INHERITANCE OF COLOR PATTERN AND SHADE OF HAIR COLOR IN HEREFORD CATTLE

By

MARION E. STANLEY

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Colorado Agricultural and Mechanical College

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INTRODUCTION

The color pattern of Hereford cattle has been established as a trade mark of the breed. Certain deviations from it have been discriminated against by purebred breeders and commercial producers, and some have associated uniformity of color with genetic purity of the breed. The deviations from the typical color pattern most often criticised in America have been "red neck" and "lineback." Red neck is the descriptive term used to indicate the absence of white hair on the crest or top of the neck. Lineback is the term used to indicate the extension of white hair behind the shoulders or on the back. Although breeders have selected against these deviations for many years, Herefords are still found which have these traits and they do not bar such individuals from registration. "Smutty" or pigmented noses and black tails are also discriminated against in Herefords, but they were not the subject of this study.

Preferences have been shown for certain shades or intensities of red hair color. These preferences have tended to change from time to time and from one section of the country to another. Some stockmen have associated the shade of red with the ability of an animal to perform efficiently in the feed lot and on the range.

Eyelid pigmentation is another trait of economic importance. It has recently been shown that the amount of eyelid pigmentation is correlated with resistance to eyelid cancer in Hereford cattle. Hereford breeders, however, have generally discriminated against appreciable amounts of pigment around the eyes.

The purposes of this study were to determine the nature of inheritance of the topline color pattern and the shade of red hair color in Hereford cattle, to obtain heritability estimates of these traits, and to determine the relationships between these traits and eyelid pigmentation.

REVIEW OF LITERATURE

The origin of the Hereford breed, according to Willham (1937), was in Herefordshire, England from stock some of which may have come from Holland. These cattle were above the average merit of cattle in England. The breeders considered their methods and systems of mating to be trade secrets, so little is known about the early development of the breed. Kinsman (1918) stated that the Hereford pattern first originated from the foundation stock of Benjamin Tomkins Jr. of King's Pyon, England, which included a red bodied, white faced bull called "Silver Bull" and three cows; one was gray, one was red with mottled face, and the other was red bodied with a white face.

Pitt (1920) described the middle red, bald-faced cattle of 1788 in England and reported that they traced to a bald-faced bull calf in the herd of a prominent breeder in 1750. The bull calf was reported to be the first one of its kind and was designated as a mutation. This origin has been questioned by some because of the large increase in numbers of white faced cattle prior to 1788. It seemed doubtful that one bull would be the progenitor of so many offspring in so short a time. Pitt noted that by 1804 the reddish-brown cattle with white faces were more common than roans or grays.

Pitt (1921) described the "typical Hereford" as a, ..."deep red beast with white face and underparts, white feet, white at the end of the tail, and with a white patch along the top of the neck and sometimes a trace of red around the eyes." Pitt further stated that the coat was a rich purple-red, and not a yellow-brown. A clean clear nose and horns free of pigment at the tips were also desired.

Inheritance of Color Characteristics in Hereford Cattle

Ibsen (1933) and Ibsen and Weber (1933) reported the Hereford pattern (S^H) to be incompletely dominant to self color (S) and completely dominant to white spotting (s). They offered crosses of Hereford x Angus and Hereford x Holstein as evidence. The first of these crosses resulted in a reduction of the white area in the offspring and the latter, a Hereford x Holstein cross, had little effect on the amount of white of the Hereford pattern. Black usually takes the place of red in these crosses because black is dominant to red.

Pitt (1921) studied the inheritance of the Hereford pattern and considered excessive white or lineback to be due to a modifying factor. An animal was considered a lineback when the white of the crest reached beyond the shoulders. She believed "lineback" to be recessive to normal Hereford pattern. The dark pigmented neck was reported to be dominant to white neck, although not completely so in all cases. She also concluded red spots around the eyes to be incompletely dominant to the absence of spots. Approximately one-quarter of the cattle showed the dominant trait. She noted that animals with the darkest hair color had red pigment around their eyes more often than the lighter colored animals. In her study, shade or intensity of red varied from a dark red which was called "claret" to a yellow-brown. The claret color was more desirable than the yellow shades which were discriminated against by the breeders. The yellow-brown color was believed to be dominant to "claret." Matings of red x red were observed to breed true; however no matings of yellow x yellow were available to substantiate this belief.

Koger and Mankin (1952) suggested that approximately three pairs of major genes were involved in controlling the shade of hair color.

Ibsen (1933) considered "brockle face" and pigmented legs as modifiers of the Hereford pattern. They were believed to be caused by the same factors since they were usually associated. They were considered to be due to a dominant factor, which would make the traits easy to eliminate by selection. Many brockle faced cattle were seen on the early Western ranges as a result of crossbreeding with Shorthorns.

Horlacher (1928) was unable to explain the presence of a black spot on the neck of a Hereford steer, since red is usually considered to act as a simple recessive to black. Some red hairs were mixed with the black hairs in the spot. The pigment of the skin under the black spot was the same as that under the red areas. No evidence of black hairs could be found on either parent and none were known to have occurred on more remote ancestors. Black spots had been known to appear occasionally on Herefords and also on red Shorthorns, and it was not known if there was a tendency for them to run in families.

Ibsen and Weber (1933) stated that black spotting often occurred in Jerseys and Ayrshires. Black hairs which were sometimes found in the tails of Herefords, they suggested, were due to a very close clumping of red pigment granules in the hair making it appear black.

Ibsen (1933) proposed that color genes are found at nineteen different loci on the chromosomes. Red genes (R) were believed to be present in all cattle with many other genes epistatic to them. The entire Hereford pattern was based on one gene (S^H) which had several modifiers. A small amount of white (LW) was believed to be dominant to (lw) for more white. Red neck (Rn) was dominant to white neck (rn) and red eye (Re) was dominant to white eye (re). Ibsen proposed the following genotypic formulae for Hereford cattle: (Alleles are given below the formula in instances where they are known.)

bb	bsbs	dd	II	nn	psps	S^HS^H	rnrn	rere	LwLw	plpl	WW	WnWn	wpwp
	Bs ?				Psps		Rnrn	Rere	Lwlw				
									lwlw				

Key to genotype above:

Black - B	Red eye - Re
Black spotting - Bs	White eye - re
Dilution - D	Little white - Lw
Intensity - I	Much white - lw
Roan - N	Pigmented legs - Pl
Pigmented (black) skin spotting - Ps	Non pigmented legs - pl
Hereford pattern - S^H	Prevents whitening - W
Red neck - Rn	Recessive white - Wn
White neck - rn	No dominant white - wp

Shrode and Lush (1947) indicated that a red coloring gene was present in all breeds and that it also caused the brownish pigment of the skin, nose, and eyelids when unaffected by other genes.

