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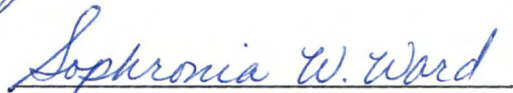
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The Graduate School

ASPECTS OF THE GENETICS OF BOVINE BLOOD SYSTEMS: LINKAGE,
HETEROSIS, GENE FREQUENCY AND ASSOCIATION WITH
PRODUCTION TRAITS

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The author wishes to dedicate this dissertation to his wife, Mary Dagley Copeland for her love, understanding, and support, and to his children, Lydia Erin and Lucas Edward Copeland.

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ABSTRACT

Data from two separate beef cattle herds, the University of Tennessee (UT) Plateau Experiment Station Angus herd and the Virginia Polytechnic Institute (VPI) and State University herd at Front Royal, Virginia, containing Angus, Shorthorns, and Herefords, were utilized to investigate some of the genetic aspects of bovine blood systems. Analyses for linkage revealed that genes responsible for blood groups are not located on the sex chromosome. Attempts to find linkage between genes responsible for the F-V and R'-S' blood systems proved inconclusive. Studies of heterozygosity in the UT Angus herd using combinations of double homozygotes and heterozygotes between the F-V and R'-S' blood systems found heterozygotes in most cases to have higher least-squares means for production traits than homozygotes. More significant differences ($.003 < P < .10$) were found between double homozygotes and heterozygotes when sire effects were removed from models than when sire effects were included, indicating that confounding of blood type and sire can be extreme. Gene frequency analyses revealed that random drift caused drastic changes in the frequency of blood type genes of the VPI herd as several significant differences ($P < .05$ or $P < .01$) in gene frequencies between years were observed. Analyses of variance were performed on various body and weight production traits to determine if associations of these existed with blood types within a system or with combinations of blood types of two systems. The Z and J systems were found involved with the majority of the associations revealed in the VPI herd. The

phenotypes Z0/Z0 and J0/J1 occurred most frequently. Numerous more associations were found in the analyses involving combinations of blood types of two systems than in analyses dealing with blood systems separately. The transferrin system and the R'-S' and F-V blood systems were found in the majority of associations in the UT herd. In a comparison of observed and expected heterozygosis of the F-V blood system in the VPI herd, significant differences ($P < .05$ or $P < .005$) were found in three of the seven years studied in Angus and in one of the seven years studied in Herefords. Expected values were almost always less than observed values, but the intensity of inbreeding was probably not sufficient to reduce the frequency of heterozygotes appreciably, if at all.

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CHAPTER I

INTRODUCTION

Bovine blood systems have been the subject of much research during the last forty years. Studies have been initiated to find associations between blood phenogroups and quantitative production traits and disease resistance. Numerous journal articles have illustrated the practical importance of blood phenogroups in the investigations of freemartin calves, breed relationships and parentage disputes.

If associations can be proven to exist between production traits and blood groups, some additional progress might be made in the improvement of these traits by selection. With the advent of genetic engineering, knowledge concerning the linkage and location of genes may become more important. Information of this type is lacking in cattle genetics. Hopefully, this dissertation may provide some insight into these and other areas of the genetics of cattle.

Two herds provided the data used in this study, the Angus herd at the University of Tennessee Plateau Experiment Station (UT herd) and the Virginia Polytechnic Institute and State University Front Royal herd (VPI herd). The VPI herd consisted of animals of three breeds: Angus, Shorthorn, and Hereford. The objectives of this study were to:

1. Determine if blood type genes are sex-linked.
2. Determine if the genes responsible for the F-V and R'-S' systems are linked.

3. Determine if any associations exist between blood types within a system and quantitative variables in the VPI herd and between double combinations of blood systems phenogroups and quantitative variables in the UT and VPI herds.
4. Measure differences between calves with double heterozygous and those with homozygous blood type genotypes in the F-V and R'-S' blood systems with respect to quantitative variables in the UT Angus herd.
5. Quantify genetic random drift by studying the frequencies of the various blood phenogroups within blood group systems in successive calf crops in the VPI herd .

CHAPTER II

REVIEW OF LITERATURE

1. GENERAL INFORMATION

Blood typing in animals had been initiated by the late 1890's, and, by 1900, it was known that the injection of blood from one animal into that of a second animal would stimulate the production of antibodies against entities in the donor's blood. Also known was the fact that these antibodies would lyse donor red blood cells in the presence of a complement (Spooner, 1967). By 1900, scientists had documented the use of iso-immunization for producing antibodies as well as the hemolysing technique for researching blood groups in animals (Stormont, 1978). The discovery of the human ABO blood groups by Landsteiner (1901), while a finding of great importance in itself, served to retard advancements made in animal blood typing. During the next forty years, researchers directed their efforts to identifying agglutinins in animals similar to the anti-A and anti-B found in man (Spooner, 1967). By the late 1930's and early 1940's, significant studies were being conducted at the University of Wisconsin by M. R. Irwin and his colleagues, C. Stormont and L. C. Ferguson. These researchers, using isoimmune antisera and hemolytic tests, made great contributions concerning blood groups and systems in cattle and other livestock species.

The blood type of an animal is determined by the known blood factors located on the erythrocytes as determined by tests made with

appropriate reagents (Stormont, et al., 1951). Reagents are obtained from isoimmune antisera which have been produced by a cow injected with the red blood cells of another cow. Reagents may be produced also by the injection of cattle blood into that of rabbits and sheep.

