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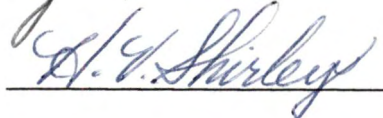
I am submitting herewith a dissertation written by Adeeb D. S. Kharoofa entitled "Evidence for Sex Linkage in the Heredity of Quantitative Traits in Beef Cattle." I have examined the final copy of this dissertation for form and content and recommend that it be accepted in partial fulfillment of the requirements for the degree of Doctor of Philosophy, with a major in Animal Science.



Robert R. Shrode, Major Professor

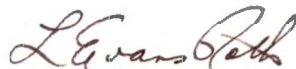
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EVIDENCE FOR SEX LINKAGE IN THE HEREDITY OF
QUANTITATIVE TRAITS IN BEEF CATTLE

A Dissertation
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Doctor of Philosophy
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ABSTRACT

To assess the relative influences of sex linkage and maternal effects, sire-son, sire-daughter, dam-son, and dam-daughter correlations of Birth Weight and weaning and post-weaning (to a year of age) Body Weight, Gain, Average Daily Gain, Heart Girth, Body Length, Hip Width, Hip Height, Fat Thickness, Type Score, Condition Score, and Frame Score of 1903 Angus calves and 1126 Polled Hereford calves were calculated after least-squares adjustment to remove variation in weaning and post-weaning traits due to differences in age of dam and age of calf. Sex-linkage effects appear to be important in Weaning Body Weight, Weaning Gain, Weaning Average Daily Gain, Post-Weaning Weight, Life-Time Average Daily Gain, Post-Weaning Heart Girth, and Post-Weaning Hip Width in Angus. None of the traits seem to show any important sex-linkage effect in Polled Herefords. Maternal effects appear to be important only in Post-Weaning Body Length in Angus and Weaning Fat Thickness, Post-Weaning Weight, Life-Time Average Daily Gain, Post-Weaning Type Score, and Post-Weaning Condition Score in Polled Herefords. Sex-linkage and/or maternal effects are appreciable in Weaning Weight, Weaning Gain, Weaning Average Daily Gain, Weaning Heart Girth, Weaning Body Length, Post-Weaning Weight, and Life-Time Average Daily Gain in Angus. However, in Polled Herefords, sex-linkage and/or maternal effects together are important in Birth Weight, Weaning Hip Width, Weaning Fat Thickness and Post-Weaning

Type Score. Sex linkage and sex linkage confounded with maternal effects as one value appear to be greater in Angus than in Polled Herefords with respect to the majority of the traits while maternal effects appear to be greater in Polled Herefords than in Angus with respect to most of the traits. The majority of the assessments decrease in both breeds between weaning and post-weaning with respect to sex-linkage effects, maternal effects, and sex-linkage and/or maternal effects with some differences between the two breeds, possibly due to the fact that Angus are earlier maturing than Polled Herefords in both sexes, and the heritability of rate of maturing in Angus appears, from research of others, to be more than twice that in Polled Herefords.

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CHAPTER I

INTRODUCTION

If parent and offspring of opposite sex consistently resemble one another with respect to some traits more than do parents and offspring of the same sex, sex-linked genes affecting the traits may be responsible for such a phenomenon. Wright's (1921) coefficient of relationship is a correlation between genotypes of individuals related in the same manner as the pair in question. However, the calculation is based on the slightly erroneous assumption that all of the heredity is autosomal, that is, that a gamete produced by a diploid individual contains a sample half of that individual's heredity. For sex-linked genes, however, the asymmetrical chromosomal complement of males and females makes it necessary to distinguish the sexes of the relatives. There are four kinds of parent-offspring relationships: father-son, father-daughter, mother-son, mother-daughter. Since a mammalian male transmits none of his sex-linked heredity to his sons and all of his sex-linked heredity to his daughters and since all of a mammalian male's sex-linked heredity was received from his dam, the coefficient of relationship between mammalian parent and offspring of opposite sex would be slightly larger than the coefficient of relationship between mammalian parent and offspring of the same sex if sex-linkage were taken into account in the calculations. To the extent that the heredity of quantitative traits in mammals is sex-linked, this effect would

be expected to cause correlations between phenotypes of parent and offspring of opposite sex to be larger than those between phenotypes of parent and offspring of the same sex. Of course, part of the correlation between phenotypes of mammalian dams and offspring of both sexes is caused by maternal effects, and this must be taken into account in any consideration of parent-offspring correlations. Evidence for sex-linkage and maternal effects in the heredity of quantitative traits was sought by calculating all possible correlations between phenotypes of parent and offspring of the same sex and comparing them with all possible corresponding correlations between phenotypes of parent and offspring of opposite sex, using data accumulated on body measurements and weight and gain variables in the Plateau Experiment Station Angus and the Tobacco Experiment Station Polled Hereford herds. Appropriate comparisons of these correlations were considered as tests of the hypothesis that sex-linked heredity influences the phenotypic expression of quantitative traits in beef cattle.

CHAPTER II

REVIEW OF LITERATURE

Among the very early investigators who held that the sire has a greater influence on the quality of the offspring than does the dam, Cole (1925) may be mentioned. Among the investigators who considered the dam to be of greater importance is Gaines (1922) who believed performance to be transmitted by the female rather than by the male. Gowen (1920) believed that the offspring receives its characters from the sire and dam in equal proportions. Graves (1925), Copeland (1927) and Gowen (1927) all indicated sire and dam to be of equal importance in the transmission of factors for milk traits. On the whole, the evidence Smith and Robinson (1933) summarized, mentioned here with others, indicated equal transmission by the two parents. Lawritson, et al. (1919) concluded that factors for good records are transmitted by the sire to his daughters and by the dam to her sons.

Of the sex chromosomes of a mammalian female, neither can come from her paternal grandsire. Hence, a study of correlations between individuals and their grandparents might produce evidence of sex-linkage. If the phenotypic correlations with each of the four grandparents are approximately equal, then sex-linked factors, if any affect the trait in question, play no important part. If, on the other hand, they do have an appreciable effect, the correlation

between females and their paternal grandsires should be less than correlations with other grandparents. Smith and Robinson (1931) and Madsen (1932) published positive evidence relating to the part that sex-linked factors may play. The results of all of these investigations show that, of the four grandparents, the paternal grandsire has less influence upon the yield of his granddaughters than do the other grandparents. The diagram in Figure 1 shows how each of the grandparents affects grandoffspring with respect to sex-linked genes.

Gowen (1933) reported that in comparisons of the correlation between sire's conformation and that of his daughters with the correlation between dam's conformation and that of her daughters, the average correlation between daughters and sires for like measurements was 0.39 and that between dams and daughters was 0.45. These correlations are not significantly different. The conformation traits included in this study were: weight, wither height, depth at withers, heart girth, paunch girth, width at hips, body length, and rump length.

Pahnish et al. (1961) drew attention to several reports on different traits in cattle showing evidence of a greater influence of sires on female progeny than on male progeny. They obviously felt justified in the belief, shared by most writers on the subject, that, as sex-linkage has for so long been accepted as unimportant in quantitative inheritance, it is unlikely to appear suddenly in several traits at once.

