	24
10 & 11	155	1011	70
12+	95	994	53
Condition			
Very thin	79	839	-102
Thin	315	889	-52
Average	708	981	40
Above average	269	1055	114
Nursing Status			
Wet	687	930	-11
Dry	684	952	11
Over-all Mean	1371	941	

Table 4. Least-squares means and constants for cow weight by season, age, and nursing status subclasses: Model B.

Variable	Number of Cows	Weight(lbs.) Mean	Weight(lbs.) Constant
Seasons			
Winter	407	889	-71
Spring	206	957	- 3
Summer	203	1014	54
Fall	555	980	20
Age			
2	64	842	-118
3	144	871	-89
4	224	896	-64
5	177	961	1
6	151	977	17
7	169	999	39
8	105	998	38
9	87	1010	50
10 & 11	155	1037	77
12+	95	1009	49
Nursing Status			
Wet	687	937	-23
Dry	684	983	23
Over-all Mean	1371	960	

than summer weights which was probably due to sparse, low quality fall pasture that did not furnish sufficient nutrients for maintenance.

Seasonal differences in Model B followed the same general trend as in Model A; however, the divergence was wider among subclasses. When flesh condition was disregarded (Model B) cows that were weighed during the winter season were 16 pounds lighter than when they were adjusted for differences in flesh condition. On the other hand, those weighed during the spring, summer, and fall were 29, 42 and 21 pounds heavier. This indicates that adjusting for flesh condition removes part of the variation due to differences among seasons which is in agreement with Marlowe (1962). Brinks *et al*. (1962) found that young Hereford cows added body weight during the period of March through October. Also, Fitzhugh (1965) reported that beef cows of various breeds tended to gain weight during the lactation period. Neither Brinks *et al*. (1962) nor Fitzhugh (1965) considered differences in flesh condition in their studies. Brown and Franks (1964) reported no appreciable differences between spring and fall weights and body measurements of three year-old cows.

Least-squares constants from Model A for age classes indicated that cattle continue to increase in weight up to eight years of age. The 10 and 11 year-old cows were actually the heaviest group, which may have resulted from selection for larger body size by the breeders. Differences among year groups were significant through age six with the exception of the three and four year-old cows. Weights of 10 and 11 year-old cows were significantly greater than other age groups, except for those 12 years or older. When adjustments were not made for flesh condition (Model B) constants for age groups were essentially unchanged except that differences between two and three year-olds became significant.

Cows that were nursing calves were approximately 22 pounds lighter than dry cows in Model A and 46 pounds lighter in Model B. Differences in weights of wet and dry cows within age groups were widely distributed, (see Table 1A of the appendix). The differences in weight of wet and dry cows for two, eight, nine, and 10 & 11 year-olds, were 88, 56, 46 and 24 pounds, respectively. Other reports indicate that cows gain weight up to eight years and decline thereafter (Knox, 1945; Brinks, 1962; Maddox, 1964; Fitzhugh, 1965). In the present study, differences in the upper age groups generally were not significant (except for 10 and 11 year-old cows), which suggests that these differences are probably due to dissimilarities in flesh condition. The weight differences between wet and dry cows were somewhat low compared to those reported by Brown and Franks (1964). Marlowe (1962) found nursing status to be an insignificant source of variation when differences in flesh condition were removed, while in this study it was significant in both cases. The discrepancy may have been due to the fact that nursing status subclasses consisted of only two categories in this study; wet and dry cows, whereas Marlowe (1962) used four classes: heifers, wet, dry, and cows heavy with calf. Other workers have considered previous parity as a source of variation in cow weight, which is essentially the nursing status of the cow one year prior to weighing. Their reports have indicated this to be an important source of variation (Maddox, 1964; Fitzhugh, 1965).

Differences due to condition (Model A) were distinct. Very thin cows were 50, 142, and 216 pounds lighter than those in thin, average, and above average flesh condition, respectively. This is in good agreement with work reported by Marlowe (1962).

Least-squares constants for herds were not fitted since this source of variation was absorbed. An estimate of herd differences was derived by summing the adjusted weights (Model A) for each herd and computing a simple average. The over-all adjusted means of cow weight calculated by this method were essentially the same as those computed by standard procedures (Table 5). Size of herd ranged between 16 and 424 cows. Adjusted weights varied between 842 and 1040 pounds. No apparent relationship existed between size of herd and cow weight, which would indicate that managers of larger herds were not more selective for this trait than managers of smaller herds.

B. Factors that affect grade of beef cows.

Least-squares analysis of variance for Models A and B for grade of beef cows is presented in Table 6. Condition and season were significant environmental effects ($P < .01$) in Model A; however, season became non-significant when condition score was not fitted (Model B). On the other hand, age was not an important source of variation in Model A but was significant ($P < .05$) in Model B. Nursing status and first order interactions were not significant in either model.