Pound (1932) stated that (Re) sometimes produces pigmentation in the skin of the eyelid instead of causing red hair around the eyes. He believed "lineback" was due to a recessive factor since parents, neither of which showed the trait, have produced linebacked calves. Pound further stated that evidence obtained from crosses with other breeds showed that many Herefords carry a "brindling" gene (Br), which does not appear in the phenotype of purebred Herefords.

Ibsen and Riddell (1931) noted that self colored cattle had pigmentation in the hoofs, nose, tongue, lining of the mouth, and nictitating membranes, and that spotted cattle were partially or completely devoid of pigment in these areas. The extent of pigmentation was closely related with the amount of the spotted areas.

Bogart and Ibsen (1937) studied the pigmentation contained in hair which varied in color. They found that the shade of red depended upon the intensity of the diffused red pigment and on the quantity and distribution of black pigment. The black pigment was found in all colors of hair including white, and the shade depended upon the intensity of clumping of the granules and their location within the hair and skin. A darker appearance was given by granules in the cortex than those in the medullary portion of the hair. Several distinct shades of red pigment were found in some animals; however, only one dark red pigment was present in Hereford cattle. Variations of intensity of color within the breed must have been the result of the amount and distribution of the black clumping. Red pigment has been found in hair which appeared entirely black, but was always masked regardless of its intensity; therefore, it had no effect upon the intensity of black, which was found to be uniform in this respect. From a microscopic study it was found that red pigment was a non-granular substance which was completely diffused within the hair. This caused it to have a transparent appearance. It sometimes appeared to be granular in the skin.

Heritability Estimates

Pound (1928) classified color in Herefords as dark red, medium red, and yellow-red. None of the six possible mating combinations including these shades of color bred true. He computed an heritability estimate of .44 for shade of red by regression of offspring on the mid-parent color scores involving 406 matings.

Hellstrom (1951) computed heritability estimates for shade of red from data which included 369 dam-offspring comparisons at the Colorado Experiment Station. The estimates from intra-sire regression of offspring on dam and paternal half-sib correlations were .63 and .49, respectively.

Koger and Mankin (1952) computed heritability estimates for shade of red of .73 and .75 by intra-sire regression of 437 offspring on dam, and regression of offspring on mid-parent for the New Mexico Experiment Station herd for the period from 1947 through 1950.

Anderson _et al._ (1957b) estimated the heritability for the amount of eyelid pigment to be .44 by using regression of offspring on dam with data from 733 offspring. An heritability estimate of .46 was found from paternal half-sib intra-class correlations from 953 offspring by 116 sires. Some evidence of a maternal effect was found from reciprocal matings. The incidence of pigment was higher in the progeny when the dam was the more highly pigmented of the two parents.

Relationships Involving Certain Color Traits in Hereford Cattle

The opinion has been expressed that light colored Hereford cattle gain more rapidly than those that are darker. Stanley and McCall (1945), at the Arizona Experiment Station, classified Hereford steers as having light, medium, and dark colored hair. Light red steers in a type study made larger gains and yielded higher grading carcasses than medium colored and dark colored steers. However, this did not hold true for steers in a progeny test in which darker steers graded significantly higher in the carcass and the correlation between hair color and daily gain was almost zero.

Hellstrom (1951) computed correlations between certain economic characteristics and shade of hair color for 80 Hereford steers. The correlations between shade of red and weaning score, rate of gain, and carcass grade were low. A correlation of .28 ($P < .05$) was found between the number of days on feed and shade of hair color. This correlation indicated that the number of days on feed was less for darker steers than the lighter ones. Steers were taken off feed and slaughtered when they reached a grade of "good" or higher. The correlation between feed lot efficiency and hair color was -.43 ($P < .05$). This indicated that the lighter colored steers were more efficient in the feed lot than the darker steers. These correlations between performance traits and shade of hair color could however, have been due to sire effects or to pre-test environmental differences.

Hurt (1956) scored red color as light, medium, and dark and found no relationship between shade of red and performance in the feed lot or performance on the range. His study included 187 long yearling steers from 1947-54, and 132 steer calves from 1949 through 1955.

Sawyer <u>et al</u>. (1948) rated cows and calves at weaning time as yellow, light, medium, and dark red. They found that dark red calves were heavier at weaning and that yellow cows weaned heavier calves, but neither of these associations were statistically significant. Yellow cows weaned heavier heifer calves and lighter steer calves than did dark red cows.

Anderson et al. (1957a) found evidence of an association between a decreasing amount of eyelid pigmentation and an increase in the number of lesions on the eyelids. The correlation between these traits was significant at the $P < .01$ level.

Influence of Sex and Age on Shade of Hair Color

Koger and Mankin (1952) found no differences between shade of color of Hereford steers and heifers, but calves scored darker than cows. They also noted that mature cows scored darker in good-years than in drought years when the nutritional level was lower. Hellstrom (1951), however, found the mean for color of calves to be slightly lighter than for cows.

Ibsen (1933) noted that in red breeds of cattle it is usual for the males to attain a deeper shade of red than the females as maturity is reached.

MATERIALS AND METHODS

This study was conducted to determine the heritability of the topline color pattern and the heritability of red hair shade in Hereford cattle. The association of these traits with eyelid pigment was also studied.

The data were from three Hereford herds at the Fort Reno Experiment Station. Two herds were registered (Project 670 and Project 873) and the other herd was a high grade herd (Project 650). Sires produced and used in the 670 herd were sometimes used in the 650 herd.

This study was conducted during the fall of 1956 and the spring of 1957. Offspring produced during the four years (1954-57) were included when both sire and dam could be identified. The mature cows and their calves were scored at weaning time in October of 1956. The yearling heifers and the bulls were scored when they were weighed during the fall of 1956. The 1957 spring calves and the fall calves in Project 873 were scored in June of 1957. The spring calves ranged from a few days to about 3 months of age at scoring. The animals were scored in a chute under as nearly the same lighting conditions as possible. All aged cattle were identified by number brands and calves were identified by eartag numbers and/or tattoos.

Each animal was scored visually for topline pattern by evaluating the amount of white on the neck, shoulders, and back. The system of classification contained nine classes with each class having a numerical value. The three classes that would be discriminated against as having too little white or none at all were scored as 1, 2, and 3; the three classes that would generally be considered as desirable were scored as 4, 5, and 6; and the three classes that would be objectionable because of excess white were scored as 7, 8, and 9. The following standard was used:

Numerical Score	Description of topline pattern
1	Red neck - no white present on topline
2	White flecks or small white spots on neck
3	White patches on neck but not enough to be desirable
4	Desirable but white still sparing
5	Desirable
6	Desirable but more white on neck than necessary
7	White extending past shoulders or small spots on the back or loin
8	Large white spots on the back or loin
9	Lineback with white covering a large area of the back

Individual animals were scored for shade of color by comparing the hair of each with a color standard. The color standard contained seven hair samples which divided the range of color into 7 distinct classes. The classes were assigned numerical values ranging from one for the lightest shade (yellow) to seven for the darkest shade of red. The samples were glued to a heavy white card in order of shade so that the scorer could quickly match the hair of the animal with the sample that was nearest the same shade. The color standard was kept in a heavy manila envelope to prevent samples from bleaching between the times they were used.