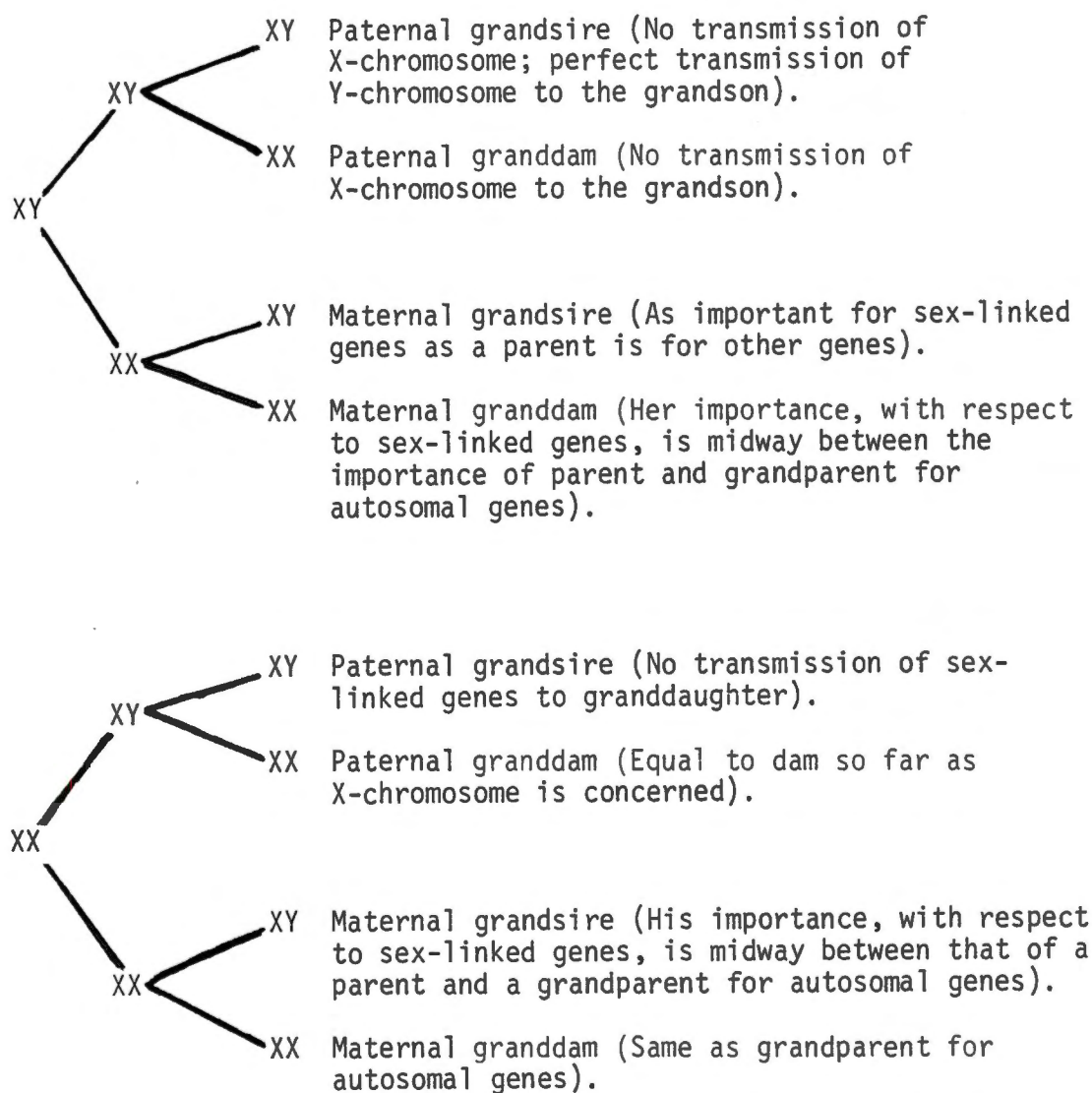


FIGURE 1. Effect of Grandparents on Grandoffspring. From Lush (1945).

Beilharz (1963) advanced the hypothesis that sex chromosomes have an effect on the organism that is greater than that of normal autosomes, and discussed at length in a paper published a year earlier (Beilharz, 1962) the calculated correlations and regressions involving 223 cows' lifetime records, own first lactation, mother's, each grandmother's, and mother's and father's paternal half-sisters' (half-aunts) lifetime performance. The results showed that the correlation with mothers' performance is significant and the greatest of the relationships with relatives. The next highest correlation, significant in fat tests, is that with half-aunts on the maternal side. The correlation with half-aunts on the father's side is very low, and this regression, in the case of both milk yield and fat test, is slightly negative. This is a result one would expect with sex linkage.

For autosomal genes, the correlations between parent and offspring and between full sibs are the same, all being 0.5 in a random mating population. This value of 0.5 is expected when variation in the trait studied is determined by autosomal genes with additive effects. Obviously, there is no genetic correlation between mammalian sire and son produced by sex-linked genes because the son receives his sire's Y chromosome which is believed to carry little or no euchromatin in most mammalian species. The contribution of sex-linked genes to the correlation between mammalian dam and daughter is the same as in the case of autosomal genes because the daughter receives an X chromosome from each parent, just as she receives

one member of each pair of autosomes from each parent. Accordingly, the genetic parent-offspring correlations in mammals with respect to sex linkage can be reasoned to be as follows:

Father-son	$r = 0$	
Father-daughter	$r = \sqrt{1/2}$	
Mother-son	$r = \sqrt{1/2}$	
Mother-daughter	$r = 1/2$	(Li, 1955)

Contributory genes located on the X chromosome increase certain correlation coefficients (i.e., those for father-daughter, mother-son, and sister-sister pairs) and reduce others (i.e., those for father-son and brother-sister pairs). Genes located on the Y chromosome would reverse this trend in the parent-offspring pairs, but they would accentuate the reduction of the brother-sister coefficients. Penrose (1967) presented correlation coefficients expected for traits determined by genes with additive quantitative effects as shown in Table 1.

TABLE 1. Correlations Expected for Additive Quantitative Traits

Type of Pair	Autosomal Genes	Sex-Chromosomal Genes		
		X Alone Effective	X and Y With Equal Effects	Y Alone Effective
Father-son	0.5	0.00	0.50	1.00
Father-daughter	0.5	0.71	0.50	0.00
Mother-son	0.5	0.71	0.50	0.50
Mother-daughter	0.5	0.50	0.50	0.50
Brother-brother	0.5	0.50	0.75	1.00
Brother-sister	0.5	0.35	0.25	0.00
Sister-sister	0.5	0.75	0.75	0.75

Mather and Jinks (1963) reported that the characteristic of sex-linked inheritance is that the sister-sister correlation is higher than that between brothers (and may be much greater than 0.5 which is the maximum value for autosomal genes) but the cross-sex correlation is lower than either same-sex correlation. The actual value of the correlation coefficients will, of course, vary with the effect of autosomal genes and nonheritable agencies affecting the characters, but, assuming these to be the same in both sexes, the magnitude rank: r_{ss} , r_{bb} , r_{sb} will hold.

Garn and Rohman (1962) reported observations on the correlation between sibs with respect to three characters which may be considered as reflecting developmental timing in man, and they showed that the correlation between sisters is markedly higher than sibs of unlike sex, which, in turn, is slightly higher than that between brothers (Table 2).

TABLE 2. Garn and Rohman Correlation Coefficients

Characters	Sister-Sister	Sister-Brother	Brother-Brother
Ossification rate	0.62	0.40	0.39
Ossification timing	0.54	0.47	0.40
Tooth calcification	0.41	0.24	0.22

It may not be generally realized that failure to detect evidence for sex linkage in quantitative characters is not evidence for the absence or unimportance of sex linkage. Beilharz (1961) showed that the conditions in which an experiment can demonstrate absence of appreciable sex linkage are rather strict. For instance, both sexes of progeny must be studied and compared for sex linkage to be separated from nongenetic maternal influence (cytoplasmic transmission and maternal environment). In some poultry studies, the criterion for the presence of sex linkage was a greater influence of the sires than of the dams on pullets. It is obvious that, in many cases, a true genetic difference between sire's and dam's influence may have been masked by the simultaneous presence of non-genetic maternal influence. Some studies involved data on one sex only while other studies included data on both sexes and claimed evidence of important sex linkage in several traits.

Generally, the best criterion for demonstrating the importance of sex linkage is the comparison of the relative amounts of influence the heterogametic parent has on the two sexes of progeny. For some traits, this may have to be evaluated through breeding tests. In mammals, there are several reports of important maternal influence on body weight, in which the progeny have not been separated into sexes. In these reports, it is impossible to separate genetic sex linkage from non-sex-linked maternal effects. Some workers combine both sexes into one population for analysis so that sex linkage must overcome non-genetic maternal influence before it can be seen as an increased sire influence (Beilharz, 1960).