This is somewhat contrary to work reported by Marlowe (1962). He found that adjusting for flesh condition essentially removed the variation due to season, age, and nursing status. His results appear to be more logical. A cow should not vary in grade between seasons or between stages of gestation and lactation if she maintains an average flesh condition. This is particularly

Table 5. Unadjusted and adjusted means of cow weights and grades within herds: Model A.

Herd	Number of Cows	Weight[a] (pounds) Unadjusted	Adjusted	Grade[b] (grade point) Unadjusted	Adjusted
1	16	951	933	11.3	11.5
2	34	851	842	12.0	11.5
3	35	1087	997	12.9	12.1
4	52	1013	978	11.5	11.4
5	71	1068	1040	12.4	11.5
6	77	975	991	11.8	11.2
7	81	1066	996	12.0	11.4
8	90	906	887	10.6	12.4
9	112	1062	990	13.2	12.5
10	113	1035	979	13.3	12.7
11	115	915	906	12.3	12.3
12	151	1062	966	11.8	11.5
13	424	869	894	10.3	10.1
Total	1371	965	941	11.6	11.4

[a] Standard deviation = 86 pounds.
[b] Standard deviation = 1.1 grade points.

Table 6. Analysis of variance for grade of beef cows.

Source of Variation	Degrees of Freedom	Model A Mean Squares	Model B Mean Squares
Total	1370		
Herds	12	99.15	159.28
Sires:Herds	364	2.07	2.44
Within Sires:Herds	995		
-- Season	3	9.94**	2.83
-- Age	9	1.09	3.21*
-- Condition	3	79.02**	---
-- Nursing Status	1	0.17	3.77
-- A x C	27	1.51	---
-- C x NS	3	0.65	---
-- A x NS	9	1.18	0.60
-- Residual	939	1.30	1.65

* $P < .05$
** $P < .01$

true for cows over five years of age. Other workers have found season and nursing status to have a major effect on grade of beef cows but they did not attempt to make any adjustment for flesh condition (Gifford et al.,1951; Brown et al., 1953). Yet, differences in experimental procedure for sub-dividing seasons, age groups, and nursing status into subclasses, plus differences between classifiers, could have accounted for the discrepancies between the results obtained by Marlowe (1962) and those from this study.

Least-squares means and constants for grade are presented in Table 7 for Model A and in Table 8 for Model B. Constants for interactions are presented in Table 1A of the appendix for Model A and in Table 2A for Model B. In Model A, cattle graded during the winter season were approximately one grade point higher than those graded during the spring season. This was probably due to a large proportion of the cattle being in the later stages of gestation during the winter and there would be a tendency on the part of the grader to classify them comparatively higher than if they were less feminine. Also, this may have been due to the fact that a large number of cows graded in the spring were in the early stage of lactation. Even though most of

Table 7. Least-squares means and constants for grade by season, age, condition, and nursing status: Model A.

Variable	Number of Cows	Grade[1] Mean	Constant
Season			
Winter	407	11.90	0.60
Spring	206	10.93	-.37
Summer	203	11.19	-.11
Fall	555	11.18	-.12
Age			
2	64	11.24	-.06
3	144	11.20	-.10
4	224	11.35	0.05
5	177	11.58	0.28
6	151	11.22	-.08
7	169	11.50	0.20
8	105	11.47	0.17
9	87	11.35	0.05
10 & 11	155	11.03	-.27
12+	95	11.06	-.24
Condition			
Very thin	79	10.10	-1.20
Thin	315	10.77	-.53
Average	708	11.75	0.45
Above average	269	12.58	1.28
Nursing Status			
Wet	687	11.33	0.03
Dry	684	11.27	-.03
Total	1371	11.30	

[1] Grade point where 10 = good, 11 = good plus, and 12 = choice minus.

Table 8. Least-squares means and constants for grade by season, age, and nursing status: Model B.

Variable	Number of Cows	Grade (grade points)	
		Mean	Constant
Season			
Winter	407	11.79	0.19
Spring	206	11.42	-.18
Summer	203	11.76	0.16
Fall	555	11.43	-.17
Age			
2	64	11.41	-.19
3	144	11.28	-.32
4	224	11.55	-.05
5	177	11.81	0.21
6	151	11.70	0.10
7	169	11.97	0.37
8	105	11.73	0.13
9	87	11.75	0.15
10 & 11	155	11.46	-.14
12+	95	11.34	-.26
Nursing Status			
Wet	687	11.51	-.09
Dry	684	11.69	0.09
Total	1371	11.60	

them were in average flesh condition (see Table 1), their gaunt appearance may have caused them to grade somewhat lower.