The values for eyelid pigment were obtained by estimating the percentage of the eyelid that was pigmented by counting the number of units covered by pigment on a scale which divided lid length into 100 equal units. The average percentage for both eyes was used in correlations with topline pattern and shade of hair color.

The repeatability of the scoring methods for topline pattern and shade of hair color was determined by scoring 36 cows and 51 calves on two different occasions which were approximately one month apart. Scoring was by the same person each time. This interval probably had no great effect on either of the traits. The correlation between the two pattern scores for cows was .83 and that between the two shade scores was .57. The correlations for both traits were somewhat higher for calves, being .90 for pattern and .64 for shade. The four correlations were highly significant as were the pooled correlations of .87 and .60.

Repeatability of scores over different seasons was obtained from correlations between fall scores and spring scores on the same animal. Cows and heifer calves, which were scored in the fall of 1956 and kept as replacements, were scored again for topline pattern and shade of hair color during the spring of 1957. The correlations are shown in table I. The correlations for mature cows were comparable to those obtained from the scores made one month apart. Correlations for the two groups of calves were low for shade of hair color.

Preliminary analyses were conducted to determine the effect of sex on the scores for topline pattern and shade of hair color. Differences in the pattern and shade scores of 556 calves of different sexes were tested by analysis of variance. Males tended to be slightly darker in color and had less white in the pattern than heifers but these differences were not significant. The mean score for pattern was 4.89 for males and 5.09 for females. The mean shade score was 3.43 for males and 3.23 for females.

TABLE I CORRELATIONS BETWEEN FALL AND SPRING SCORES ON THE SAME ANIMAL

Herd	Class	Year calved	Number	Correlation coefficients for pattern	Correlation coefficients for shade
650	cows	1948	108	.90**	.67**
650	cows	1954	38	.95**	.60**
650	heifers	1955	32	.93**	.77**
650	calves	1956	43	.85**	.21
670	cows	1946-54	72	.76**	.65**
670	calves	1956	25	.90**	.21
873	cows	1946-52	59	.75**	.66**

**Significant at $P < .01$

Methods of Computing Heritability Estimates

Heritability estimates were calculated for pattern and shade from intra-sire regression of offspring's score on dam's score, by paternal half-sib intra-class correlations, and by regression of the offspring's score on mid-parent's score. Data from 517 parent-offspring comparisons were used in computing the first two estimates. Mid-parent scores were available for only 419 comparisons since some sires were not scored for the two traits.

The nested classification shown in Appendix A was used to compute heritability estimates. The data were grouped by sires within age-of-dam, herd, age, and seasons. The classification contained 58 sire-groups, 15 age-of-dam groups, 10 herd-groups, 6 age-groups, and 2 season-groups.

An intra-sire regression of offspring's score on dam's score was computed from covariances and variances from the nested classification. This removed the average effects due to each of these sources of variation. Since the average genetic relationship between dam and offspring was assumed to be .5 the regression was multiplied by two to obtain an estimate of heritability.

The same nested classification was used for computing heritability estimates from paternal half-sib intra-class correlations. Another method was utilized whereby all offspring of each sire were grouped into a single class without respect to other sources of variation. Paternal half-sib correlations were multiplied by four to obtain heritabilities since the average genetic relationship between half-sibs was assumed to be .25.

Regressions of offspring score on mid-parent score were obtained from covariances and variances involving the average scores of the two parents and the offspring scores for the traits in question. These regressions yield direct estimates of heritability.

Methods of calculating standard errors for the heritability estimates are shown in Appendix C.

The proceedure followed for determining the weighted number of progeny per sire ($\bar{k}$) is given in Appendix B.

Correlations Between Traits

Correlations between topline pattern and eyelid pigmentation, shade of hair color and eyelid pigmentation, and topline pattern and shade of hair color were calculated within groups and then pooled over all groups. Data from 585 animals were available for the first two correlations and data from 974 animals were used in the last correlation. Eyelid pigmentation data were not available for all animals that were scored for the other two traits.

RESULTS AND DISCUSSION

The distribution of pattern scores for calves and their dams is shown in table II. Only the 1956 and 1957 calves were included since the individuals from other years were not scored as calves. The mean topline pattern score was 5.04 for calves and was 5.14 for cows. This difference was not statistically significant when tested by analysis of variance. Class 7 appears to be too large in every case for the scores to fit a normal distribution. This may be due to the fact that any animal with a discontinuous white mark behind the shoulders was placed in class 7, even if only a few white hairs were present, whereas only animals with a large amount of white on the crest and neck were placed in class 6.

TABLE II DISTRIBUTION OF TOPLINE PATTERN SCORES OF COWS AND CALVES FOR 1956 AND 1957

	Pattern scores										Mean
	1	2	3	4	5	6	7	8	9	Total	score
Cows	6	9	14	32	156	32	50	6	1	312	5.14
Calves (1956)	3	10	17	14	101	12	35	2	3	197	5.05
Calves (1957)	4	8	8	10	169	6	28	4	0	237	5.03

Table III shows that calves were lighter in shade of red than cows. The mean score for calves was 3.22 compared to 3.79 for their dams.

These data were also for the years 1956 and 1957. This difference was significant at the one percent level of probability.

TABLE III DISTRIBUTION OF SHADE OF HAIR COLOR SCORES OF COWS AND CALVES FOR 1956 AND 1957

	Shade scores								Mean
	1	2	3	4	5	6	7	Total	score
Cows	14	43	66	93	68	23	5	312	3.79
Calves (1956)	19	29	41	59	38	11	0	197	3.51
Calves (1957)	31	49	69	70	17	1	0	237	2.98

Heritability Estimates from Intra-Sire Regression of Offspring's Score on Dam's Score

The intra-sire regression of offspring's score on dam's score for pattern was .336 as shown in table IV. The regression coefficient when multiplied by two, yielded a heritability estimate for pattern of .67 $\pm$ .08. In the variance analysis for pattern, the between-sire differences were significant ($P < .01$), indicating that hereditary differences were important. Differences due to the other sources of variation were within the realm of chance.

The intra-sire regression of offspring's score on dam's score for shade was .297, which yielded a heritability estimate of .59 $\pm$ .07. This estimate was obtained from table V by the same method as outlined for pattern and included the same dam-offspring comparisons. This estimate is comparable to those of .63 and .73 reported by Hellstrom (1951) and Koger and Mankin (1952), respectively, using the method of regression of offspring on dam.