Spooner (1967) explained that a blood type is a protein carbohydrate association found on the surface of red blood cells. Structurally different proteins are encountered, and it is these differences which give rise to different antigens and, thus, different blood types.

Cattle erythrocytes, unlike those of humans, pigs, chickens, and horses, do not agglutinate easily. As a result, agglutination techniques are not used. Instead, hemolytic tests are conducted (Stormont, 1967; Spooner, 1967). Hemolysis, however, will not take place unless a complement is added to the antibody-erythrocyte mixture. The complement used most often is fresh rabbit serum, although, originally, guinea pig serum was used (Stormont, 1967, 1978; Mishra et al., 1974).

At the present time, eleven genetic systems of blood groups are recognized. These are symbolically designated as A, B, C, F-V, J, L, M, S, Z, R'-S', and T. A system is composed of blood groups known as phenogroups that are determined by a set of multiple alleles. Each phenogroup is composed of blood factors. Each factor is inherited as a single Mendelian dominant in contrast with its absence (recessive to presence), and blood factors belonging to the same genetic system are inherited by means of allelic genes (Stormont, 1967; Miller, 1966).

Cattle blood types are extremely complicated as is exemplified by the B system which is known to contain over 300 alleles in one allelic series. Following B in complexity are C, A, S, F-V, R'-S', J, L, T, and Z, respectively. Even though complex, the blood groups of cattle are better known than those of any other organism yet studied, apart from man (Cooper and Rendel, 1968). Stormont (1967) estimated that nearly two trillion blood types are theoretically possible. This number is considered to be far greater than the total number of cattle which have ever lived.

Transferrin polymorphisms also are well defined in cattle. Transferrins are iron binding globulins present in blood serum. Four co-dominant allelic genes designated as Tf^A, Tf^{D1}, Tf^{D2}, and Tf^E are responsible for serum transferrin polymorphism (Makarechian and Howell, 1967). As a result, ten transferrin types, AA, AD₁, AD₂, AE, D₁D₁, D₁D₂, D₁E, D₂D₂, D₂E, and EE are possible. Transferrin polymorphisms are detected and typed by electrophoretic procedures.

2. BLOOD TYPE AND PRODUCTION ASSOCIATIONS

According to Oosterlee (1964), there are several possibilities on which associations between blood and serum groups and other genetically determined characteristics can be based. These are linkage of loci, pleiotrophic effects of genes, and the possibility that the antigenic substance or the genetically determined serum groups occur also in tissues other than blood and have a physiological function.

A great deal of research in dairy cattle has involved searching for associations between blood types and milk and butter fat production. Rendel (1961), working with Swedish Red and White and the Swedish Friesian breeds, found an association between the B allele BO_1YD' and butterfat percentage. He found that heifers carrying this allele had, on the average, a fat percentage .19 unit higher than that of their paternal half sibs lacking this allele. He found also that the presence of the J gene had an effect of increasing butterfat. His results with the L system were conflicting. Within groups of paternal half sibs of Swedish Red and White cattle, the L gene seemed to exert a depressing influence on fat percentage while in the Swedish Friesian cattle, the daughters from sires having L had significantly higher fat percentages than those from sires lacking L. Concerning the J gene, Mishra et al. (1974) found Indian cattle possessing this factor to be superior in performance with respect to economic traits over those lacking it.

Rausch et al. (1968) investigated the relationship between blood type and predicted differences in production of Holstein sires. They found alleles in the B and L systems related to predicted differences for milk. In the B system the least-squares constant for the BO_1Y_2D' phenogroup was 305 ± 118 kg milk higher than the constant for the $OxE'_3G'O'$ phenogroup. Regarding the L system, they found that milk production of females from bulls lacking L exceeded that of females sired by bulls carrying L by 55 ± 27 kg. Differing from these findings concerning the BO_1Y_2D phenogroup is the report of Brum et al. (1968) of a least-squares constant of $-.009 \pm .072$ fat percentage

units. Kaczmarek et al. (1972) also found no association between BO_1Y_2D' and butterfat yield. However, several others have reported on the superiority in fat percentage of cattle with this allele. Conneally and Stone (1965), Neimann-Sorensen and Robertson (1961), and Andresen et al. (1959) reported cows with these alleles to be superior in fat percentage.

Other B alleles, such as GD' , have been found associated with high fat percentage while the allele $O_1T_1E_3'K$ has been associated with low fat percentage (Neimann-Sorensen and Robertson, 1961). Nair (1957) reported a decrease in fat percentage in cows with the B phenogroup $BGIO_1T_2A_1'$. This lack of agreement concerning various B alleles led Brum et al. (1968) to suggest that this probably should be expected since some B alleles are often either not present or are not present in high enough frequencies to permit reliable estimates of effects in different samples of dairy cattle.

Brum et al. (1968) in Ohio, conducted research on a large number of Holsteins to determine if associations exist between blood types and lactation traits. Researching several blood systems, their findings indicated significant milk and fat yield differences between genotypic classes of the F-V system. They found F^V/F^V as being highly superior to either F^F/F^F or F^F/F^V . Least-squares constant estimates were reported as being -191 for F^F/F^V , -80 for F^F/F^F , and 271 for F^V/V^V kg milk and -4.3 for F^F/F^F , -9 for F^F/F^V , and 13.3 for F^V/F^V kg fat. The S system also exhibited significant differences with respect to fat yield with S^H' being superior to $S^{SH'}$ and S^S . S^H' had a least-squares constant of 18.1 ± 7.7 kg while $S^{SH'}$ and S^S had constants of

-5.3 ± 8.1 and -12.8 ± 6.7 kg, respectively. Regarding the A system, these researchers concluded that, generally, the constant estimates revealed that the alleles A^A and A^{AH} are more desirable for fat and milk yields than are A^D and A^{DH} .