Age differences were not significant in Model A but were significant at the .05 level in Model B. There was a general trend for the youngest and the oldest cattle to grade somewhat lower than those ranging in age from five through nine years, with the average difference being about 0.20 grade point.

Considerable differences among condition subclasses were found. Cattle that were very thin or thin graded approximately 1.6 and 1.0 grade points below those in average condition; whereas, those above average graded 0.8 of a grade point higher. Fat cattle, or those which would approach show condition, were not included in this study due to the small numbers available.

As mentioned previously, average adjusted grades among herds were not obtained directly but were computed by an alternative procedure (see Table 5). Herd averages varied between 10.1 and 12.7 grade points. There appeared to be no correlation between size of herd and average grade of the cows. The over-all unadjusted and adjusted average grades were 11.6 and 11.3, respectively.

From the above analyses it can be concluded that adjusting for season and flesh condition will eliminate a large portion of the variation in grade of beef cows due to temporary environmental effects. If flesh condition is not considered, age of cow should be taken into account. These findings are in good agreement with those reported by other workers (Gifford et al., 1951; Brown et al., 1953; Marlowe, 1962).

C. Factors affecting condition of beef cows.

Least-squares analysis of variance for flesh condition from Model B is presented in Table 9. The temporary environmental effects of season and nursing status were highly significant ($P < .01$). Also, age was significant at the .05 level of probability.

Least-squares means and constants for condition score by season, age, and nursing status subclasses are presented in Table 10. Constants for age by nursing status interaction are given in Table 2A of the appendix. The adjusted mean condition score for all cows was 2.76 grade points which is slightly below average flesh condition (3.0). This was due largely to the fact that no cows scored as fat (5.0) were included in the study.

Seasonal differences were significant ($P < .01$) between cows scored during the winter and those scored

Table 9. Analysis of variance for condition score: Model B.

Source of Variation	Degrees of Freedom	Condition Mean Squares
Total	1370	
Herds	12	11.49
Sires:Herds	364	0.592
Within Sires:Herds	994	
-- Season	3	5.06**
-- Age	9	0.99*
-- Nursing Status	1	7.69**
-- A x NC	9	0.33
Residual	972	0.44

* $P < .05$
** $P < .01$

Table 10. Least-squares means and constants for condition score by season, age, and nursing status: Model B.

Variable	Number of Cows	Condition(grade points) Mean	Constant
Season			
Winter	407	2.33	-.44
Spring	206	2.91	0.15
Summer	203	3.08	0.32
Fall	555	2.73	-.03
Age			
2	64	2.59	-.17
3	144	2.60	-.16
4	224	2.65	-.11
5	177	2.77	0.01
6	151	2.73	-.03
7	169	2.68	-.08
8	105	2.90	0.14
9	87	2.71	-.05
10 & 11	155	3.07	0.31
12+	95	2.74	-.02
Nursing Status			
Wet	687	2.63	-.13
Dry	684	2.89	0.13
Total	1371	2.76	

during the spring, summer, or fall. Spring scores did not differ significantly from summer or fall scores. Summer and fall scores differed by 0.35 of a grade point, which was significant ($P < .05$).

Age groups less than five years of age were considerably thinner than other age groups. Ten and eleven year-old cows scored the highest for flesh condition and were approximately 0.31 of a grade point above the average. Wet cows were 0.26 of a grade point lower in flesh condition than dry cows.

There are no other reports in the literature related to factors affecting the flesh condition of beef cows. Several articles, however, have indicated that season, age, and nursing status affect cow weight and body measurements. The results of this investigation support the findings of Marlowe (1962), in that these factors may well influence cow weight through their influence on flesh condition rather than skeletal growth. This is especially apparent in females scored during the winter season and those that were nursing calves.

D. Components of variance and covariance.

The procedure for obtaining components of variance and covariance involved adjusting data for fixed effects, including interactions. This was accomplished by reversing the signs and applying the constants previously described for Models A and B, respectively, to the actual cow weights, grades, and condition scores. Data used in Model C were adjusted by applying the least-squares constants obtained in Model A. The adjusted mean squares for herds, among sires within herds, and within sires within herds were then equated to their expectations in order to obtain the components of variance and covariance. The variance and covariance components for Models A, B, and C are given in Table 11.

The coefficients of the variance components (k values) which make up the expected mean squares for each source of variation are listed on the far right of Table 11 and their respective values appear in footnotes. The values k_1, k_3 and k_4 are weighted average number of cows per sire, sires per herd, and cows per herd, respectively. The coefficients k_0 and k_2 are adjustments for confounding between fixed and random variables resulting from estimating the least-squares constants for fixed effects within sires and herds, respectively. Generally, these values are considered unity (Model C) which is incorrect when using unbalanced data. Assuming these values to be unity will inflate the among sire component of variance in proportion to the within sire component and in turn will bias heritability

Table 11. Components of variance and covariance for Models A, B, and C.