The variance analysis showed a statistically significant difference ($P < .01$) due to age of dam within herd, age, and season. The mean shade scores for calves from 73 two-year-old heifers were 2.76, 3.25 for calves from 20 three-year-old cows, and 3.33 for calves from 424 mature cows. The effect of age of dam might have been caused by nutritional differences among the offspring. Heifers as a rule do not give as much milk as mature cows. Their calves had rough coats with dull, lifeless hair. This would have caused them to score lower in shade than calves from mature cows. Sire differences for shade were significant ($P < .01$) indicating that hereditary factors exert a real influence on the shade of red hair color in Hereford cattle.

Heritability Estimates from Paternal Half-sib Intra-class Correlations

Heritability estimates were computed from paternal half-sib intra-class correlations as given by Snedecor (1956).

$$r_I = \frac{\sigma_s^2}{\sigma_e^2 + \sigma_s^2}$$

σ_e^2 = component of variance between calves within sires

σ_s^2 = component of variance between sires

The intra-class correlation from the nested classification was .088 for pattern, which multiplied by four yielded a heritability estimate of $.35 \pm .21$ (table VI). Since sires were confounded with the other variables, the estimate of .35 was smaller than would apply to a random group of sires because a portion of the sire variance was removed in the nested classification. This resulted in 58 sire groups although there were only 38 different sires in the study.

TABLE IV VARIANCE AND COVARIANCE ANALYSIS OF TOPLINE PATTERN FOR DAMS (X) AND CALVES (Y)

	D/F	Mean squares and cross products: ms(X)	xy	ms (Y)	Reg. coef.	Heritability estimate
Between seasons	1	1.159	-1.711	2.522		
Between ages, within seasons	4	1.125	- .208	2.823		
Between herds, within ages	4	2.069	.552	1.508		
Between age of dams, within herds	5	3.309	.075	3.696		
Between sires, within age of dams	43	1.787	.663	3.579**		
Within sires	459	1.664	.559	1.694	.336	.67

**Significant at $P < .01$

TABLE V VARIANCE AND COVARIANCE ANALYSIS OF SHADE OF HAIR COLOR FOR DAMS (X) AND CALVES (Y)

		Mean squares and cross products				
	D/F	ms (X)	xy	ms (Y)	Reg. coef.	Heritability estimate
Between seasons	1	4.664	12.850	35.409		
Between ages, within seasons	4	3.343	2.182	6.498		
Between herds, within ages	4	4.643	-6.249	11.090		
Between age of dams, within herds	5	5.165	4.590	9.736**		
Between sires, within age of dams	43	2.146	1.162	2.710**		
Within sires	459	1.569	.466	1.274	.297	.59

**Significant at $P < .01$

A second estimate was obtained from a variance analysis in which all offspring were grouped into 38 sire groups without regard to season, age, age of dam, or herd as shown in table VII. This yielded an intra-class correlation for pattern of .106 and a heritability estimate of .42 ± .20.

The intra-class paternal half-sib correlation of .089 for shade of hair color by the nested classification gave a heritability estimate of .36 ± .20. The second method gave a correlation of .140 and a heritability estimate of .56 ± .18. The analyses for shade are shown in tables VIII and IX. These estimates are in general agreement with the one of .49 from a paternal half-sib correlation given by Hellstrom (1951).

The method of analysis which involved the 38 actual sire groups was considered a better basis for estimating heritability for both topline pattern and shade of hair color than the nested classification. Forty-four full-sibs were involved in these analyses. Their influence did not appear to alter appreciably the heritability estimates, hence no adjustments were made for their presence. The paternal half-sib estimates for pattern were lower than those from the regression of offspring on dam or regression of offspring on the mid-parent, which might indicate some maternal effect upon topline pattern.

Heritability Estimates from Regression of
Offspring's Score on Mid-parent Score

The regression coefficients of 419 offspring scores on mid-parent scores were .542 ± .073 for topline pattern and .485 ± .076 for shade of red. These are direct estimates of heritability. Pound (1928)

TABLE VI HERITABILITY ESTIMATE OF TOPLINE PATTERN BY PATERNAL HALF-SIB INTRA-CLASS CORRELATION USING A NESTED CLASSIFICATION

	D/F	Mean square	Expected mean square	Variance component	Intra-class r	Heritability estimate
Between sires, within age of dams	43	3.358	$\sigma_e^2 + 11.488\ \sigma_s^2$	1.885	.088	.35
Within sires	459	1.694	σ_e^2	1.694		

TABLE VII HERITABILITY ESTIMATE OF TOPLINE PATTERN BY PATERNAL HALF-SIB INTRA-CLASS CORRELATION

	D/F	Mean square	Expected mean square	Variance component	Intra-class r	Heritability estimate
Between sires	37	4.369	$\sigma_e^2 + 13.366\ \sigma_s^2$	2.682	.106	.42
Within sires	479	1.687	σ_e^2	1.687		

TABLE VIII HERITABILITY ESTIMATE OF SHADE OF HAIR COLOR BY PATERNAL HALF-SIB INTRA-CLASS CORRELATION USING A NESTED CLASSIFICATION

	D/F	Mean square	Expected mean square	Variance component	Intra-class r	Heritability estimate
Between sires, within age of dams	43	2.710	$\sigma_e^2 + 11.488\ \sigma_s^2$	1.436	.089	.36
Within sires	459	1.274	σ_e^2	1.274		

TABLE IX HERITABILITY ESTIMATE OF SHADE OF HAIR COLOR BY PATERNAL HALF-SIB INTRA-CLASS CORRELATION

	D/F	Mean square	Expected mean square	Variance component	Intra-class r	Heritability estimate
Between sires	37	4.551	$\sigma_e^2 + 13.366\ \sigma_s^2$	3.116	.140	.56
Within sires	479	1.435	σ_e^2	1.435		

obtained a heritability estimate for shade of .44 by regression of offspring on mid-parent. Koger and Mankin (1952) found an estimate of .75 for shade by the same method.

Distribution of Scores

Lush (1945) states that the mean of a population for any trait may be changed rapidly by selection when the heritability of the trait is high. Heritability estimates obtained in the present study ranged from .35 to .67 for pattern and from .36 to .59 for shade, which would mean that progress from phenotypic selection would be expected to be rapid for both traits. Selection by breeders for desirable topline pattern has apparently not been very successful for fixing the desired trait. The distribution of offspring scores for topline pattern from various combinations of parents, which is given in table X, shows that 70 percent of the offspring from all matings were desirably marked while 30 percent were either red necked or linebacked. Only seventy-five percent of the offspring from desirably marked parents were classified as desirable. When the parents were both perfectly marked (scores of 5) the number of desirable offspring (scores 4, 5, and 6) was only 76 percent, indicating that intensive selection would not entirely eliminate the undesirable traits.