Similarly, in birds, there are reports in which, because sexes have not been separated, or only one sex weighed, differences in non-additive gene effects between reciprocal crosses cannot be analyzed into sex linkage or other gene interaction (Kan et al., 1959; Morely and Smith, 1954). Beilharz (1962) stated that in many reports of body inheritance, which show no evidence of sex linkage, one or more of the following reasons may apply:

1. Sex linkage is not detectible due to the nature of the data, e.g., unsexed progeny.
2. X chromosomes of a breeding population may be uniform for factors determining body weight.
3. Genotype-environment interactions may obscure sex-linked genes affecting body weight; e.g., McDonald (1957 a and b) showed that dietary cysteine determined whether a particular sex-linked genetic difference in growth rate was observed in poultry.

Kidwell et al. (1960) estimated the relative importance in rats of additive, non-additive, maternal, and sex-linkage effects in inheritance. This study showed sex linkage negligible by the method of Henderson (1948).

Brumby (1960) concluded that in mice, sex linkage is unimportant in body weight inheritance.

Damon et al. (1961) reported that in beef cattle, there is little, if any, influence of sex-linked genes on 180-day weight, slaughter calf grade, slaughter grade, rate of gain or weight per day of age.

Shahrودي (1972) found that in beef cattle (Angus and Hereford), generally, sex-linked effects were small and nonsignificant in his study of different periods of cumulative weight and different periodic gains, in addition to birth weight, weaning weight, and suckling gain. However, this effect was highly significant on weaning weight and the second 42-day periodic gain. The constant estimated for sex-linkage effect was quite large in weaning weight. As a cause of variation in weaning weight, sex-linkage effect accounted for 3.24 percent of the total variation.

Many reports, including Morris and Skaller (1958) in chickens, Johnson and Asmundson (1957) in turkeys, Falconer (1951) and Chai (1958) in mice, and Yao and Eaton (1954) in rabbits, made no reference to sex linkage in body weight inheritance. Other studies in poultry, e.g., Hale (1959), Morris (1959), and Yao (1959), failed to show evidence for sex linkage.

Henderson (1961) reported that hatching power in chickens is not sex-linked. In other words, the dam and sire are of equal importance in the transmission of hatching power.

Beilharz (1960) suggested sex-linked inheritance of body weight in poultry and rabbits. A year later Beilharz (1961) presented some evidence of important sex linkage in body weight in mice and sheep.

Many studies suggest the presence of sex linkage in poultry; e.g., Ghigi (1948), King and Bruckner (1952), Osborne (1953, 1955), and Goodman and Jaap (1961), reported that sex-linked genetic effect

appeared to be important in egg weight in fowl. Other studies, e.g., Ubbels and Albada (1948), Greenwood and Blyth (1951), Warren (1958), and Kawahara (1965) found a possibility of sex-linked genes affecting sexual maturity in poultry.

Niesel (1941) reported that the correlation of the performance of ancestors of the cock with performance of the progeny was 0.67 ± 0.08 , while the correlation of the performance of ancestors of the hens with that of the progeny was 0.38 ± 0.12 . He considered this to be evidence of strong sex-linked inheritance of laying capacity as opposed to autosomal influences.

Kaufman (1948) explained that the difference in body size between Greenleg and Bantam fowls may be due to the cumulative action of two pairs of genes, one autosomal, the other sex-linked. Also, Brunson et al. (1956), Jaap and Grimes (1956), Jerome et al. (1956), Beilharz (1960), and Khan et al., (1973) agreed that sex-linked genes affect body weight. Hay (1950) indicated that sex-linked genes may be operating to regulate fertility in the fowl. Godfrey (1953, 1957) suggested that sex-linked genes affect growth rate in the fowl.

Thomas et al. (1958) reported that comparisons of heritability estimates from male and female progeny data for the characters of body weight at different ages, gain, feed consumption, and feed conversion during different periods provide some evidence that sex-linked genes are of considerable importance in the expression of these characters in broilers.

Redman and Shoffner (1961) reported that sex linkage, as indicated by average sire variance components, was present in specific gravity of eggs, egg shell color, and egg weight.

Goodman and Jaap (1961) stated that sex-linked genetic effects appeared to be of importance in egg production, as well as egg weight and egg shape index at 40 weeks of age. Egg shape index at 30 weeks of age did not show any appreciable sex linkage.

Hole et al. (1958) stated that the sire influenced age at first egg, plumage, and the moult to a greater degree than did the dam, which may indicate sex linkage. Shell quality did not differ appreciably in crossbreds and purebreds.

Boyer et al. (1963) reported that an appropriate diet permits the manifestation of sex-linked variability in meat traits.

Merritt (1966) found, in the fowl, estimates of heritability of male's 42-day weight, 63 day body weight, breast angle, keel length, and shank length based on the sire component of variance to be only slightly smaller than the corresponding estimates for females, but the difference between male and female estimates based on the dam component are, except for breast angle, more than twice the appropriate standard error and statistically nonsignificant. These differences are consistent with relatively large sex-linkage effects.

Collin and Hans (1968) found that liver weight is affected by sex-linked genes.

Lokanath et al. (1978) stated that sex-linkage and maternal effects accounted for 6.95 and 3.78 percent, respectively, of the variation in hatchability.

In the biometrical area, investigation of genotypic correlations between relatives under the assumption of autosomal transmission, Fisher's (1918) and Wright's (1921) papers are the classical ones. Fisher (1918) obtained many ancestral and collateral-relative correlations under conditions of random mating considering dominance and interaction among loci. Wright (1921) obtained correlations among relatives of many kinds in populations randomly or assortively mating or in which inbreeding was occurring with gene effects additive, i.e., no dominance or non-allelic gene interaction. Charles (1933) found collateral and ancestral correlations of sex-linked transmission, irrespective of sex. In this study, he considered the correlation between relatives without regard to the sex of the individuals in each pair or to the sex of their common ancestor and concluded that sib correlations might be higher than parent-offspring correlations when there is dominance with respect to autosomal genes or when there is a contribution of sex-linked genes, irrespective of dominance effect. Wright (1933) evaluated the correlation between uniting gametes and between zygotes in terms of gene frequencies and finite population numbers of males and females to study the changes in heterozygosis. Wright (1935) dealt with the simple formula for the inbreeding coefficient (F) and coefficient of relationship ($r_{z_1 z_2}$). These were derived also by Wright (1951) under the assumption of sex-linked inheritance, using a path coefficient analysis. Lush (1948) presented a formula for the correlation between parent and offspring under the assumption

of t autosomal genes and s sex-linked genes using the method of path coefficients. Kempthorne (1954) solved the general problem of partitioning the total genotypic variance and obtaining the genotypic covariance between relatives. Cockerham (1956) stated a few simple effects of autosomal linkage on covariances among relatives.

Penrose (1967) concluded that there is no indication of any influence from genes on the X or Y chromosomes in the hereditary variations of the finger-tip ridge-count in humans, using in his study, correlations between parent and offspring and between sibs.

Thomas et al. (1958) pointed out that, in poultry, comparison of the sire and dam components of variance shows that the distribution of the additively genetic variance arising from genes on the sex chromosome is different from that from genes on autosomes. Considering only sex-linked genes in the analysis of female progeny, one-half of this variance is in the sire component, none is in the dam component, and the remainder is in the variance between full sibs. Thus, the genetic variability due to sex-linked genes contributes only to heritability estimated from the sire component estimated from female progeny.

In the analysis of only male progeny, the additively genetic variance is distributed one-quarter each to the sire component of variance and the variance between full sibs, and the remaining one-half to the dam component of variance. In contrast to the results for female progeny, the effect of sex-linked genes in male progeny

is to make heritability from the dam component of variance larger than that from the sire component of variance.