Hargrove et al. (1980) reported on associations of blood and milk protein with reproductive performance in Holsteins. More than 32,000 services in 15,000 service periods of 6,000 cows with semen from 700 sires contributed to the data used. The S system, having statistically significant influence on five of ten traits, was the system exerting the most influence. Traits significantly affected were conception rate in all services by female phenotype, male phenotype, male by female phenotype combined; conception rate in first service by female phenotype and probability of conception by female phenotype. S negative cows had the lowest conception rates, while those with the S phenotype U_1' had the highest. Intermediate was S phenotype UH' . In the F-V system, matings between F/V heterozygotes had higher conception rates than did matings between F/F homozygotes and between F/V and F/F individuals.

Fewer studies have been undertaken concerning blood types and production traits in beef cattle. Sanders (1981), working with the Angus herd at the Plateau Experiment Station obtained results which suggested associations between blood groups and production traits. She found significant least-squares mean differences between blood groups in the S system with respect to postweaning average daily gain from weaning to time of postweaning data collection ($P < .03$), lifetime average daily gain from birth to approximately one year of age

($P < .01$), and average daily gain from birth to weaning, which was adjusted for age of dam and sex of calf ($P < .06$). Significant differences were found also with respect to adjusted 365-day weight. Within the C system, Sanders found that cattle having C_1E/C_2EW and C_1/C_1EW had significantly higher average daily gain from birth to weaning than did those having other C blood types. She reported significantly different least-squares means of heart girth at weaning and shape ratio among blood groups of the F-V system. F^4/F^4 calves had significantly smaller ($P < .008$) heart girths at weaning and had smaller values ($P < .02$) also for shape ratio.

According to Mather (1977), conflicting results have been obtained when studying transferrin types along with production traits. He reported several researchers finding Tf^A superior to Tf^D with respect to fat production while others have found the opposite. There seems to be agreement that Tf^E is least preferred. Kiddy et al. (1975) suggested these differences may be due to breed differences. However, there is evidence contradicting this suggestion. While the study by Kiddy et al., showed Tf^D to be superior in Holsteins, Brum et al. (1968) and Young and Hunter (1966) found Tf^A to be superior to Tf^D in Holsteins.

The research by Kiddy et al. (1975) analyzed transferrin type with respect to predicted differences for milk, fat, first-lactation milk and fat, and daughter average fat percentage in Holsteins, Guernseys, and Jerseys. After removing sire effects from their model, they found significant differences ($P < .05$) among genotypes with respect to predicted differences for milk in Holsteins and Guernseys

and predicted differences for fat in first-lactation heifers in Holsteins and Jerseys. In Holsteins, Tf^{DD} individuals had higher predicted differences for milk than Tf^{AA} individuals. Tf^{AD} individuals being intermediate suggests an additive effect. In Guernseys and Jerseys, the finding was opposite, with Tf^{AA} individuals being superior to Tf^{DD} individuals.

Brum et al. (1968), also working with Holsteins, obtained results which revealed Tf^A to be more desirable than Tf^D with respect to fat and milk yields. They analyzed five transferrin types, Tf^{AA} , Tf^{AD} , Tf^{AE} , Tf^{DD} , and Tf^{DE} , and reported least-squares constants of 348 kg, 158 kg, -56 kg, -42 kg, and -409 kg, respectively, for milk and 13.8 kg, 5.5 kg, -5.1 kg, 1.7 kg, and -16.0 kg, respectively, for fat.

Hargrove et al. (1980) found heterozygous bulls, Tf^{AD} , to have higher conception rates than bulls carrying other transferrin types. Tf^{AD} had the highest conception rate, 54 percent over all services, followed by Tf^{DD} , 52 percent; Tf^{AA} , 50 percent; and Tf^{DE} , 48 percent.

In Canada, Makarechian and Howell (1967) working with 763 feedlot steers of which 618 were grade Herefords, searched for a relationship between production traits, carcass characteristics and transferrin type. Least-squares estimates of feedlot gains and carcass traits showed no significant association with any transferrin type.

With Angus, Sanders (1981) found significant differences ($P < .02$) among least-squares means of average daily gain from birth to weaning. Animals Tf^2/Tf^3 gained significantly less than did animals of types Tf^2/Tf^2 and Tf^1/Tf^2 . Tf^1/Tf^1 animals gained significantly less than did those of the type Tf^1/Tf^2 . Significant differences were

found also among least-squares means of 205-day weaning weight, adjusted for age of dam and sex of calf. Once again, animals of the Tf^2/Tf^3 transferrin type were found to gain significantly less than their contemporaries, and animals of the Tf^1/Tf^1 type weighed significantly less at 205 days than animals of the Tf^1/Tf^2 type.

Ashton (1960) studied 141 British bulls with established contemporary comparisons. Statistically significant difference ($P < .01$) between Tf^{AA} and Tf^{DD} was found with respect to milk production, with Tf^{DD} being superior. Average contemporary comparisons were 178.5 kg for 30 Tf^{DD} bulls, 125.2 kg for 61 Tf^{AD} bulls, and 57 kg for 39 Tf^{AA} bulls.