The number of matings in this study was not large enough in some classes to furnish conclusive evidence as to the nature of inheritance of topline pattern or shade of hair color. No mating of a completely red necked sire and a completely red necked dam was present which would be a critical test if red neck was due to a recessive gene.

TABLE X. THE TOPLINE PATTERN SCORES OF CALVES FROM PARENTS WITH VARIOUS PATTERN COMBINATIONS

Scores of Parents ♂ ♀	Average score of parents	Scores of calves 1	2	3	4	5	6	7	8	9	Total number of calves	Average score of calves
R x R												
2 x 1	1.5	1									1	1.00
2 x 2	2.0	2		1		1					4	2.50
2 x 3	2.5			2							2	3.00
3 x 2	2.5	1									1	1.00
D x D												
4 x 5	4.5			1	1	17	3	2	1		25	5.28
5 x 4	4.5	2	3	3	2	17		3			30	4.37
4 x 6	5.0					7	2	1			10	5.40
6 x 4	5.0			1			1		1		3	5.67
5 x 5	5.0		8	10	9	94	5	15	1		142	4.89
5 x 6	5.5		2	2		20	2	3	2		31	5.13
6 x 5	5.5					6	2	3			11	5.73
L x L												
7 x 7	7.0									1	1	9.00
7 x 8	7.5					1					1	5.00
R x D												
2 x 4	3.00			1		2					3	4.33
2 x 5	3.50	3	1	1	4	5	1	1			16	3.88
3 x 4	3.50		1		1	2	1				5	4.40
3 x 5	4.00		2	1	1	6		2			12	4.58
2 x 6	4.00		1					1			2	4.50
3 x 6	4.50					1					1	5.00

Continued

R includes scores 1, 2, and 3
D includes scores 4, 5, and 6
L includes scores 7, 8, and 9

TABLE X (continued)

Scores of Parents ♂ ♀	Average score of parents	Scores of calves 1	2	3	4	5	6	7	8	9	Total number of calves	Average score of calves
D x R												
4 x 1	2.5					1					1	5.00
4 x 2	3.0					1		1			2	6.00
5 x 1	3.0	1	1		1	4					7	3.86
5 x 2	3.5		1	1	1	5					8	4.25
4 x 3	3.5				1	2		1			4	5.25
5 x 3	4.0	1				10					11	4.64
6 x 2	4.0					1					1	5.00
6 x 3	4.5				1						1	4.00
R x L												
2 x 7	4.5		1		1	4		3			9	5.22
3 x 7	5.0			1		2		1			4	5.00
L x R												
7 x 3	5.0					1					1	5.00
D x L												
4 x 7	5.5					2	1	1		1	5	6.40
5 x 7	6.0	1		1	3	25		12	1		43	5.42
6 x 7	6.5					2	2	2			6	6.00
5 x 8	6.5					4		1			5	5.40
6 x 8	7.0							2			2	7.00
5 x 9	7.0							1			1	7.00
L x D												
7 x 4	5.5					2					2	5.00
7 x 5	6.0					1		2			3	6.33
7 x 6	6.5					2					2	5.00
		12	21	26	26	248	20	58	6	2	419	

R includes scores 1, 2, and 3
D includes scores 4, 5, and 6
L includes scores 7, 8, and 9

The distribution of shade of hair color scores for offspring from various combinations of parents is shown in table XI. The skewed distribution of scores toward the lighter shades can be partially accounted for by the effect of age of dam on the shade of hair color of the calf, since calves from heifers had lighter mean scores than calves from mature cows.

Correlations Between Topline Pattern Scores, Shade of Hair Color Scores, and Eyelid Pigmentation Scores

A total of 585 animals were used in the correlations between topline pattern and eyelid pigmentation, and shade of hair color and eyelid pigmentation. Eyelid pigmentation scores were not available for all cows in this study and the 1957 calves were not scored for eyelid pigmentation.

Correlations between topline pattern scores and eyelid pigmentation scores are shown in table XII for eleven groups of cattle. Only the correlation of .25 for the 650 group of cows was significant at the 5 percent level. All other correlations were small and not significant. The pooled correlation of $.06 \pm .04$ was not significant. The positive sign of the correlation indicates there was some tendency for animals with linebacks to have more eyelid pigmentation. Topline pattern and eyelid pigmentation do not appear to be controlled by the same genes since very little correlation exists between the two traits.

Correlations between shade of red and eyelid pigmentation scores in table XIII were significant for three groups at $P < .05$. Two of these were positive correlations. However, the correlation between these traits for the heifers born in 1955 in the 650 herd was a $-.41$. This

TABLE XI THE SHADE OF HAIR SCORES OF CALVES FROM PARENTS WITH VARIOUS SHADE COMBINATIONS

Scores of Parents ♂ ♀	Average score of parents	Score of calves 1	2	3	4	5	6	7	Total number of calves	Average score of calves
2 x 1	1.5	1		2					3	2.33
2 x 2	2.0	2			2				4	2.50
3 x 1	2.0	2	1	3	1				7	2.58
2 x 3	2.5	1	1			1			3	2.67
3 x 2	2.5	6	4	6	3				19	2.32
4 x 1	2.5	1		2	1				4	2.85
2 x 4	3.0	1	1	1	3	1			7	3.29
4 x 2	3.0	5	6	3	3				17	2.24
3 x 3	3.0	6	4	3	8				21	2.62
5 x 1	3.0	1	1						2	1.50
2 x 5	3.5				3	1			4	4.25
5 x 2	3.5	1	3	4	1				9	2.56
3 x 4	3.5		13	16	12	2			43	3.07
4 x 3	3.5	5	6	10	9	2	1		33	3.00
2 x 6	4.0				2	1			3	4.33
3 x 5	4.0	2	6	4	8	7	1		28	3.54
5 x 3	4.0	3	6	5	5	3			22	2.95
4 x 4	4.0	12	4	15	17	6	1		55	3.07
3 x 6	4.5		1		2	2	1		6	4.33
4 x 5	4.5	2	10	5	19	6	1		43	3.47
5 x 4	4.5	1	4	5	7	9	1		27	3.81
3 x 7	5.0					1	1		2	5.50
4 x 6	5.0	3	1	2	4	5	1		16	3.63
5 x 5	5.0	2	3	7	6	5	3		26	3.69
4 x 7	5.5		1		2	2			5	4.00
5 x 6	5.5		3	4	2	1			10	3.10
		57	79	97	120	55	11	0	419	

TABLE XII CORRELATIONS BETWEEN TOPLINE PATTERN SCORES (X) AND EYELID PIGMENTATION SCORES (Y)