Heritability in the narrow sense, i.e., the proportion of variation due to additively genetic variation, is usually calculated as follows, assuming that the variation is not sex-linked:

$$h^2 = \frac{4S}{S + D + Q} \quad \text{or} \quad h^2 = \frac{4D}{S + D + Q}$$

where,

S = estimated component of variance due to differences between sires,

D = estimated component of variance due to differences between dams,

Q = estimate of variance between full sibs,

and,

S + D + Q = total phenotypic variance.

The logic for this calculation is the fact that the additively genetic variation in a population mating at random comes from various sources as follows: one-fourth from sires, one-fourth from dams, and one-half from chance during the reduction division in gametogenesis (Wright, 1921). These formulas apply whether the population is of mixed sexes or of a single sex.

Where additively genetic variation is assumed to stem from the segregation of X-chromosome loci only, the situation in a population of males differs from that in a population of females.

Using Wright's approach, as before, the following solutions are obtained from completely sex-linked additive variation in a randomly mating population:

1. In the male (X_{-}) additive variation is derived as follows:

None from sires (S)

1/2 from dams (D)

1/2 from chance

Thus, the heritability estimate is $h_D^2 = \frac{2D}{S + D + Q}$

2. In the female (XX) additive variation is derived as follows:

1/2 from sires (S)

1/4 from dams (D)

1/4 from chance

Thus, the heritability estimates are:

$$h_S^2 = \frac{2S}{S + D + Q} \text{ or } h^2 = \frac{4D}{S + D + Q} .$$

The effect of sex-linked genes on the comparison of estimates of heritability from progenies of different sexes is not straight forward. Heritability based on the sire component of variance should be highest when estimated from female progeny since the sire is assumed to contribute no sex-linked genes to male offspring. The larger heritability from the dam component of variance, however, should be estimated from the male progeny because one-half the additively genetic variance falls into the dam component of variance estimated

from male progeny and only one-fourth into that estimated from female progeny.

Estimates of heritability of certain traits in beef cattle appear to be higher in heifers than in bulls (Diven et al., 1960; Pahnish, et al., 1961; Roberson, et al., 1963; Pahnish, et al., 1964; Al-Mallah, 1975; and Chihasz, 1980). A possible reason for these differences could be sex-linked genes contributing importantly to the phenotypes of the traits.

Differences in reciprocal crosses depend primarily on sex-linked traits and maternal effects in animal breeding experiments. Eisen et al. (1966) established four biological models for detecting sex linkage and maternal effects from homogametic and heterogametic female species with male or female progenies. It was found that neither the statistical models used by Henderson (1948) or the one used by Griffing (1956) is adequate to separate maternal effects from sex-linked effects. Two of Eisen's models which correspond to beef cattle breeding experiments are:

1. Homogametic female species with male progeny:

$$Y_{ij} = m + A_i + A_j + M_j + L_j + S_{ij} + E_{ij}$$

2. Homogametic female species with female progeny:

$$Y_{ij} = m + A_i + L_i + A_j + M_j + L_j + S_{ij} + E_{ij}$$

where,

Y_{ij} = mean of quantitative variable measured on individuals resulting from crossing i^{th} and j^{th} lines,

A_i, A_j = the cumulative additive effect of autosomal genes in the i^{th} and j^{th} lines,

L_i, L_j = the cumulative additive effect of sex-linkage in the i^{th} and j^{th} lines,

M_j = the average maternal effect in j^{th} line,

S_{ij} = specific combining ability,

E_{ij} = error.

CHAPTER III

MATERIALS AND METHODS

The data used in this study were collected from two breeds of cattle, Angus and Polled Hereford. A total of 1903 Angus calves were born from 1969 to 1980 at The University of Tennessee Plateau Experiment Station at Crossville. A total of 1126 Polled Hereford calves were born from 1969 to 1980 at The University of Tennessee Tobacco Experiment Station at Greenville. These two herds were the experimental material in Tennessee's contribution to project S-10, the Southern Regional Beef Cattle Breeding Project.

A limited breeding season was used at both stations, the calves being born in January, February, and March each year. Calves were kept with their dams until weaning without creepfeed. Cows were segregated according to the sex of the calf they were nursing on approximately July 1 of each year. At weaning, the calves were placed in dry lots according to sex and size. At this time, the feeding regimes of heifer and bull calves were different. The heifer calves were each fed daily a ration of corn silage ad libitum, two pounds of hay, two pounds of grain, and one-half pound of protein supplement. This ration was designed to produce an average daily gain of about one pound per day which would consist of a limited amount of fat. The bull calves were fed a more liberal ration. They were fed daily corn silage ad libitum with about two pounds of hay and about one pound of a 14-percent protein grain mixture

per Cwt of live weight. These rations were fed until the first of April, at which time the yearling replacement heifers were placed upon pasture, and no more supplemental feeding was provided until the next winter.

A total of 3029 calves' records was available for this study. The variables recorded were Birth Weight, Weaning Weight, Post-Weaning Weight, Weaning Gain, Post-Weaning Weight, Weaning Average Daily Gain, Post-Weaning Average Daily Gain, Life-Time Average Daily Gain, Fat Thickness, Frame Score, Type Score, Condition Score, and four body measurements taken at weaning and post-weaning times, including Heart Girth, Body Length, Hip Width, and Hip Height.

The description of these variables is as follows:

1. Birth Weight, unit, lb
2. Weaning Weight, at average of 231 days of age, unit, lb
3. Post-Weaning Weight, at average of 365 days of age, unit, lb
4. Weaning Gain, calculated by subtracting Birth Weight from Weaning Weight, unit, lb
5. Post-Weaning Gain, calculated by subtracting Weaning Weight from Post-Weaning Weight, unit, lb
6. Weaning Average Daily Gain, calculated by dividing the Weaning Gain by Weaning Age, unit, lb
7. Post-Weaning Average Daily Gain, calculated by dividing the Post-Weaning Gain by the difference between Post-Weaning Age and Weaning Age, unit, lb

8. Life-Time Average Daily Gain, calculated by dividing the difference between Post Weaning Weight and the Birth Weight by the total number of days from birth to the end of the Post-Weaning period, unit, lb

9. Fat Thickness, the ultrasonically measured thickness of subcutaneous fat, unit, mm

10. Type Score, a subjective estimate of general conformation, subjective score, 1 to 16.

11. Condition Score, the conventional subjective appraisal of fatness, subjective score, 1 to 16.

12. Frame Score, subjective score, 1 to 5.

13. Heart Girth, body circumference just posterior to the front legs, measured with a metal tape, unit, in

14. Body Length, the distance down the midline of the back from the center of the top of the shoulder to the posterior prominence of the pin bone as measured with a metal tape, unit, in

15. Hip Width, the horizontal distance between the lateral prominences of the hip bones, measured with a metal tape, unit, in

16. Hip Height, the vertical distance between the ground and the dorsal edge of the hip bone as measured with a precision caliper, unit, in

Data were analyzed with an IBM 360/65 computer using Statistical Analysis System (SAS) programs. All records were adjusted by using constants obtained by least-squares procedures to remove variation due to differences in age of calf and age of dam. All possible

correlations between phenotypes of parent and offspring of opposite sex and of the same sex were obtained. Estimates of the part of correlation caused by sex linkage and/or maternal effect were obtained by subtracting sire-son correlations from dam-son correlations, the part of correlation caused by maternal effect alone was obtained by subtracting sire-daughter correlations from dam-son correlations, and the part of correlation caused by sex linkage alone was obtained by subtracting sire-son correlations from sire-daughter correlations. The sum of the last two differences should equal the first one.