Working with Jerseys and Australian Illawarra Shorthorn cows in Queensland, Ashton et al. (1964) again found Tf^{DD} superior to Tf^{AA} . In this study, the effects of transferrin type on lactation length, milk yield, butter fat yield, and butter fat percentage were assessed by a least-squares multiple linear regression analysis. The results in the two breeds did not differ significantly. The data from both breeds were pooled together, and it was found that, generally, Tf^{DD} cows had lactations 13.9 days longer ($P < .01$) than Tf^{AA} cows and yielded 449.7 lb more ($P < .01$) milk. Again, cows Tf^{AD} were intermediate.

3. LINKAGE RELATIONSHIPS

Linkage refers to genes being located on the same chromosome. Genes located on the sex chromosome are said to be sex-linked, while

linked genes found on chromosomes other than the sex chromosome are linked autosomally.

Chickens, as would be expected, having a shorter generation interval and the ability to produce large numbers of progeny, are excellent organisms for genetic research. Of our livestock species, much more is known of linkage groups in chickens than in all the mammalian livestock species combined. Numerous studies have dealt with the sex-linkage of genes in chickens. Some of these may prove to be very important in areas of research other than genetics. For example, Becon and Craig (1966) reported the histocompatibility locus to be located on the sex chromosome of chickens. This finding is important as the presence of this gene would presumably result in tissues of females being antigenically rejected if they were to be transplanted in males. Research such as this may prove important to medical science in the search for more successful transplanting of organs and tissues.

Several of the genes known to be sex-linked in the fowl are involved with pigmentation. These include genes responsible for barring of feathers (Spillman, 1908), gold and silver hackle feathers (Sturtevant, 1912), inhibitor of dermal melanin (Serebrovsky and Wassina, 1922), albinism (Muller and Hutt, 1941), and blue dilution (Munro, 1946). Other fowl genes found to be sex-linked include those for nakedness (Hutt and Sturkie, 1938), dwarfism (Hutt, 1959), winglessness (Lancaster, 1968), and coloboma (Abbott et al., 1970).

As a result of the numerous studies concerning sex-linked genes, a fairly well developed map of the sex chromosome has been drawn for

the domestic fowl. A review of linked genes and chromosome maps was made by Somes (1970).

Several researchers have reported on the linkage of blood groups of fowl. No genes responsible for fowl blood groups are now known to be sex-linked. Briles et al. (1967) determined the P blood group locus is linked to that of naked neck by 29.1 ± 1.4 map units and that the H blood locus is linked to the locus of white skin by 22.1 ± 1.6 units. These researchers provided information also that suggests linkage of the B blood group locus and that of polydactyly, of the H blood locus and that of muffs, and of the P blood locus with loci of the J blood group and white skin.

Schierman and Nordskog (1963) reported the C blood group locus to be linked to the gene for crest with a crossover percentage of 38.9 and that the A blood group locus is linked with the blue plumage color locus with a linkage of 33.8-unit map distance between them. However, Somes (1970) stated that several attempts to confirm these relationships have been unsuccessful. Briles (1968) published evidence suggesting a very close linkage between the A and E blood group loci. He reported a crossover percent of $.49 \pm .09$.

According to Hutt (1964), not a single case of linkage has been incontrovertibly established in cattle, horses, sheep or swine. However, linkages have been reported in such species.

Interestingly, all linkage groups reported in swine include blood group loci. The C and J blood group loci were found to be closely linked by Andresen and Baker (1964). They determined a recombination value of 5.3 ± 1.1 percent. Andresen (1966) provided evidence that

the K blood group locus is linked with the locus for hematin binding globulins in pigs, with a recombination frequency of $3.6 \pm .7$ percent. Working with pigs of the Danish Landrace breed, Andresen (1970a) reported the H blood group locus and the locus for 6-phosphogluconate dehydrogenase (6-PGD) to be linked with a recombination frequency of 3.4 percent. Andresen (1970b) found also that the H blood group locus is linked with the locus for the enzyme phosphohexose isomerase (PHI). From 78 Duroc offspring from double backcross matings an estimate of 2.6 percent recombination frequency was obtained. This linkage group became of much interest with the findings that H and PHI are closely associated with reactivity of pigs to halothane exposure (Juneja et al., 1983). Animals that are halothane-positive, those that react when exposed to halothane, may have a greater tendency to develop porcine stress syndrome (Juneja et al., 1983). The halothane-positive reaction is believed to be determined by a recessive allele at a single locus that has been designated HAL (Smith and Bampton, 1977). Rasmusen et al. (1980) indicated that the locus for HAL is linked with the loci for the H blood group and PHI. Rasmusen (1981) reported that the S locus, which has a suppressant effect on the expression of the A-O blood group locus, is located between the loci for HAL and the H blood group. Juneja et al. (1983) reported that accumulated evidence suggests an order of PHI - HAL - S - H - 6PGD for this linkage group. These researchers found the pig serum protein locus, Po-2, to be linked to this linkage group and indicated its locus to be between the loci of the H blood group and 6-PGD.