MODEL A

Source	df	Weight	%	Weight x Grade	Grade	%	k values[1]
Total	1370	10,004	100	52.6	2.3	100	---
Herd	12	1,726	17	29.5	.8	34	k_2, k_3, k_4
Among Sires	364	782	8	4.7	.2	8	k_0, k_1
Within Sires	939	7,496	75	18.4	1.3	58	---

[1] $k_0 = 1.1158$, $k_1 = 3.398$, $k_2 = 2.781$, $k_3 = 10.076$, $k_4 = 97.712$

MODEL B

Source	df	Weight	%	Weight x Grade	Weight x Condition	Grade	%	Grade x Condition	Condition	%	k values[1]
Total	1370	15,667	100	124.1	55.1	3.2	100	.7	.5	100	---
Herd	12	4,353	28	66.5	17.9	1.3	42	.3	.0	0	k_2, k_3, k_4
Among Sires	364	830	5	7.7	1.7	0.2	6	.0	.0	0	k_0, k_1
Within Sires	972	10,484	67	49.9	35.5	1.7	52	.4	.5	100	---

[1] $k_0 = 1.066$, $k_1 = 3.398$, $k_2 = 2.580$, $k_3 = 10.076$, $k_4 = 97.712$

MODEL C

Source	df	Weight	%	Weight x Grade	Grade	%	k values[1]
Total	1370	11,124	100	56.0	2.4	100	---
Herd	12	2,882	26	33.0	1.0	40	k_2, k_3, k_4
Among Sires	364	1,158	10	5.7	0.2	10	k_0, k_1
Within Sires	994	7,084	64	17.3	1.2	50	---

[1] $k_0 = 1.00$, $k_1 = 3.398$, $k_2 = 1.00$, $k_3 = 10.076$, $k_4 = 97.712$

and genetic correlation estimates upward, i.e. if the true value is greater than unity. A comparison of parameter estimates from Model A (k_0 = 1.1158, and k_2 = 2.781) and Model C (k_0 = k_2 = 1) illustrates the magnitude of these biases. Also, it can be seen by comparing the size of the k_0 and k_2 values in Models A and B, that the more adjusting involved the larger the accumulative error.

The proportions of the total variation in cow weight, grade, and condition explained by differences among herds, among sires within herds, and within sires for Models A, B, and C, are also given in Table 11. The same proportions for unadjusted data are presented in Table 12. These percentages point out that adjusting cow weights, grades, and condition scores for temporary environmental effects decreases the estimates of the herd and among sire components of variance and increases the within sire component. By comparing Models A and B it can be seen that the more adjustments involved the more extensive these increases and decreases become. Also, a comparison of the percentages of variation accounted for by the herd, among sire, and within sire components in Models A and C, illustrates the approximate adjustments made in these components when the coefficients k_0 and k_2 take on values other than one.

Table 12. Nested analysis of variance of cow weight, grade, and condition.[1]

Source	df	Mean Square	Variance Component	Per Cent
		WEIGHT		
Total	1370	23,043	24,251	100
Herd	12	846,091	8,147	34
Sires:Herds	364	25,062	3,735	15
Within Sires	994	12,368	12,368	51
Error Standard Deviation = 111 pounds				
Coefficient of Variation = 11.52				
		GRADE		
Total	1370	2.989	3.184	100
Herd	12	134.350	1.339	42
Sires:Herds	364	2.286	0.184	6
Within Sires	994	1.662	1.662	52
Error Standard Deviation = 1.3				
Coefficient of Variation = 11.12				
		CONDITION		
Total	1370	0.63	0.66	100
Herd	12	14.79	0.14	21
Sires:Herds	364	0.66	0.06	9
Within Sires	994	0.46	0.46	70
Error Standard Deviation = 0.675 grade point				
Coefficient of Variation = 23.69				

[1] Values computed from unadjusted data.

E. Heritabilities, and genetic, phenotypic, and environmental correlations between weight, grade, and condition.

One of the purposes of this study was to determine if the magnitude of these parameter estimates change when (1) flesh condition is and is not considered a fixed environmental effect, and (2) when different statistical procedures are employed.

Exactly the same data were used in Models A, B, and C. In Model A, flesh condition was considered a fixed independent variable, whereas in Model B it was considered a dependent variable. Both models were analyzed according to Method II of Henderson (1953) whereby adjustments were made for fixed effects and k_0 and k_2 values were calculated. Models A and C differ in that the cow weights in Model C were adjusted for fixed effects by using the constants obtained in the analysis of Model A. Then a simple nested analysis of variance and covariance was used to obtain the sire and within sire components of variance and covariance. In this case the coefficients k_0 and k_2 were considered unity. Heritability estimates and correlation coefficients were computed by paternal half-sib analysis for each of the three models.