The null hypothesis, $H_0: r_1 = r_2$, was tested by using Fisher's Z transformation, the following test statistic for the equality of two correlations was used.

$$z = \frac{\frac{1}{2} \log_e \frac{1 + r_1}{1 - r_1} - \frac{1}{2} \log_e \frac{1 + r_2}{1 - r_2}}{\sqrt{\frac{1}{n_1 - 3} + \frac{1}{n_2 - 3}}}$$

CHAPTER IV

RESULTS

Obviously, there is no genetic correlation between mammalian sire and son produced by sex-linked genes because the son receives only his sire's Y chromosome which in most mammalian species is believed to carry little or no euchromatin. The contribution of sex-linked genes to correlation between mammalian dam and daughter is the same as in the case of autosomal genes because the daughter receives an X chromosome from each parent, just as she receives one member of each pair of autosomes from each parent. Accordingly, the genetic parent-offspring correlations in mammals with respect to sex-linkage can be reasoned to be as follows:

Father-son	$r = 0$	
Father-daughter	$r = \sqrt{1/2}$	
Mother-son	$r = \sqrt{1/2}$	
Mother-daughter	$r = 1/2$	(Li, 1955)

Thus, it seems logical to expect the father-daughter correlation to be larger than the father-son correlation if sex-linked heredity affects the trait in question.

Among sire-offspring correlations (Tables 3-6) involving weaning and post-weaning data on all the performance and measurement variables in both breeds, values of the sire-daughter correlations are larger than those of sire-son correlations in general, and significant differences which were observed in weaning Body Weight, Weaning

TABLE 3. Coefficients of Correlation Between Parents and Offspring with Respect to Angus Weaning Variables and Various Differences Among Them

Variable	Sire		Dam		Sex-Linkage and/or Maternal Effect		Maternal Effect		Sex-Linkage Effect	
	Son	Daughter	Son	Daughter	Dam-Son	Minus Sire-Son	Dam-Son	Minus Sire-Daughter	Sire-Son	Minus Sire-Daughter
Birth Weight	0.116	0.095	0.181	0.154	0.065		0.086		-0.021	
Body Weight	-0.101	0.039	0.138	0.232	0.239**		0.099		0.140*	
Gain	-0.125	0.011	0.105	0.188	0.230**		0.094		0.136*	
Average Daily Gain	-0.119	0.014	0.097	0.186	0.216**		0.083		0.133*	
Heart Girth	-0.046	0.027	0.083	0.061	0.129*		0.056		0.073	
Body Length	-0.047	0.026	0.111	0.191	0.158*		0.085		0.073	
Hip Width	0.128	0.011	0.063	0.094	-0.065		0.053		-0.117	
Hip Height	0.030	0.097	0.117	0.048	0.087		0.020		0.067	
Fat Thickness	0.092	0.180	-0.082	0.103	-0.174		-0.262*		0.088	
Type Score	-0.023	0.064	0.026	-0.036	0.049		-0.038		0.087	
Condition Score	0.026	-0.025	-0.093	0.054	-0.119		-0.068		-0.051	
Frame Score	0.004	0.160	0.140	0.061	0.136		-0.020		0.156	

* .01 < P < .05

** P < .01

TABLE 4. Coefficients of Correlation Between Parents and Offspring with Respect to Polled Hereford Weaning Variables and Various Differences Among Them

Variable	Sire		Dam		Sex-Linkage and/or Maternal Effect		Maternal Effect		Sex-Linkage Effect	
	Son	Daughter	Son	Daughter	Dam-Son	Minus Sire-Son	Dam-Son	Minus Sire-Daughter	Sire-Son	Minus Sire-Daughter
Birth Weight	0.007	0.085	0.199	-0.045	0.192**	0.114	0.114	0.078	0.078	0.078
Body Weight	-0.128	-0.122	-0.015	0.009	0.113	0.107	0.107	0.006	0.006	0.006
Gain	-0.137	-0.143	-0.038	0.036	0.099	0.105	0.105	-0.006	-0.006	-0.006
Average Daily Gain	-0.131	-0.134	-0.046	0.035	0.085	0.088	0.088	-0.003	-0.003	-0.003
Heart Girth	-0.007	0.011	0.058	0.084	0.065	0.047	0.047	0.018	0.018	0.018
Body Length	0.057	0.022	0.062	-0.043	0.005	0.040	0.040	-0.035	-0.035	-0.035
Hip Width	-0.129	-0.117	0.017	0.012	0.146	0.134	0.134	0.012	0.012	0.012
Hip Height	0.125	0.025	0.175	0.152	0.050	0.150	0.150	-0.100	-0.100	-0.100
Fat Thickness	-0.009	-0.017	0.332	0.299	0.341**	0.349**	0.349**	-0.008	-0.008	-0.008
Type Score	0.045	-0.013	0.085	0.069	0.040	0.098	0.098	-0.058	-0.058	-0.058
Condition Score	-0.053	-0.006	0.028	0.113	0.081	0.034	0.034	0.047	0.047	0.047
Frame Score	0.099	0.114	0.042	-0.056	-0.057	-0.072	-0.072	0.015	0.015	0.015

* .01 < P < .05

** P < .01

TABLE 5. Coefficients of Correlation Between Parents and Offspring with Respect to Angus Post-Weaning Variables and Various Differences Among Them

Variable	Sire		Dam		Sex-Linkage and/or Maternal Effect		Maternal Effect		Sex-Linkage Effect	
	Son	Daughter	Son	Daughter	Dam-Son Minus Sire-Son	Dam-Daughter Minus Sire-Daughter	Dam-Son Minus Sire-Daughter	Dam-Son Minus Sire-Daughter	Sire-Son	Sire-Daughter Minus Sire-Son
Body Weight	-0.037	0.186	0.209	0.290	0.246**	0.023	0.023	0.023	0.223**	0.223**
Gain	0.010	0.103	0.086	0.154	0.076	-0.017	-0.017	-0.017	0.093	0.093
Average Daily Gain	0.014	0.111	0.066	0.148	0.052	-0.045	-0.045	-0.045	0.097	0.097
L.T. ADG	-0.048	0.172	0.174	0.283	0.222**	0.002	0.002	0.002	0.220**	0.220**
Heart Girth	0.046	0.316	0.092	0.236	0.046	-0.224**	-0.224**	-0.224**	0.270**	0.270**
Body Length	0.035	-0.048	0.081	0.039	0.046	0.129*	0.129*	0.129*	-0.083	-0.083
Hip Width	0.060	0.285	-0.054	0.163	-0.114	-0.339**	-0.339**	-0.339**	0.225**	0.225**
Hip Height	0.141	0.207	0.124	0.097	-0.017	-0.083	-0.083	-0.083	0.066	0.066
Fat Thickness	-0.191	-0.112	-0.267	-0.162	-0.076	-0.155*	-0.155*	-0.155*	0.079	0.079
Type Score	-0.006	-0.046	0.047	0.108	0.053	0.093	0.093	0.093	-0.040	-0.040
Condition Score	0.212	0.108	0.032	0.025	-0.180**	-0.076	-0.076	-0.076	-0.104	-0.104
Frame Score	0.039	0.160	0.043	0.039	0.004	-0.117	-0.117	-0.117	0.121	0.121

* .01 < P < .05

** P < .01

TABLE 6. Coefficients of Correlation Between Parents and Offspring with Respect to Polled Hereford Post-Weaning Variables and Various Differences Among Them

Variable	Sire			Dam		Sex-Linkage and/or Maternal Effect		Maternal Effect		Sex-Linkage Effect	
	Son	Daughter		Son	Daughter	Dam-Son	Sire-Son	Dam-Son	Sire-Daughter	Sire-Son	Minus Sire-Son
Body Weight	0.215	-0.108		0.080	0.182	-0.135*		0.188**		-0.323**	
Gain	0.069	0.101		-0.020	0.180	-0.089		-0.121		0.032	
Average Daily Gain	0.075	-0.046		-0.058	0.114	-0.133		-0.012		-0.121	
L.T. ADG	0.199	-0.092		0.068	0.195	-0.131		0.160*		-0.291**	
Heart Girth	0.122	-0.021		0.080	0.151	-0.042		0.101		-0.143*	
Body Length	0.112	0.098		0.030	0.092	-0.082		-0.068		-0.014	
Hip Width	0.251	0.231		0.178	0.244	-0.073		-0.053		-0.020	
Hip Height	0.034	0.118		0.129	0.231	0.095		0.011		0.084	
Fat Thickness	-0.021	0.057		0.028	0.099	0.049		-0.029		0.078	
Type Score	0.006	-0.035		0.165	0.080	0.159*		0.200**		-0.041	
Condition Score	-0.072	-0.107		0.076	0.062	0.148		0.183*		-0.035	
Frame Score	0.106	0.177		0.156	0.263	0.050		-0.021		0.071	

* .01 < P < .05

** P < .01

Gain, Weaning Average Daily Gain, Post-Weaning Weight, Life-Time Average Daily Gain, Post-Weaning Heart Girth, and Post-Weaning Hip Width in Angus could result from sex linkage of some genes which affect the traits in question. None of the comparisons show any important differences in Polled Herefords.