Rasmusen (1982) working with Duroc, Yorkshire, and Duroc-Yorkshire crossbred pigs, determined that the H blood group locus is linked with the loci for the C and J blood groups. He reported very small frequencies of recombination between H and C and between H and J, $.424 \pm .030$ and $.417 \pm .035$, respectively. This information enlarges the linkage group of PHI - HAL - S - H - Po-2 - 6PGD, with the two blood loci being added. To the knowledge of the author, this linkage group represents the largest linkage group known in mammalian livestock. Only in chickens are larger linkage groups now known.

Few cases of linkage in horses and cattle have been reported. This is to be expected because of the longer generation intervals and smaller numbers of progeny produced per reproductive cycle in horses and cattle.

Working with Shetland ponies, Trommerhausen-Smith (1978) reported linkage to exist between genes responsible for tobiano coat spotting and serum albumin. Observing comparisons of allelic segregation patterns, she reported the linkage to be tight between these two loci.

Sandberg (1974) found linkage between the K blood group locus and the 6-PGD locus in horses with an estimated recombination frequency of $.24 \pm .02$. Chi-square values obtained showed good agreement between the segregation data observed and those expected under the assumption of linkage being statistically significant ($P < .001$).

Interestingly, the findings of other researchers concerning the 6-PGD locus also involve linkage with blood factors. As mentioned previously, in swine, the 6-PGD locus has been found to be linked with the H blood group locus. In humans the 6-PGD locus is thought to be

linked with that for the Rh factor. The occurrence of linkage between the 6-PGD locus and blood group loci of different species may be of some evolutionary significance but probably is more likely to be due to chance (Sandburg, 1974).

In cattle, the gene responsible for streaked hairlessness was reported by Eldridge and Atkeson (1953) to be sex-linked. These researchers observed this condition in Holstein-Friesian cattle and found that the hairless streaks occurred only in females directly descended from a single cow. Accumulated evidence suggested that the condition was lethal in males. Deviation from the normal 1:1 sex ratio was noticed in calves born to affected dams, as nearly two female births per male birth were reported.

In France, Drieux et al. (1950) studied a syndrome known as congenital hypotrichosis with anadontia in crossbred calves from matings of Maine-Anjou-Normandy cows to a Charolais bull. Based on only three observations involving male calves, these investigators reached the conclusion that the responsible gene is sex-linked recessive. The basis for this conclusion was the fact that only male calves were involved, the mother of one of the three males having the condition was a daughter of the cow that produced the other two, and all other calves sired by the Charolais bull were normal with respect to this syndrome. In support of this conclusion, Hutt (1953) discussed a similar syndrome in humans known as anhydrosis with anadontia. This condition in humans has received much attention and is known to be sex-linked.

Morrill (1945) reported bovine polydactylism to be sex-linked. He reached this conclusion from the fact that only the male progeny of a particular cow and her daughter were affected. He considered the condition to be produced by a single gene which is dominant in the male and recessive to the gene for normal toe condition in the female. If the gene is sex-linked, it would not have to be dominant for the condition to develop in the male, for mammalian males carry only a single sex chromosome and would develop the extra toe regardless of the dominance or recessiveness of the gene. Shrode and Lush (1947) suggested that this might be a case in which the dominance is reversed between the sexes.

Concerning the linkage of bovine blood group genes, Hines et al. (1981) provided some recent information. Using sequential probability tests, they tested the probability of linkage between members of pairs of eighteen loci. The informative statistic in this test is known as the lod, which is the logarithm of the probability ratio formed by dividing the probability under a chosen recombination fraction by the probability under a .5 recombination fraction. Lod scores equal to or greater than 3.0 were interpreted as evidence of linkage while lod scores equal to or less than -2.0 provided the basis for exclusion of linkage as close or closer than indicated by the test recombination fraction. Scores between -2 and +3 were considered to be suggestive of linkage. Using this test, these researchers reported lod scores that supported linkage between the A blood group and hemoglobin loci and between the J blood group and the milk protein B-lactoglobulin

loci. Blood group loci found to have suggestions of linkage with one another included B with C and B with L.

Neimann-Sorensen and Robertson (1961) searched for linkage between blood group genes and genes affecting production characters. No evidence of any linkage was found.

4. BLOOD GROUP HETEROSIS

Heterosis, also known as hybrid vigor, is one of the great enigmas of genetics. Two theories have been advanced to explain heterosis. The theory of dominant genes is based on the belief that recessive genes have depressing effects on the measures of vigor, such as growth and viability, whereas, dominant genes tend to raise the level of vigor. In general terms, the more dominant genes, the greater the vigor. The second theory is that of overdominance. Hutt (1964) explained overdominance as a situation in which the different genes of allelic pairs compete with one another to determine the phenotype. The conflict between the alleles makes for greater biochemical activity which may increase vigor. Hutt (1964) mentioned also that the drawback to this theory is the fact that few examples are known in which heterozygosity at one locus increases vigor more than homozygosity at the locus.