In Model D, heritability was estimated by doubling the intra-sire regression of offspring on dam. Observations on 198 dam-daughter pairs by 63 sires were used in this analysis. The effects of season, age, condition, nursing status, and two-way interactions were adjusted, using correction factors obtained from the analysis of Model A.

Heritability estimates and correlation coefficients computed from the various models are presented in Table 13. Heritability estimates for cow weight obtained from Models A, B, and C, were 0.38±0.11, 0.29±0.11 and 0.56±0.11 respectively. The estimate from Model B was approximately one standard error less than the estimate calculated from Model A. It can be seen from Table 11 that, by not adjusting the cow weights for flesh condition, all variances increased but the within sire component increased to a greater extent than the among sire component. This is to be expected since there are fewer degrees of freedom involved in the latter. It should be noted that the k_0 value of 1.1158 in Model A decreased to 1.066 in Model B which would tend to offset, but only slightly, the comparatively large decrease in the among sire component of variance.

The difference in the magnitude of the heritability estimates from Models A and C is approximately two standard errors or 0.18 percentage points. This demonstrates the difference in the magnitude of parameter estimates resulting from exactly the same data but derived from application of

Table 13. Heritabilities and genotypic, phenotypic, and environmental correlations for Models A, B, C, And D.

Trait	Heritability Estimates	Correlations		
		Genotypic	Phenotypic	Environmental
		Model A		
Weight	0.38±0.11	---	---	---
Weight-Grade	---	0.39±0.18	0.21	0.07
Grade	0.49±0.11	---	---	---
		Model B		
Weight	0.29±0.11	---	---	---
Weight-Grade	---	0.60±0.18	0.40	0.29
Weight-Condition	---	0.32±0.23	0.51	0.59
Grade	0.43±0.11	---	---	---
Grade-Condition	---	0.21±0.21	0.44	0.58
Condition	0.31±0.11	---	---	---
		Model C		
Weight	0.56±0.11	---	---	---
Weight-Grade	---	0.33±0.12	0.21	0.01
Grade	0.67±0.13	---	---	---
		Model D		
Weight	0.22±0.14	---	---	---
Grade	0.10±0.06	---	---	---

two different, but often used statistical procedures. The difference between estimates obtained from Models B and C is simply a compounded result of the differences between Models A and B, and A and C.

All estimates are somewhat low for mature cow weight compared to estimates reported by other workers. Lickley et al. (1960) reported a value of 0.72 based on an average of three weights taken at four, five, and six years of age. Brinks et al. (1962) reported similar estimates for spring and fall weights of Hereford cows of 0.75 and 0.73, respectively. These were based on multiple weights and would be expected to exceed the ones found in this study by approximately $nh^2/1+(n-1)r$ (Lush, 1948), where h^2 = heritability of single records, r = repeatability, and n = number of records per cow. However, Brinks et al. (1962) also reported estimates based on single observations of spring and fall weights of 0.57 and 0.62. These are in good agreement with the estimate derived in Model C. Fitzhugh (1965) reported considerably higher heritability estimates from paternal half-sib analysis based on single cow weights measured at the time of calving and weaning of 0.96 and 0.74, respectively. However, the author suggested possibly a sire by year interaction may have existed which would have overestimated the sire component of variance.

The heritability for cow weight obtained by intra-sire regression of offspring on dam (Model D) was 0.22±0.14. This estimate is somewhat lower than the ones published by Fitzhugh (1965). He reported 0.42 and 0.44 for cow weight taken at the time of calving and weaning, respectively.

Heritability estimates for grade from Models A, B, and C were 0.49±0.11, 0.43±0.11 and 0.67±0.14, respectively. Differences in estimates between models followed the same general trend as for cow weight; this is as it should be since precisely the same statistical procedures were used. No direct comparisons of these estimates can be made; however, they are somewhat higher than those reported for grade of yearling and 18-month old heifers by Carter and Kincaid (1959), Roberson _et al_. (1963), Brinks _et al_. (1964). Repeatability estimates for grade, which range between 0.40 and 0.60 and should approximate the upper limits of heritability, suggest that the estimates from Models A, B, and C are reasonable (Gifford _et al_., 1951, and Brown, 1953). Moderately high heritability estimates indicate that mass selection for this trait would be quite effective.

The estimate by intra-sire regression of offspring on dam from Model D was 0.10±0.06, which is considerably lower than expected. This was probably due to sampling error resulting from using a sample of data that was too small to derive reliable estimates of heritability by regression analysis (Searle, 1962).