Part of the correlation between phenotypes of dam and offspring could be caused by maternal effect. Consideration of differences between dam-son correlation and sire-daughter correlation is the only way to assess maternal effect unconfounded with sex-linkage (Tables 3-6). These differences were significant only for Post-Weaning Body Length in Angus and for Weaning Fat Thickness, Post-Weaning Weight, Life-Time Average Daily Gain, Post-Weaning Type Score, and Post-Weaning Condition Score in Polled Herefords.

Dam-son correlation and sire-son correlation should be the same unless sex-linkage and/or maternal effects (transmitted cytoplasmically or from maternal environment) are involved. Appreciable differences in these correlations were observed (Tables 3-6) in Weaning Weight, Weaning Gain, Weaning Average Daily Gain, Weaning Heart Girth, Weaning Body Length, Post-Weaning Weight, and Life-Time Average Daily Gain in Angus. However, in Polled Herefords, sex-linkage and/or maternal effects together were significantly important in Birth Weight, Weaning Hip Width, Weaning Fat Thickness, and Post-Weaning Type Score.

There is no logical explanation for significant negative differences as measures of sex-linkage effect, maternal effect, or

sex-linkage and/or maternal effect together except, that in both breeds, the males were earlier maturing than the females even though the bulls were 60 percent heavier at maturity, and these differences are greater in Polled Herefords than in Angus (Brown et al., 1972).

Sex-linkage effect appears to be greater in Angus than in Polled Herefords for most of the traits studied, but Table 7 shows the relative magnitude of measures of sex-linkage effect calculated from weaning correlations as compared to those calculated from post-weaning correlations with +'s indicating a greater value in the post-weaning data, e.g., Body Weight, Heart Girth, and Hip Width in Angus. This may be caused by differences in maturity between linear growth variables and thickness growth variables (Guilbert and Gregory, 1952). However, sex-linkage effect in Body Weight, Heart Girth and Hip Width, along with Average Daily Gain and Condition Score appear to decrease from weaning to post-weaning in Polled Herefords. This may be explained by the fact that Angus are earlier maturing than Herefords in both sexes, and the heritability of rate of maturing in Angus is more than twice that in Herefords (Brown et al., 1972).

Maternal effects appear to be greater in Polled Herefords than in Angus on most of the traits. Table 8 shows that Body Length, Fat Thickness and Type Score in Angus appear to be subject to greater maternal effect at post-weaning than at weaning, while maternal effect on other traits decreases from weaning to post-weaning. In Polled Herefords, the variables which show greater maternal effect at post-weaning are Body Weight, Heart Girth, and score variables.

TABLE 7. Correlation Differences Between Post-Weaning and Weaning Variables with Respect to Sex-Linkage Effect

	Sex-Linkage Effect ¹	
	Angus	Polled Hereford
Body Weight	+	-
Gain	-	+
Average Daily Gain	-	-
Heart Girth	+	-
Body Length	-	+
Hip Width	+	-
Hip Height	-	+
Fat Thickness	-	+
Type Score	-	+
Condition Score	-	-
Frame Score	-	+

¹+ indicates greater affect in post-weaning data.
 - indicates smaller effect in post-weaning data.

TABLE 8. Correlation Differences Between Post-Weaning and Weaning Variables with Respect to Maternal Effect

Trait	Maternal Effect ¹	
	Angus	Polled Hereford
Body Weight	-	+
Gain	-	-
Average Daily Gain	-	-
Heart Girth	-	+
Body Length	+	-
Hip Width	-	-
Hip Height	-	-
Fat Thickness	+	-
Type Score	+	+
Condition Score	-	+
Frame Score	-	+

¹+ indicates greater effect in post-weaning data.

- indicates smaller effect in post-weaning data.

These differences between the two breeds and the variables could be explained on the same basis as sex-linkage effect differences.

Sex linkage confounded with maternal effects as one value is greater in Angus, in general, than in Polled Herefords for the majority of the traits, and these values decrease in both breeds between weaning and post-weaning (Table 9).

TABLE 9. Correlation Differences Between Post-Weaning and Weaning Variables with Respect to Sex-Linkage and/or Maternal Effect

Trait	Sex-Linkage and/or Maternal Effect ¹	
	Angus	Polled Hereford
Body Weight	+	-
Gain	-	-
Average Daily Gain	-	-
Heart Girth	-	-
Body Length	-	-
Hip Width	-	-
Hip Height	-	+
Fat Thickness	+	-
Type Score	+	+
Condition Score	-	+
Frame Score	-	+

¹+ indicates greater effect in post-weaning data.
 - indicates smaller effect in post-weaning data.

CHAPTER V

DISCUSSION

Only two reports from the review of literature were of studies in beef cattle, namely, Damon et al. (1961) and Shahrودي (1972). In both reports, the two sexes were combined and used to detect maternal effect and sex-linkage, using the statistical models of Henderson (1948) in the study of Damon et al. (1961) or a combination of Eisen's (1966) two models in Shahrودي's (1972) study. Thus, the estimate of variation due to maternal effects would actually include variation due to true maternal effects plus that resulting from sex-linkage effects.

Only Birth Weight and Weaning Weight from the list of variables considered in the present study were included in Shahrودي's (1972) report. His results with respect to sex-linkage agree with the present study Angus results shown in Table 3, and, with respect to maternal effect, he found an important effect in both traits. Tables 3 and 4 do not show any important maternal effect alone on these two traits, while they do show an important effect on Birth Weight in Polled Herefords and on Weaning Weight in Angus for sex-linkage and/or maternal effects as one value.

In general, when sex-linkage plays a significant role in the inheritance of a beef cattle trait, the rate of genetic progress

from selection could be increased by concentrating attention on the daughters (the homogametic sex progeny) of prospective sires. If evidence indicates an important contribution of sex-linked genes to the heredity of a quantitative trait in beef cattle, bulls possessing the most desirable sex-linked genes would be those whose daughters have the highest averages for the trait in question. Thus, ranking of bulls as prospective sires would be based, to a greater extent, on the ranking of their daughter averages for such traits than for traits which do not appear to be influenced significantly by sex-linked genes.

CHAPTER VI

SUMMARY

Data on birth weight and on weaning traits and post-weaning traits were recorded from 1903 Angus calves and 1126 Polled Hereford calves born during a period of twelve years (1969 to 1980). The traits were Birth Weight, Body Weight Gain, Average Daily Gain, Heart Girth, Body Length, Hip Width, Hip Height, Fat Thickness, Type Score, Condition Score, and Frame Score

All records were adjusted by using constants obtained by least-squares procedures to remove variation due to differences in age of calf and age of dam. All possible correlations between phenotypes of parent and offspring of opposite sex and of the same sex were calculated. Measures of the influence of sex-linkage and/or maternal effects were obtained by subtracting sire-son correlations from dam-son correlations, a measure of maternal effects alone was obtained by subtracting sire-daughter correlations from dam-son correlations, and a measure of sex-linkage effects alone was obtained by subtracting sire-son correlations from sire-daughter correlations.