W. E. Briles has published numerous papers and abstracts concerning the effects of heterozygosity in the B blood group system on several production characteristics in chickens. Studying three inbred Leghorn lines, Briles et al. (1953) reported that, in two of the lines, male chicks heterozygous for the B blood group alleles were

significantly heavier at nine weeks of age than those that were homozygous. Heavier weights of female chicks heterozygous for the B system also were reported, but these were not significantly different from those of homozygous females. Briles and Krueger (1955) studied hatchability and chick survival data from three related inbred lines of White Leghorns. Matings that produced only homozygotes were compared with matings that produced fifty percent heterozygotes. Matings that produced fifty percent heterozygotes had significantly higher hatchability values than matings resulting only in homozygotes. Chick survival to nine weeks of age was eight to fifteen percent greater in chicks from matings resulting in heterozygotes, but these differences were not statistically significant. Briles (1956), investigating hen-day production in two lines of inbred White Leghorns, reported that females heterozygous for the B blood group system consistently outlaid homozygous females. Briles et al. (1957) theorized that the overall superiority of the B blood group heterozygote may be due to two factors. They suspected that the superiority may stem from heterotic expression throughout the life span of the bird or that it may be due to alternate superiority of the different alleles during various phases of the life cycle or under different environmental conditions. Whatever the reason, it is interesting that in Briles' inbred lines of Leghorns, natural selection appears to have favored the heterozygous condition. A case in which natural selection favors the heterozygous state is well known in humans. This is the well known case involving the gene for sickle cell anemia and the

disease, malaria, to which heterozygotes for sickle-cell anemia are resistant.

Fewer studies have been published concerning the effects of the heterozygosity of blood systems in cattle. Working with RDM, SDM, and Jersey cattle, Neimann-Sorensen and Robertson (1961) conducted heterozygosity tests within the B, F-V, and Z systems. They determined no obvious differences in vigor between heterozygous and homozygous individuals.

Conneally (1962) found a significant excess of Z/z calves from matings segregating at the Z locus. His findings involving the Z blood system revealed that Z/z heterozygotes significantly excelled homozygous z/z cows with respect to milk yield, fat yield, and percent butterfat. He found also that embryonic mortality was significantly greater in homozygous Z/Z zygotes.

Sanders (1981), working with the UT Angus Herd at the Plateau Experiment Station, found evidence of heterozygosity superiority. She reported statistical differences between homozygotes and heterozygotes in the S, Z, and M systems. Within the S system, significant differences were found between the least-squares means of adjusted average daily gain, adjusted calf weaning weight, and adjusted post weaning weight (365-day weight adjusted for age of calf), with heterozygotes excelling homozygotes. Also, within the S system, heterozygotes had significantly larger heart girths at weaning, greater length and greater height than homozygotes. Within the Z system, Z1/Z0 individuals excelled homozygous individuals with respect to adjusted calf weaning weight. In the M system, she found heterozygous calves

to be significantly longer than calves which were homozygous. Sanders reported also several differences between heterozygotes and homozygotes that approached significance. In all cases, heterozygotes had greater values than homozygotes.

5. GENE FREQUENCY, HETEROZYGOSITY, AND HOMOZYGOSITY OF BLOOD TYPES

In the study of population genetics, gene frequencies are of paramount importance, and, as a result, several researchers have been interested in gene frequencies and the degrees of homozygosity and heterozygosity of blood group genotypes. Genetic drift is known to be one of the major factors responsible for modifying gene frequencies in small populations. Thus, genetic drift also has been of interest to population geneticists. One of the major uses made of blood group gene frequencies is their use by breed associations for registration purposes. Most breed associations now have a blood type rule that states that animals having nontraditional blood groups are ineligible for registration. It is obvious that blood group gene frequencies are important in the study and separation of breeds of livestock.

Rausch et al. (1967) compared gene frequencies of blood type systems in the Angus, Shorthorn, and Hereford breeds. Blood systems compared were the A, B, C, F-V, J, L, M, S, Z, and Tf. They reported large frequency differences among the three breeds. Making two-breed comparisons, it was found that the Angus and Shorthorn are more similar than are the Hereford and either of the other breeds. Co-dominant blood systems were tested for genetic equilibrium using the Hardy-

Weinberg model and chi-square probability estimates. Equilibrium was reported for all three breeds at these loci. Within the F-V system, an excess of heterozygotes was found, whereas, in the Tf system an excess of homozygotes was observed.

Sanders (1981) reported significant ($P < .05$ or $P < .01$) differences among successive calf crops in gene frequencies of blood group phenogroups in the UT Cumberland Plateau Angus herd, indicating significant random drift. Studying homogeneity among blood phenogroup frequencies over time, she observed only one trend, that being the decreasing trend of the S1 blood group frequency within the S system.

Sanders (1981) made a comparison also of observed and expected heterozygosis of the blood group genotypes within the F-V and R'-S' systems. Within the F-V system, no significant differences were found between observed and expected values. Due to the fact that the R'-S' system was not accurately typed with a reliable reagent, Sanders could not reach a definite conclusion regarding this system. However, she did find significant differences between observed and expected values for R'-S' genotypes in the years 1975-1979. These differences seemed to be due to the increasing frequency of the R1 allele with the corresponding stability of the R1/R1 genotype.

Briles et al. (1957) studied 73 closed populations of chickens and found that 71 clearly possessed two or more B alleles. Inbreeding was found to have a rather marked effect on the number of alleles. Lines having average inbreeding coefficients of greater than .65 uniformly possessed two alleles while three to eight alleles were observed in lines with average inbreeding coefficients of .65 or less.

The presence of two or more alleles in populations which have been subjected to inbreeding suggests some sort of balance mechanism resulting in the superiority of the heterozygote. The B blood group system in chickens constitutes a case of genetic polymorphism, and the data supplied by Briles et al. (1957) indicate that it must be of the balanced type rather than transient, in which an advantageous gene is in the process of spreading through a population. In lines possessing only two alleles, a balance between the three possible genotypes would be expected to depend on the relative superiority of the single heterozygous type over each of the two homozygous types. In lines possessing three or more alleles, the superiority of the different heterozygotes would largely determine the equilibrium frequency of each allele.