The heritability of 0.31±0.11 for condition score from Model B implies that it is as highly heritable as cow weight but slightly less than grade of beef cows. This suggests that adjusting cow weight for flesh condition may actually involve adjusting for genetic differences as well as for differences due to environment. This estimate is in line with those reported by Roberson et al. (1963) for heifers at various ages.

The genetic and phenotypic correlations estimated from Models A, B, and C were positive and moderate in size. Environmental correlations were moderately high and positive in Model B but essentially zero in Models A and C. The correlation between weight and grade in all models appears to be largely genetic, while the correlation of either of these traits with condition score was mostly environmental. Model B appeared to be the most suitable for taking into account the correlated nature of the traits considered in this study.

No other correlation estimates between cow weight, grade, and condition could be found in the literature. However, the correlation between weight and grade of heifers at younger ages have been reported. Brinks et al. (1964) reported negative genetic correlations between weaning score and weights at 12 and 18 months of age. Genetic and environmental correlations between weaning score, 18 month score, and mature spring and fall weights were small but positive. Carter and Kincaid (1959b) reported phenotypic and genetic correlations between 182-day weight and yearling grade of 0.50 and 0.28. These are in fairly good agreement with the correlations between weight and grade in Model B. On the other hand, Blackwell et al. (1962) reported negative genetic and phenotypic correlations between weaning weight and grade at weaning. Similarly, Swiger et al. (1963) found genetic correlations between weights and grades of heifers, bulls, and steers to be generally low or negative. On the other hand, Cobb et al. (1961) reported positive phenotypic correlations of 0.50 or higher among weights and scores of heifers taken at 8, 12, and 20 months of age. Koch and Clark (1955) reported genetic, phenotypic, and environmental correlations between yearling weight and scores of heifers to be 0.49, 0.61, and 0.56, respectively. These estimates are somewhat higher than those found in this study.

SUMMARY AND CONCLUSIONS

Weights, grades, and condition scores taken on 1371 Angus cows were used to estimate the genetic and environmental nature of these traits. This sample of cows represent 365 sire groups and 13 purebred herds in Virginia.

Four models were used in this study:

1. Model A - Cow weight and grade were considered dependent variables; herds and sires within herds were considered random independent variables; and season, age, condition, nursing status, and their interactions were considered fixed independent variables. Least-squares procedures involving Henderson's (1953) Method II, as described by Harvey (1960), were used to adjust for fixed effects and to obtain variance and covariance components for the random variables. Heritability estimates and correlation coefficients were obtained by paternal half-sib analysis using auxiliary computer programs.

2. Model B differed from Model A in that condition score was considered a dependent variable instead of an independent variable.

3. Model C was the same as Model A except that a different statistical procedure was used to obtain the variance and covariance components. In Model C, the coefficients for the within sire component of variance

(k_0 and k_2) were considered unity whereas as Model A they were calculated according to Method II of Henderson.

4. Model D - Heritability estimates were computed by doubling the estimate of intra-sire regression of offspring on dam from 198 dam-daughter pairs representing 63 sire groups. The dam-daughter pairs were part of the group of 1371 cows.

The results of this study indicated that season, age, condition score, nursing status, and age by nursing status interactions have a significant influence on the variation in cow weight (Model A). Season, age, and nursing status remained significant when condition score was not considered as a fixed environmental effect (Model B). However, a comparison of the magnitude of the mean squares for these effects in Models A and B indicated that season, age, and nursing status are highly confounded with condition score.

Least-squares constants for both models indicated that beef cows gain weight during the lactation period (April-October). They lose weight during the fall season and reach their lowest weights during the winter (January - March). Constants for age groups indicated that beef cows gain weight up to seven or eight years of age. Most significant gains are made at the younger ages. Differences between condition subclasses were distinct. Very thin cows were approximately 50, 142, and 216 pounds lighter than those in thin, average, and above average flesh condition. The average weight of wet and dry cows differed by approximately 22 pounds when the weights were adjusted for differences in flesh condition (Model A) and 46 pounds when not adjusted for flesh condition (Model B).

Season and flesh condition were found to have a significant effect on grade of beef cows when they were included in the same model (Model A). When condition score was not included (Model B), season was a non-significant source of variation in grade. Age had a significant effect on grade when condition score was not taken into account (Model B).

Age, season, and nursing status were found to have a significant effect on flesh condition (Model B). This indicates that adjusting cow weights and grades for these effects removes variation due to differences in fleshing rather than variation in skeletal growth.