Sex-linkage effects appear to be important in Weaning Body Weight, Weaning Gain, Weaning Average Daily Gain, Post-Weaning Weight, Life-Time Average Daily Gain, Post-Weaning Heart Girth, and Post-Weaning Hip Width in Angus. None of the traits seemed to show any important sex-linkage effect in Polled Herefords.

Maternal effects appear to be important only in Post-Weaning Body Length in Angus and Weaning Fat Thickness, Post-Weaning Weight, Life-Time Average Daily Gain, Post-Weaning Type Score, and Post-Weaning Condition Score in Polled Herefords.

Sex-linkage and/or maternal effects are appreciable in Weaning Weight, Weaning Gain, Weaning Average Daily Gain, Weaning Heart Girth, Weaning Body Length, Post-Weaning Weight, and Life-Time Average Daily Gain in Angus. However, in Polled Herefords, sex-linkage and/or maternal effects together are important in Birth Weight, Weaning Hip Width, Weaning Fat Thickness, and Post-Weaning Type Score.

Sex-linkage and sex-linkage confounded with maternal effects as one value appear to be greater in Angus than in Polled Herefords with respect to the majority of the traits while maternal effects appear to be greater in Polled Herefords than in Angus with respect to most of the traits.

The majority of the assessments decrease in both breeds between weaning and post-weaning with respect to sex-linkage effects, maternal effects, and sex-linkage and/or maternal effects with some differences between the two breeds. All the differences between the two breeds may be due to the fact that Angus are earlier maturing than Polled Herefords in both sexes, and the heritability of rate of maturing in Angus appears to be more than twice that in Polled Herefords.

LIST OF REFERENCES

REFERENCES

- Al-Mallah, M. Y. 1975. A study of sex differences in various statistics calculated from data on growing Angus bulls and heifers fed at different levels. Ph.D. Dissertation, The University of Tennessee, Knoxville.
- Beilharz, R. G. 1960. Research into sex-linked control of body-weight in poultry and rabbits. *Proc. Aust. Soc. Anim. Prod.* 3:139.
- Beilharz, R. G. 1961. The importance of sex-chromosome in quantitative inheritance. Unpublished M.Sc. thesis, University of Sydney.
- Beilharz, R. G. 1962. A review of the importance of sex-linkage in inheritance. *Proc. 12th World's Poult. Congr. Sec. Pap.* 63.
- Beilharz, R. G. 1963. On the possibility that sex-chromosomes have a greater effect than autosomes on inheritance. *Genetics* 58:441.
- Boyer, J. P., X. Delaage, and C. Calet. 1963. Influence on feed on the heritability of some chicken traits. *Proc. 11th Int. Congr. Genet.* 1:262 (Abstr.).
- Brown, J. E., C. J. Brown, and W. T. Butts. 1972. A discussion of the genetic aspects of weight, mature weight and rate of maturing in Hereford and Angus cattle. *J. Anim. Sci.* 34:525.
- Brumby, P. J. 1960. The influence of the maternal environment on growth in mice. *Heredity* 14:1.
- Brunson, C. C., G. F. Godfrey, and B. L. Goodman. 1956. Types of gene action in the inheritance of ten-week bodyweight and breast angle in broilers. *Poult. Sci.* 35:524.
- Chai, C. K. 1958. Isolation of genetic factors affecting body size in mice. *Proc. 10th Int. Cong. Gen. (Montreal).* 2:47.
- Charles E. 1933. Collateral and ancestral correlation of sex-linked transmission irrespective of sex. *J. of Genetics.* 27:97.

- Chihasz, C. P. 1980. Heritabilities and genetic correlations of selected live body measurements of purebred Angus calves. M.Sc. thesis, The University of Tennessee, Knoxville.
- Cockerham, C. C. 1956. Effects of linkage on the covariances between relatives. *Genetics* 41:138.
- Cole, L. J. 1925. Inheritance in cattle. *Proc. Scot. Cattle Breed. Conf.*, Chap. 3:26.
- Collins, W. M., and A. Hans. 1968. Changes in body and organ weights of Japanese Quail selected for 6-week body weight. *Br. Poult. Sci.* 9:231.
- Copeland, L. 1927. Inheritance of butter fat percentage in Jersey cows. *J. Dairy Sci.* 10:344.
- Damon, R. A., W. R. Harvey, C. B. Singletary, S. E. McCrain, and R. M. Crown. 1961. Genetic analysis of crossbreeding beef cattle. *J. Anim. Sci.* 20:849.
- Diven, R. H., O. F. Pahnish, C. B. Roubicek, E. S. Erwin, and H. M. Page. 1960. Heritability of vitamin A and carotenoid concentrations in bovine liver and plasma. *J. Anim. Sci.* 19:1218 (Abstr.).
- Eisen, E. J., B. B. Bohren, and H. E. McKean. 1966. Sex-linked and maternal effects in the diallel cross. *Australian J. of Biolog. Sci.* 19:1061.
- Falconer, D. S. 1951. Selection for large and small size in mice. *J. Genetics* 51:470.
- Fisher, R. A. 1918. The correlation between relatives on the supposition of Mendelian inheritance. *Trans. Roy. Soc. Edin.* 52:399.
- Gaines, W. L. 1922. Inheritance of fat content of milk in dairy cattle. *Proc. Amer. Soc. Anim. Prod.* 29.
- Garn, M. S., and C. G. Rohmann. 1962. X-linked inheritance of developmental timing in man. *Nature.* 196:695.
- Ghigi, A. 1948. Is the weight of the egg a sex-linked feature? *Off. Rep. 8th World's Poult. Congr. (Copenhagen).* 1:751.
- Godfrey, E. F. 1953. The genetic control of growth and adult body size in the domestic fowl. *Poult. Sci.* 32:248.

- Godfrey, E. F. 1957. The genetic control of body size in the domestic fowl. Diss. Abst. 17:2745.
- Goodman, B. L., and R. G. Jaap. 1961. Non-additive and sex-linked genetic effects on egg production in a randombred population. Poult. Sci. 40:662.
- Gowen, J. W. 1920. Inheritance in crosses of dairy and beef breeds of cattle. II. Transmission of milk yield to the first generation. J. Heredity. 2:365.
- Gowen, J. W. 1927. Quantitative methods of research and the problems of animal breeding. Amer. Nat. 61:420.
- Gowen, J. W. 1933. On the genetic constitution of Jersey cattle as influenced by inheritance and environment. Genetics 18:415.
- Graves, R. R. 1925. Dairy cattle breeding. Investigations of the United States Department of Agriculture. Proc. Scot. Cattle Breed. Conf. Chap. 24:299.
- Greenwood, A. W., and J. S. S. Blyth. 1951. A repeated cross between inbred lines of poultry. A. Agric. Sci. 41:367.
- Griffing, B. 1956. Concept of general and specific combining ability in relation to diallel crossing systems. Australian J. of Biological Sci. 9:463.
- Guilbert, H. R., and D. W. Gregory. 1952. Some features of growth and development of Hereford cattle. J. Anim. Sci. 11:3.
- Hale, R. W. 1959. Heritability of laying-house viability in a White Wyandott flock. Poult. Sci. 38:471.
- Hay, F. A. 1950. Is fertility in domestic fowl regulated by inheritance? Poult. Sci. 29:171.
- Henderson, C. R. 1948. Estimation of general, specific and maternal combining abilities in crosses among inbred lines of swine. Ph.D. thesis, Iowa State University, Ames, Iowa.
- Henderson, E. W. 1961. Hatching power of paternal vs. maternal first cousins in chickens. Quart. Bull. Mich. Agric. Exp. Sta. 44:328.