CHAPTER III

EXPERIMENTAL PROCEDURE

1. SOURCE OF DATA

Data collected from the University of Tennessee Plateau Experiment Station purebred Angus herd (UT herd) and the Virginia Polytechnic Institute and State University Front Royal herd (VPI herd), consisting of Angus, Shorthorn, and Hereford cattle, were used in this study. Data from the UT herd were collected from 1970 through 1979. Data collected from 1960 through 1972 in the VPI herd were used. Several differences exist as to the collection of the data in the two herds. In the UT herd, most bulls were used for only one season, whereas, in the VPI herd, a good bull may have been used for several years. Several body measurements as well as weights and average daily gains were measured in the UT herd. Body measurements were not taken in the VPI herd.

A blood sample was taken from each calf and mailed to the Texas A & M Immunogenetics laboratory, Texas A & M University, College Station, Texas, for antigenic and transferrin typing.

2. DESCRIPTION OF DATA

The variables recorded and used in the analyses from the UT herd were:

1. Birth weight (BW)
2. Weaning weight (WW)

3. Average Daily Gain from birth to weaning, adjusted for the age of dam and sex of calf (AADG)
4. Weaning Heart Girth (WHG), which was measured as the circumference immediately posterior to the shoulder.
5. Weaning Body Length (WLENGTH), which was measured on the dorsal midline from midpoint of the scapula to a line connecting the posterior prominences of the pin bones.
6. Weaning Hip Width (WHIETH), measured as the distance between the distal extremities of the tuber coxae.
7. Weaning Hip Height (WHIHT), measured as the distance from the ground to the top of the hips.
8. Postweaning weight (PWT).
9. Postweaning Average Daily Gain (PADG), which represented average daily gain from time of weaning till postweaning data collection.
10. Lifetime Average Daily Gain (LADG), which represented average daily gain from birth until animals were approximately one year of age.
11. Adjusted Weaning Weight (AWW), adjusted to 205 days, where

$$AWW = [([WW - BW]/WAGE) \times 205] + BW$$

WAGE = weaning age in days
12. 205-Day weaning weight (ACFWW) adjusted to account for age of dam and sex of calf.
13. 365-Day adjusted Weight (APWT) adjusted for age of calf at post-weaning data collection.

$$APWT = [([PWT - WW]/NPWD) \times 160] + AWW$$

NPWD = number of days between weaning and postweaning data collection.

14. Body Volume at weaning (VOL)

$$VOL = \frac{(WHG)^2}{4(3.14)} \times WLENGTH$$

15. Shape Ratio (SRATIO) see Dellmeier et al. (1979)

$$SRATIO = VOL/WHIHT$$

All body and weight measurements were recorded in pounds and inches but were converted to metric units for this analysis. Blood systems found in the UT herd are A, B, C, F-V, J, L, M, R'-S', S and Z and blood serum transferrins.

Variables collected from the VPI herd and used in the analyses were:

1. Birth weight (BW)
2. Life Time Average Daily Gain (LADG); previously described.
3. 205-Day Weaning Weight (ACFWW); previously described.
4. Pre-test Average Daily Gain (PREADG) which represents average daily gain from time of weaning until placed on test ration.
5. Test Average Daily Gain (TADG) which represents daily gain while being fed the test ration.
6. Adjusted Average Daily Gain (AADG), previously described.

Blood typing was conducted by the Texas A & M Immunogenetics Laboratory. Phenogroup codes were provided by Dr. Jerry Caldwell of ImmGen, Incorporated.

In all blood systems, the letter representing the blood group system followed by a zero indicates that the animal does not possess

an antigen within that system (Sanders, 1981). On the other hand, this may represent cases in which reagents capable of detecting an unknown antigen had not been developed. Because blood typing procedures at the time of typing were not always able to ascertain which antigens were present, blanks are found in the data.

Table 1 lists the systems typed for and phenogroups found in the UT Angus herd. The VPI herd systems typed for and phenogroups found are presented in Table 2.

3. METHODS OF ANALYSIS

Analyses of these data were conducted by several procedures. To examine the UT herd for associations among double combinations of blood types within two blood systems and quantitative production traits, analyses of variance were performed on the data to obtain least-squares means. This was accomplished by fitting mathematical models using the general linear models procedure of the Statistical Analysis System (SAS). AADG and ACFWW were considered dependent variables (Y's) in the following model:

$$Y_{ijkl} = \mu + y_i + sy_{ij} + b_k + e_{ijkl}$$

where:

Y_{ijkl} = dependent variable

μ = overall means

y_i = the effect of the i th year

sy_{ij} = the effect of the j th sire in the i th year

TABLE 1

BLOOD GROUP SYSTEM PHENOGROUPS IN ANGUS CATTLE OF THE UT HERD

SYSTEM	CODE	DECODE
A	A1	A
	A2	AH
	A3	D
B	B3	B01(I'')
	B16	B01Y2D'
	B22	B03Y1E'3G'P'Q'G''(I'')
	B39	G2Y2E'1Q'
	B45	01Q'
	B46	01A'(I'')
	B78	I2Y2E'1Y'
	B79	Y1E'3G'Y'G''
	B82	Y2
	B85	E'1
	B89	I'Q'(I')
	B90	E'30'
	B92	A'P'
	B96	O'
	B111	G3TY1A'E'3G'G''(I'')
	B144	01E'3
	B202	I2
	B206	I2E'1
	B233	E'30'G''(I'')
	B296	01E'1P'
	B306	I'
	B307	Q'
	B330	A'
	B331	01(I'')
C	C0	---
	C1	C1
	C2	C1E
	C3	C1EW
	C13	C2(C')
	C14	C2E
	C16	C2EW
	C21	C2W(R2C')
	C22	E
	C23	EW
	C27	W
	C29	WX2