Herd	Class	Years calved	D/F	Sum of squares and cross products Σx^2	Σxy	Σy^2	r
670	cows	1946-54	98	191.84	-121.96	83,490.24	-.10
670	heifers	1955	18	2.95	62.30	16,552.20	.28
670	calves	1956	77	208.76	195.20	54,688.99	.06
873	cows	1946-52	55	60.67	118.67	48,012.25	.07
873	calves	1956	29	56.77	-73.39	25,536.19	-.06
650	cows	1948	101	201.86	1230.23	120,785.23	.25*
650	cows	1954	37	87.90	287.31	38,785.23	.15
650	heifers	1955	26	78.86	-27.57	20,531.71	-.02
650	calves	1956[1]	88	189.60	-339.00	72,880.00	-.09
650	calves	1956[2]	24	69.54	-42.31	8,476.46	-.06
	Bulls		10	18.25	47.50	4,381.67	.17
Pooled			563	1167.00	1327.98	494,078.97	.06

*Significant at $P < .05$
[1]Calves from mature cows
[2]Calves from two-year-old cows

TABLE XIII CORRELATIONS BETWEEN SCORES FOR SHADE OF HAIR COLOR (X) AND EYELID PIGMENTATION SCORES (Y)

				Sum of squares and cross products			
Herd	Class	Years calved	D/F	Σx^2	Σxy	Σy^2	r
670	cows	1946–54	98	175.84	594.04	83,490.24	.16
670	heifers	1955	18	26.55	159.90	16,552.20	.24
670	calves	1956	77	159.97	492.89	54,688.99	.17
873	cows	1946–52	55	84.25	–14.25	48,012.25	–.01
872	calves	1956	29	40.84	–96.03	25,536.19	–.09
650	cows	1948	101	158.84	1085.39	120,744.03	.25*
650	cows	1954	37	31.59	234.46	38,785.23	.21
650	heifers	1955	26	50.68	–418.14	20,531.71	–.41*
650	calves	1956[1]	88	164.00	316.00	72,880.00	.09
650	calves	1956[2]	24	36.62	236.77	8,476.46	.42*
	Bulls		10	10.25	–88.50	4,381.67	–.42
Pooled			563	939.43	2502.53	494,078.97	.12**

**Significant at $P < .01$
* Significant at $P < .05$
1 Calves from mature cows
2 Calves from two-year-old cows

is probably a chance occurrence since the pooled correlation of .12 ± .04 was positive and significant at $P < .01$. This might indicate that the traits are influenced by the same genetic factors, but since the correlation is small, the rate of change in one trait from selection for the other trait would be expected to be slight. Positive correlations in this case indicate that darker Herefords tend to have more eyelid pigmentation.

Correlations between scores for topline pattern and shade of hair color were negative for most of the groups (table XIV). The only significant correlation was -.40 for the calves in 1956 from the two-year-old heifers in the 650 herd, ($P < .05$). The pooled correlation of -.07 ± .03 was also significant but very small. Correlations between topline pattern and shade of hair color suggest that the darker colored Herefords tend more toward red neck and the lighter colored Herefords tend to have more white in the topline pattern. Scores from 974 individuals in seventeen groups comprised the data which were used in these correlations.

The repeatability of the scoring methods used in this study was relatively high. The repeatability of shade score might be increased by refining the scoring techniques for shade. This might be done by taking hair samples from the same area of each individual and comparing them with a standard. In this way scoring of all samples could be done at nearly the same time and under the same amount of light. The samples should be perfectly dry at the time of scoring so that the moisture content would not affect the shade. This would reduce the effect of variable weather conditions when scoring on different days.

TABLE XIV CORRELATIONS BETWEEN TOPLINE PATTERN SCORES (X) AND SHADE OF HAIR COLOR SCORES (Y)

				Sum of squares and cross products			
Herd	Class	Years calved	D/F	Σx^2	Σxy	Σy^2	r
670	cows	1946-54	102	194.913	11.885	181.846	.06
670	heifers	1955	19	2.950	1.430	29.140	.15
670	calves	1956	80	213.610	14.878	169.524	.08
670	calves	1957	89	125.300	-4.520	140.420	-.03
873	cows	1946-52	63	64.862	-11.338	98.062	-.14
873	calves	1956	32	57.441	7.735	41.559	.16
873	calves	1956[1]	10	17.000	-3.500	2.980	-.49
873	calves	1957	36	31.710	-1.310	22.550	-.05
650	cows	1948	109	214.432	-29.973	211.856	-.14
650	cows	1954	39	101.512	-15.268	35.902	-.25
650	heifers	1955	37	114.974	2.000	76.000	.02
650	calves	1956[2]	102	212.990	-35.798	192.760	-.18
650	calves	1956[3]	30	81.719	-23.844	43.469	-.40*
650	calves	1957[2]	101	189.300	-13.400	79.200	-.11
650	calves	1957[4]	30	71.500	-6.500	18.870	-.18
650	calves	1957[3]	28	41.500	4.500	30.700	.13
	Bulls		33	40.743	-5.171	45.886	-.12
Pooled			940	1776.456	-108.194	1420.724	-.07*

*Significant at $P < .05$
[1]Fall calves
[2]Calves from mature cows
[3]Calves from two-year-old cows
[4]Calves from three-year-old cows

SUMMARY

Hereford cattle from three herds at the Fort Reno Experiment Station were scored for topline pattern, shade of hair color, and eyelid pigmentation. The data consisted of scores from 517 dams and their offspring by 38 sires. Data from 419 calves were used in the regression of calf score on mid-parent score. Heritability estimates were computed for topline pattern and shade of hair color scores. Correlations were computed between these traits and eyelid pigmentation. Methods for computing estimates of heritability were intra-sire regression of offspring on dam score, paternal half-sib intra-class correlations, and regression of offspring score on mid-parent score. The average effects due to season in which the animal was scored, age of the animal, herd, age of dam, and sires were removed before computing heritability estimates from regression of offspring on dam.

Age of the dam appeared to have an effect on the shade of hair color of the calves. Mean shade of hair color for calves from two-year-old heifers was 2.76 while means of 3.25 and 3.33 were found for calves from three-year-old cows and mature cows, respectively. In the three herds studied, cows were darker in shade of hair color than calves and had more white in the topline pattern. The mean score for topline pattern in cows was 5.14 and for shade was 3.79. Calves had a mean score of 5.04 for topline pattern and 3.22 for shade of hair color. Differences between cow scores and calf scores for shade of hair color

were statistically significant ($P < .01$). Differences between scores of calves of different sexes were not significant for either trait; however, males scored slightly darker in color and tended to have less white in the pattern. Mean scores for male calves were 4.89 for pattern and 3.43 for shade. Heifers had mean scores of 5.09 and 3.23 for pattern and shade, respectively.