- Hole, J., O. Aurlien, and F. Sannan. 1958. Pure breeds and crosses in egg production. *Meld. Norg. Landbrhogsk*, 37(9):32.
- Jaap, R. G., and J. F. Grimes. 1956. Growth rate and plumage color. *Poult. Sci.* 35:1148.
- Jerome, F. N., C. R. Henderson, and S. C. King. 1956. Heritabilities, gene interactions, and correlations associated with certain traits in the domestic fowl. *Poult. Sci.* 35:995.
- Johnson, A. S., and V. S. Asmundson. 1957. Genetic and environmental factors affecting size of body and body parts of turkeys. I. Heritability and interrelationships of body weight and live body measurements. *Poult. Sci.* 36:296.
- Kan, J., W. F. Krueger, and J. H. Quisenberry. 1959. Non-additive gene effects of six broiler traits as studied from a series of diallel matings. *Poult. Sci.* 38:972.
- Kaufman, L. 1948. Sex-linked inheritance of body weight in fowls. *Off. Rep. 8th World's Poult. Congr. (Copenhagen)* 1:291.
- Kawahara, T. 1965. Effect of heterosis and sex-linkage on sexual maturity in the domestic fowl. *Rep. Natn. Inst. Genet., Misima*, 15:50.
- Kempthorne, O. 1954. The correlation between relatives in a random mating population. *Proc. Roy. Soc. Lond. B.* 143:153.
- Khan, A. G., R. G. Jaap, and W. R. Harvey. 1973. The effect of egg weight on eight-week weight of normal and dwarf progeny from dwarf dams. *Poult. Sci.* 52:211.
- Kidwell, J. F., H. J. Weeth, W. R. Harvey, L. H. Haverland, C. E. Shelby, and R. T. Clark. 1960. Heterosis in crosses of inbred lines of rats. *Genetics* 45:225.
- King, S. C., and J. H. Bruckner. 1952. A comparative analysis of purebred and crossbred poultry. *Poult. Sci.* 31:1030.
- Lawritson, M. N., J. W. Hendrickson, and W. B. Nivens. 1919. Purebred sires effect herd improvement. *Nebraska Agric. Expt. Sta. Circ.* 8:1.
- Li, C. C. 1955. Population Genetics. The University of Chicago Press.

- Lokanath, G. R., C. R. Kanavikar, and B. S. Ramappa. 1978. Genetic studies on fertility and hatchability in a strain of cornish selected for body weight. *Indian J. of Heredity* 10(3):1.
- Lush, J. L. 1945. Animal Breeding Plans. Iowa State College Press, Ames, Iowa.
- Lush, J. L. 1948. The genetics of populations. (Mimeo.) Animal Husbandry Dept., Iowa State University of Science and Technology, Ames, Iowa.
- Madsen, K. 1932. Inheritance of milking capacity. *Nature* 129:165.
- Mather, K. and J. L. Jinks. 1963. Correlation between relatives arising from sex-linked genes. *Nature* 198:314.
- McDonald, M. W. 1957a. Methionine supplement in chicken diets. I. Effect of supplementary methionine and choline on growth and folic acid requirements of White Leghorn chickens. *Aust. J. Agric. Res.* 8:318.
- McDonald, M. W. 1957b. Methionine supplements in chicken diets. II. A breed difference in growth response to DL. methionine. *Aust. J. Agric. Res.* 8:587.
- Merritt, E. S. 1966. Estimates by sex of genetic parameters for body weight and skeletal dimensions in a random bred strain of meat type fowl. *Poult. Sci.* 45:118.
- Morley, F. H. W., and J. Smith. 1954. A comparison between reciprocal crosses of Australorp and White Leghorns. *N.S.W. Ag. Gazette* 55:1.
- Morris, J. A. 1959. Heritability of chick viability for two breeds of the domestic fowl. *Poult. Sci.* 38:481.
- Morris, J. A., and F. Skaller. 1958. Single crossing between White Leghorn and Australorp. *Aust. J. Agric. Res.* 9:842.
- Niesel, M. P. 1941. Investigations on the sex-linked inheritance of laying capacity in domestic hens. *Arch. Kleintierz* 2:329.
- Osborne, R. 1953. The inheritance of egg weight in the domestic fowl: Further evidence of sex-linkage. *Poult. Sci.* 32:60.
- Osborne, R. 1955. Sex-linked association of egg weight and body weight in Brown Leghorn. *Proc. Roy. Soc. Edinb. B.* 65:317.

- Pahnish, O. F., E. B. Stanley, R. Bogart, and C. B. Roubicek. 1961. Influence of sex and sire on weaning weights of south-western range calves. *J. Anim. Sci.* 20:454.
- Pahnish, O. F., R. L. Roberson, R. L. Taylor, J. S. Brinks, R. T. Clark, and C. B. Roubicek. 1964. Genetic analysis of economic traits measured in range-raised Herefords at pre-weaning and weaning ages. *J. Anim. Sci.* 23:562.
- Penrose, L. S. 1967. Finger-print pattern and sex chromosomes. *The Lancet.* 1:298.
- Redman, C. E., and R. N. Shoffner. 1961. Estimates of egg quality parameters utilizing a polyallel crossing system. *Poult. Sci.* 40:1662.
- Roberson, R. L., O. F. Pahnish, R. L. Taylor, J. S. Brinks, R. T. Clark, and A. M. Lane. 1963. Genetics of grade, condition and weight in range cattle. *J. Anim. Sci.* 22:822 (Abstr.).
- Shahroudi, F. E. 1972. Genetic analysis of maternal ability and evaluation of some environmental factors affecting pre-weaning performance of beef cattle. Ph.D. thesis, Oregon State University, Corvallis, Oregon.
- Smith, A. D., and O. J. Robison. 1931. The inheritance of milk yield. *Intern. Dairy Cong.* pp.4.
- Smith, A. D., and O. J. Robison. 1933. The Genetics of Cattle. *Bibliographia Genetica* 10. The Hague, Martinus Nijhoff.
- Thomas, C. H., W. L. Blow, C. Cockerham, and E. W. Glazener. 1958. The heritability of body weight, gain, feed consumption, and feed conversion in broilers. *Poult. Sci.* 37:862.
- Ubbels, P., and M. V. Albada. 1948. Observations made during investigation on breeding and inheritance at the State Poultry Breeding Institute at Beekbergen. Beekbergen: State Poultry Breeding Institute.
- Warren, D. C. 1958. A half century of advances in the genetics and breeding improvement of poultry. *Poult. Sci.* 37:3.
- Wright, S. 1921. System of mating. I-V. *Genetics* 16:97.
- Wright, S. 1933. Inbreeding and homozygosis. *Proc. Nat. Acad. Sci.* 19:411.

- Wright, S. 1935. The analysis of variance and correlation between relatives with respect to deviations from an optimum. *J. Genetics* 30:243.
- Wright, S. 1951. The genetical structure of populations. *Ann. Eugen.* 15:323.
- Yao, T. S. 1959. Additive and dominance effects of genes in egg production and 10-week body weight of crossbred chickens. *Poult. Sci.* 38:284.
- Yao, T. S., and N. S. Eaton. 1954. Heterosis in the birth weight and slaughter weight in rabbits. *Genetics* 39:667.

VITA

Adeeb D. S. Kharoofa was born in Mosul, Iraq, January 23, 1950. He entered the College of Agriculture, University of Mosul, Iraq in September, 1968 and received the Bachelor of Science degree in Animal Science in June, 1972. In September, 1972 he attended graduate school at the University of Baghdad, Iraq. He received the Master of Science degree in Animal Breeding in June, 1975. In January, 1979 he accepted a scholarship to continue his formal education toward the Doctor of Philosophy degree in Animal Breeding at The University of Tennessee, Knoxville, and was graduated in December, 1982.

On January 31, 1977 the author married Fatin F. Ismael. They are the proud parents of a son, Yazn A. D. Kharoofa, born March 2, 1979 and a daughter, Marwa A. D. Kharoofa, born September 6, 1980.

He is a member of the Iraqi Agricultural Engineering Organization and Iraqi Teacher Organization.