Paternal half-sib heritability estimates for cow weight using Models A, B, and C were 0.38 ± 0.11, 0.29 ± 0.11, and 0.56 ± 0.11, respectively. Estimates for grade from the same models were 0.49 ± 0.11, 0.43 ± 0.11, and 0.67 ± 0.13, in that order. Estimates from Model A should be the most reliable. The estimates for cow weight are low compared to those reported by other workers. The differences in the estimates from Models A, B, and C, illustrate that variation in heritability estimates is not entirely due to genetic differences. Considerable variation can occur depending on how much adjustment has been made for fixed effects, and the methods used in estimating the variance and covariance components.

The heritability estimates of cow weight and grade obtained by intra-sire regression of offspring on dam were 0.22 ± 0.14 and 0.10 ± 0.06, respectively. These estimates are somewhat lower than those reported by other workers.

The paternal half-sib heritability estimate for condition score was 0.31 ± 0.11, which implies that adjusting cow weights and grades for condition may actually involve adjusting for genetic differences as well as differences due to environmental influences.

The correlation between weight and grade of beef cows was found to be largely genetic whereas the correlation between condition and cow weight or grade was primarily environmental.

The general conclusions from this study were:

1. (a) Season, age, condition, and nursing status significantly affect the variation in cow weight. Adjusting cow weights for condition will greatly reduce the

variation due to differences among seasons and between nursing status classification, but not to the extent that these effects become insignificant.

(b) Season, age, and condition significantly influenced the grade of beef cows. Nursing status was not an important source of variation in this trait.

(c) Season, age, and nursing status significantly influenced the condition of beef cows.

2. (a) The paternal half-sib heritability estimate of cow weight, was approximately 0.38 when corrections were made for errors contributed to adjusting for temporary environmental effects of season, age, condition, nursing status, and two-way interactions (Model A - statistical procedure used was Henderson's Method II). When cow weights were adjusted for season, age, and nursing status but not for condition and its respective interactions (Model B), the heritability estimate was roughly 0.29. This indicates that differences due to condition were comparatively larger within sire groups than between sire groups. The heritability of cow weight was approximately 0.56 when no corrections were made for adjusting for season, age, condition, nursing status, and two-way interactions (Model C).

The over-all results indicated that heritability estimates of mature weight of beef cows may vary in magnitude from moderate to high. The size of the heritability estimate for this trait, when estimated by paternal half-sib analysis, depends on how much adjustment has been made for environmental effects and whether corrections have been made for errors involved in estimating the adjustment factors. Unless corrections are made for errors made in adjusting the data for fixed effects, the sire components of variance and covariance will be inflated and genetic parameters will be biased upward.

The heritability of cow weight was 0.22 when computed by doubling the intra-sire regression of offspring on dam (Model D).

(b) The heritability estimates of grade of beef cows, computed from Models A, B, C, and D were 0.49, 0.43, 0.67 and 0.10. The above explanation for the variation in the magnitude of the heritability of cow weight, also applies to this trait.

(c) The heritability of flesh condition in beef cows was found to be approximately 0.31 (Model B). This suggests that adjusting cow weights and grades for differences in flesh condition as a preliminary step toward computing genetic parameters may not be warranted. This type of adjustment would tend to remove genetic variation as well as that due to environment.

3. The correlation between weight and grade of beef cows was found to be largely genetic whereas the correlation between condition and cow weight or grade was primarily due to environment.

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A P P E N D I X

Table 1A. Estimated least-squares constants for interactions for cow weight (lbs.) and grade (grade points): Model A.

Coded Variable	Weight Constant	Grade Constant	Coded Variable	Weight Constant	Grade Constant
Age Condition			11-1	12	.07
			11-2	-17	.14
			11-3	5	-.13
2-1	-15	-.29	11-4	0	-.08
2-2	32	-.15			
2-3	35	.16	Condition-		
2-4	-52	.28	Nursing Status		
3-1	68	-.17	1-2	12	.06
3-2	-34	.20	1-3	-12	-.06
3-3	-41	-.34	2-2	6	-.08
3-4	6	.31	2-3	- 6	.08
4-1	18	.03	3-2	- 6	.03
4-2	-11	-.10	3-3	6	-.03
4-3	-11	.10	4-2	-12	-.02
4-4	4	-.02	4-3	12	.02
5-1	- 7	.41			
5-2	- 1	-.19	Age-		
5-3	- 3	-.03	Nursing Status		
5-4	11	-.20	2-2	-44	.01
6-1	-17	-.58	2-3	44	-.01
6-2	9	-.08	3-2	- 2	.17
6-3	-11	.39	3-3	2	-.17
6-4	20	.27	4-2	11	-.05
7-1	-11	-.46	4-3	-11	.05
7-2	10	-.14	5-2	8	.10
7-3	15	.13	5-3	- 8	-.10
7-4	-14	.48	6-2	4	-.01
8-1	12	.46	6-3	- 4	.01
8-2	-21	.42	7-2	1	-.04
8-3	- 6	-.39	7-3	- 1	.04
8-4	15	-.49	8-2	28	.04
9-1	-103	.04	8-3	-28	-.04
9-2	49	.06	9-2	-23	-.25
9-3	47	.25	9-3	23	.25
9-4	7	-.35	10-2	12	.21
10-1	43	.46	10-3	-12	-.21
10-2	-16	-.15	11-2	5	-.17
10-3	-30	-.13	11-3	- 5	.17
10-4	3	-.19			