The pooled correlation between pattern score and eyelid pigmentation was .06 and was not significant. A significant ($P < .01$) pooled correlation of .12 was found between shade score and amount of eyelid pigment. The correlation for topline pattern and shade of hair color was -.07. It was significant at the 5 percent level.

Heritability estimates were .67 ± .08 for topline pattern and .59 ± .07 for shade of hair color by intra-sire regression of offspring's score on dam's score. Paternal half-sib estimates from the same corrected data were .35 ± .21, and .36 ± .20 for pattern and shade, respectively. Paternal half-sib estimates of .42 ± .20 and .56 ± .18 were calculated from the uncorrected data for pattern and shade, respectively. Regression of offspring scores on mid-parent scores yielded heritability estimates of .54 ± .07 and .48 ± .08 for pattern and shade, respectively.

LITERATURE CITED

Anderson, D. E., J. L. Lush and D. Chambers. 1957a. Studies on bovine ocular squamous carcinoma ("cancer eye") II. Relationship between eyelid pigmentation and occurrence of cancer eye lesions. J. Animal Sci. 16:739.

Anderson, D. E., D. Chambers and J. L. Lush. 1957b. Studies on bovine ocular squamous carcinoma ("cancer eye") III. Inheritance of eyelid pigmentation. J. Animal Sci. 16:(in press).

Bogart, R. and H. L. Ibsen. 1937. The relation of hair and skin pigmentation to colour inheritance in cattle, with some notes on guinea-pig hair pigmentation. J. Genetics 35:31.

Hazel, L. N. and C. E. Terrill. 1945. Heritability of weaning weight and staple length in range Rambouillet lambs. J. Animal Sci. 4:347.

Hellstrom, C. F. 1951. The heritability of hair color in Hereford cattle and the correlation between color and selected feedlot and carcass characteristics of steers. M.S. Thesis, Colo. A. & M. College.

Hetzer, H. O., G. E. Dickerson and J. H. Zeller. 1944. Heritability of type in Poland China swine as evaluated by scoring. J. Animal Sci. 3:390.

Horlacher, W. R. 1928. Exceptional color inheritance in Hereford cattle. J. Heredity 19:10.

Hurt, P. 1956. Color doesn't affect Hereford production. New Mexico Extension News 36:5 No. 2.

Ibsen, H. L. 1933. Cattle inheritance. I. Color. Genetics 18:441.

Ibsen, H. L. and W. H. Riddell. 1931. Recessive white spotting in cattle. Anatomical Record 51:116 (abstract).

Ibsen, H. L. and A. D. Weber. 1933. The genetics of the Hereford pattern. Proc. Am. Soc. An. Prod. p. 291.

Kinsman, W. 1918. Hereford color. Breeder's Gazette 74:650.

Knapp, B. Jr. and A. W. Nordskog. 1946. Heritability of live animal scores, grades, and certain carcass characteristics in beef cattle. J. Animal Sci. 5:194.

Koger, M. and J. D. Mankin. 1952. Heritability of intensity of red color in Hereford cattle. J. Heredity 43:15.

Lush, J. L. 1945. Animal Breeding Plans 3rd Ed. The Iowa State College Press, Ames, Iowa.

Pitt, F. 1920. Notes on the inheritance of colour and markings in pedigree Hereford cattle. J. Genetics 9:281.

Pitt, F. 1921. Notes on the inheritance of colour and markings in pedigree Hereford cattle in England. International Review of Science and Practice of Agriculture p. 1298.

Pound, E. O. 1928. Sidelight on Hereford color. Am. Hereford J. 19:84 No. 5.

Pound, E. O. 1932. Sidelight on the markings of Herefords. Am. Hereford J. 22:16 No. 21.

Sawyer, W. A., R. Bogart and M. M. Oloufa. 1948. Weaning weight of calves as related to age of dam, sex and color. J. Animal Sci. 7:514 (abstract).

Shrode, R. R. and J. L. Lush. 1947. The genetics of cattle. Advances in Genetics 1:209.

Snedecor, G. W. 1956. Statistical Methods. 5th Ed. The Iowa State College Press, Ames, Iowa.

Stanley, E. B. and R. McCall. 1945. A study of performance in Hereford cattle. I. Progeny testing of Hereford sires. II. Type as an indicator of performance. Ariz. Agr. Exp. Sta. Tech. Bul. 109:35.

Willham, O. S. 1937. A genetic history of Hereford cattle in the United States. J. Heredity 28:283.

A P P E N D I X

APPENDIX A

TABLE XV NESTED CLASSIFICATION OF TOPLINE PATTERN SCORES FOR DAMS (X) AND CALVES (Y)

Total			Season scored			Year of birth(Y)			Herd			Age of dam			Sire			
No.	ΣX	ΣY	No.	ΣX	ΣY	No.	ΣX	ΣY	No.	ΣX	ΣY	No.	ΣX	ΣY		No.	ΣX	ΣY
						1954			650			Cows			901	11	57	37
															D247	9	47	50
						37	192	171	37	192	171	37	192	171	CK	12	58	54
															182	5	30	30
						1955			650			Cows			901	10	53	42
															120	5	30	23
						29	159	134	29	159	134	29	159	134	2-19	5	32	28
															2-42	6	29	27
															182	3	15	14
									650			Cows			D-95	9	44	50
															2-19	19	98	111
									89	467	459	63	339	332	2-42	4	21	19
			Fall (1956)												4-50	13	71	57
															3-11	5	27	24
															4-08	5	27	25
			254	1324	1249										4-25	8	51	46
												2 yr. olds			3-09	13	66	57
												26	128	127	3-11	13	62	70
						1956			670			Cows			901	16	72	69
															D-95	11	53	57
						188	973	944	79	401	384	76	386	375	D247	11	55	62
															120	14	74	57
															4-24	10	53	58
															4-34	14	79	72
												2 yr. olds						
												3	15	9	4-50	3	15	9
									873			Cows			4-68	4	21	18
															I-35	5	28	25
									20	105	101	20	105	101	4-26	5	25	26
Total															4-07	3	18	17
															4-38	3	13	15
517	2670	2579				1955			670			Cows			D247	9	47	46
															120	2	11	10
						17	91	86	17	91	86	17	91	86	BL	6	33	30
						1956			873			Cows			I-17	5	25	25
						9	49	51	9	49	51	9	49	51	I-58	4	24	26
									650			Cows			D-84	19	104	99
															D-95	13	74	68
									114	591	564	69	376	338	4-34	11	55	51
															4-50	12	74	53
															4-68	14	69	67
												3 yr. olds			P472	5	21	28
												20	96	95	C785	15	75	67
			Spring (1957)									2 yr. olds			4-16	13	60	69
												25	119	131	4-20	12	59	62
			263	1346	1330				670			Cows			420A	7	36	34
															D247	20	98	108
									89	434	451	70	339	360	450A	10	53	59
						1957									469A	11	59	59
															A-2	22	93	100
						237	1206	1193				2 yr. olds			450A	5	25	25
															A-2	4	20	23
												19	95	91	4-50	10	50	43
									873			Cows			5-21	8	43	49
															5-61	4	21	18
									34	181	178	34	181	178	5-74	4	20	19
															445	8	41	42
															517	6	33	28
															529	4	23	22