Table 2A. Estimated least-squares constants for interactions for cow weight (lbs.), grade (grade points), and condition (grade points): Model B.

Coded Variables	Weight Constant	Grade Constant	Condition Constant
Age-Nursing Status			
2-2	-22	0.02	0.03
2-3	22	-.02	-.03
3-2	- 8	0.12	0
3-3	8	-.12	0
4-2	15	0.03	0.10
4-3	-15	-.03	-.10
5-2	3	0.07	-.01
5-3	- 3	-.07	0.01
6-2	- 3	-.06	-.06
6-3	3	0.06	0.06
7-2	- 1	-.07	-.01
7-3	1	0.07	0.01
8-2	25	0.05	0
8-3	-25	-.05	0
9-2	-11	-.14	0.05
9-3	11	0.14	-.05
10-2	- 6	0.11	-.14
10-3	6	-.11	0.14
11-2	8	-.12	0.04
11-3	- 8	0.12	-.04

HERITABILITY ESTIMATES AND GENETIC, PHENOTYPIC, AND ENVIRONMENTAL CORRELATIONS BETWEEN WEIGHT, GRADE, AND CONDITION OF ANGUS COWS

by

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An abstract of a

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(Animal Breeding)

APPROVED: ______________________
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The objectives of this study were: (1) to estimate the effects of certain non-genetic sources of variation in weight, grade, and condition of beef cows; (2) to estimate the heritability of weight, grade, and condition of beef cows; and (3) to estimate the genetic, phenotypic, and environmental correlations between weight, grade, and condition of beef cows.

Weights, grades, and condition scores taken on 1371 Angus cows were used to evaluate the genetic and environmental nature of these traits. This sample of cows represented 365 sire groups.

Four models were used in this study:

1. Model A - Cow weight and grade were considered dependent variables; herds and sires within herds were considered random independent variables; and season, age, condition, nursing status, and their interactions were considered fixed independent variables. Least-squares procedures involving Henderson's (1953) Method II were used to adjust for fixed effects and to obtain variance and covariance components. Heritability estimates and correlation coefficients were obtained by paternal half-sib analysis.

2. Model B differed from Model A in that condition

score was considered a dependent variable instead of an independent variable.

3. Model C was the same as Model A except that the coefficients (k_o and k_2) for the within sire (σ_W^2) component of variance included in the among sire and herd adjusted expected mean squares (EMS) were considered unity whereas as in Model A they were calculated according to Method II of Henderson.

4. Model D - Heritability estimates were computed by doubling the estimate of intra-sire regression of offspring on dam from 198 dam-daughter pairs representing 63 sire groups. The dam-daughter pairs were part of the group of 1371 cows.

The results of this study indicated that season, age, condition score, nursing status, and age by nursing status remain significant when condition score was not considered as a fixed environmental effect (Model B). However, a comparison of the magnitude of the mean squares for these effects in Models A and B indicated that season, age, and nursing status are highly confounded with condition score.

Season and flesh condition were found to have a significant effect on grade of beef cows when they were included in the same model (Model A). When condition score was not included (Model B) age had a significant effect on grade.

Age, season, and nursing status were found to have a significant effect on flesh condition (Model B).

Paternal half-sib heritability estimates for cow weight using Models A, B, and C were 0.38$\pm$0.11, 0.29$\pm$0.11, and 0.56$\pm$0.11, respectively. Estimates for grade from the same models were 0.49$\pm$0.11, 0.43$\pm$0.11, and 0.67$\pm$0.12, in that order. Estimates from Model A should be the most reliable. The differences in the estimates from Models A, B, and C, illustrate that variation in heritability estimates is not entirely due to genetic differences. Considerable variation can occur depending on how much adjustment has been made for fixed effects, and the methods used in estimating the variance and covariance components.

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The paternal half-sib heritability estimate for condition score was 0.31$\pm$0.11, which implies that adjusting cow weights and grades for condition may actually involve adjusting for genetic differences as well as differences due to environmental influences.

The correlation between weight and grade of beef cows was found to be largely genetic whereas the correlation between condition and cow weight or grade was primarily environmental.