TABLE XVI NESTED CLASSIFICATION OF SHADE OF HAIR COLOR SCORES FOR DAMS (X) AND CALVES (Y)

Total No.	Total ΣX	Total ΣY	Season scored	No.	ΣX	ΣY	Year of birth (Y)	No.	ΣX	ΣY	Herd	No.	ΣX	ΣY	Age of dam	No.	ΣX	ΣY	Sire	No.	ΣX	ΣY
517	2016	1682	Fall (1956)	254	1015	894	1954	37	165	150	650	37	165	150	Cows	37	165	150	901	11	46	45
																			D247	9	38	35
																			CK	12	58	53
																			182	5	23	17
							1955	29	111	86	650	29	111	86	Cows	29	111	86	901	10	44	31
																			120	5	18	15
																			2-19	5	11	11
																			2-42	6	24	18
																			182	3	14	11
							1956	188	739	658	650	89	351	322	Cows	63	248	223	D-95	9	38	28
																			2-19	19	75	67
																			2-42	4	11	12
																			4-50	13	53	49
																			3-11	5	22	24
																			4-08	5	21	16
																			4-25	8	28	27
															2 yr. olds	26	103	99	3-09	13	52	53
																			3-11	13	51	46
											670	79	324	254	Cows	76	312	245	901	16	55	33
																			D-95	11	38	37
																			D247	11	47	33
																			120	14	55	44
																			4-24	10	48	38
																			4-34	14	69	60
															2 yr. olds	3	12	9	4-50	3	12	9
											873	20	64	82	Cows	20	64	82	4-68	4	15	16
																			I-35	5	16	21
																			4-26	5	15	21
																			4-07	3	9	10
																			4-38	3	9	11
			Spring (1957)	263	1001	788	1955	17	72	47	670	17	72	47	Cows	17	72	47	D247	9	39	20
																			120	2	7	7
																			BL	6	26	20
							1956	9	32	34	873	9	32	34	Cows	9	32	34	I-17	5	19	19
																			I-58	4	13	15
							1957	237	897	707	650	114	421	371	Cows	69	260	253	D-84	19	73	71
																			D-95	13	43	45
																			4-34	11	45	48
																			4-50	12	45	45
																			4-68	14	54	44
															3 yr. olds	20	80	65	P472	5	22	15
																			C785	15	58	50
															2 yr. olds	25	81	53	4-16	13	44	25
																			4-20	12	37	28
											670	89	354	225	Cows	70	295	184	420A	7	31	27
																			D247	20	80	38
																			450A	10	46	24
																			469A	11	52	31
																			A-2	22	86	64
															2 yr. olds	19	59	41	450A	5	17	14
																			A-2	4	10	10
																			4-50	10	32	17
											873	34	122	111	Cows	34	122	111	5-21	8	32	26
																			5-61	4	10	12
																			5-74	4	18	14
																			445	8	32	29
																			517	6	19	16
																			529	4	11	14

APPENDIX B

METHOD OF COMPUTING $\bar{k}$ VALUES

The value of $\bar{k}$, which is a weighted number of progeny per sire, and is used in computing paternal half-sib correlations was obtained by the following formula given by Hetzer <u>et al</u>. (1944).

$$\bar{k} = \frac{\sum\left(\frac{\sum k^2}{\sum k}\right)_c - \sum\left(\frac{\sum k^2}{\sum k}\right)_g}{Nc - Ng}$$

$\sum\left(\frac{\sum k^2}{\sum k}\right)_c$ = the number of progeny per sire, per season, etc. i.e.

$$\left(\frac{11^2}{11}\right) + \left(\frac{9^2}{9}\right) + \left(\frac{12^2}{12}\right) + \ldots + \left(\frac{4^2}{4}\right) = 517$$

$\sum\left(\frac{\sum k^2}{\sum k}\right)_g$ = number of progeny per sire, per season etc. squared, divided by the total number of progeny i.e.

$$\frac{(11)^2 + (9)^2 + (12)^2 + \ldots + (4)^2}{11 + 9 + 12 + \ldots + 4} = 22.46$$

Nc = the number of sire subclasses.

Ng = the number of groups with 2 or more sire subclasses.

k = the number of observations in a sire group.

c = sire subclass.

g = group containing sire subclasses.

APPENDIX C

STANDARD ERRORS FOR HERITABILITY ESTIMATES

Standard errors for heritability estimates by intra-sire regression of offspring on dam score and paternal half-sib intra-class correlations were calculated from formulas used by Hazel and Terrill (1945).

The formula used for intra-sire regression of offspring on dam score was as follows:

$$S.E. = \sqrt{\frac{BB' - cov(b)^2}{(B')^2 \quad (nk - n - 1)}}$$

B = the mean square within sires of the adjusted y value.

B' = the mean square within sires of the x value.

cov $(b)^2 = \Sigma xy$ divided by the degrees of freedom within sires.

n = the number of sires in each year.

k = the weighted number of calves per sire.

This standard error was multiplied by two since the intra-sire regression was multiplied by two.

The standard errors for paternal half-sib intra-class correlations were multiplied by four as were the half-sib correlations. The following formula was used to compute standard error.

$$S.E. = \frac{B \ (B + kA)}{(A + B)^2 \sqrt{(\frac{1}{2}) \ (k - 1) \ kn}}$$

A = mean square between sires of the adjusted y value.

B = mean square within sires of the adjusted y value.

k = the weighted number of calves per sire.

n = the number of sires in each year.

The standard errors for regression of offspring on the mid-parent scores were calculated as set forth by Snedecor (1956).

VITA

Marion E. Stanley

Candidate for the Degree of

Master of Science

Thesis: INHERITANCE OF COLOR PATTERN AND SHADE OF HAIR COLOR IN HEREFORD CATTLE

Major Field: Animal Breeding

Biographical:

Personal Data: Born near New Raymer, Colorado, November 1, 1931, the son of Edward B. and Velma E. Stanley

Education: Received the Bachelor of Science degree from Colorado Agricultural and Mechanical College, with a major in Animal Husbandry in June, 1954.

Experiences: Entered the United States Army in 1954 and was separated in 1956.

Date of Final Examination: October 19, 1957

THESIS TITLE: INHERITANCE OF COLOR PATTERN AND SHADE
OF HAIR COLOR IN HEREFORD CATTLE

AUTHOR: Marion E. Stanley

THESIS ADVISER: Dr. Doyle Chambers

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TYPIST: Mrs. Robert L. Noble