TABLE 1 (Continued)

SYSTEM	CODE	DECODE
	C30	WX2L'
	C32	X2
	C33	X2L'
	C34	C1X2
	C39	C2EWX2
	C45	C1W
	C51	C1EX2
F-V	F1	F
	F2	V
J	J0	---
	J1	J
L	L0	---
	L1	L
M	M0	---
	M1	M1
	M2	M2M'
R'-S'	R1	R'
	R2	S'
S	S0	---
	S1	SH'
	S2	UH'
	S4	U'
	S6	H'
	S12	SH' S''
Z	Z0	---
	Z1	Z
Transferrins	Tf1	A
	Tf2	D
	Tf3	E

TABLE 2

BLOOD GROUP SYSTEM PHENOGROUPS IN ANGUS, SHORTHORN, AND HEREFORD
CATTLE OF THE VPI HERD

SYSTEM	CODE	DECODE
A	A1	A
	A2	AH
	A3	D
B	B0	---
	B3	B01(I'')
	B16	B01Y2D'
	B22	B03Y1E'3G'P'Q'G''(I'')
	B39	G2Y2E'1Q'
	B49	01Q'
	B65	P(I'')
	B68	PI'(I'')
	B79	Y1E'3G'Y'G''
	B80	Y1D'
	B81	Y1D'I'
	B82	Y2
	B85	E'1
	B89	I'Q'(I')
	B90	E'30'
	B91	Q(I'')
	B92	A'P'
	B93	A'O'P'(I'')
	B96	O'
	B104	BG2KA'O'A''(I'')
	B111	G3TY1A'E'3G'G''(I'')
	B144	01E'3
	B164	B
	B235	PQE'1*
	B239	Y1(I'')
	B268	BY1EI'Y*
	B402	BY2P'Y''(I'')
C	C0	---
	C1	C1
	C3	C1EW
	C6	C1RW
	C10	C1R
	C13	C2(C')
	C16	C2EW
	C21	C2W(R2C')
	C22	E

TABLE 2 (continued)

SYSTEM	CODE	DECODE
	C27	W
	C29	WX2
	C31	X1
	C32	X2
F-V	F2	F2
	F4	V
J	J0	---
	J1	J
L	L0	---
	L1	L
M	M0	---
	M1	M1
S	S1	SH'
	S2	UH'
Z	Z0	---
	Z1	Z

b_k = the effect of the kth blood group combination within
blood group system

e_{ijkl} = residual error

The dependent variables (Y's) were PADG, LADG, WHG, WLENGTH, WHIHT, and SRATIO in the model:

$$Y_{ijklmno} = \mu + y_i + sy_{ij} + d_k + x_l + a_m + b_n + e_{ijklmno}$$

where:

$Y_{ijklmno}$ = dependent variable

μ = overall mean

y_i = the effect of the ith year

sy_{ij} = the effect of the jth sire in the ith year

d_k = effect of the kth age of dam

x_l = effect of the lth sex of calf

a_m = the effect of the mth age of calf

b_n = the effect of the nth blood group combination within
blood group system

$e_{ijklmno}$ = residual error

The dependent variable (Y) was APWT in the following model:

$$Y_{ijklmn} = \mu + y_i + sy_{ij} + d_k + x_l + b_m + e_{ijklmn}$$

where:

Y_{ijklmn} = dependent variable

μ = overall means

y_i = the effect of the ith year

sy_{ij} = the effect of the jth sire in the ith year

d_k = the effect of the kth age of calf

x_l = the effect of the lth sex

b_m = the effect of the mth blood group combination within blood group system.

e_{ijklmn} = residual error

Similar models were utilized to analyze data from the VPI herd. For this herd blood types within a system as well as double combinations of blood types within two systems were analyzed to determine associations between blood polymorphisms and quantitative production traits. The dependent variables (Y's) were ACFWW and AADG in the following model:

$$Y_{ijkl} = \mu + y_i + s_j + b_k + e_{ijkl}$$

where: Y_{ijkl} = dependent variable

μ = overall mean

y_i = the effect of the ith calf crop year

s_j = the effect of the jth sire

b_k = the effect of the kth blood group within a system or the effect of the kth blood group combination within a combination of system.

e_{ijkl} = residual error

Dependent variables (Y's) were LADG, PRETADG, and TADG in the model:

$$Y_{ijklmno} = \mu + y_i + s_j + d_k + x_l + a_m + b_n + e_{ijklmno}$$

where:

$Y_{ijklmno}$ = dependent variable

μ = overall mean

y_i = the effect of the ith calf crop year

s_j = the effect of the jth sire

d_k = the effect of the kth age of dam

x_l = the effect of the lth sex

a_m = the effect of the mth age of calf

b_n = the effect of the nth blood type or blood type
combination

$e_{ijklmno}$ = residual error

The variable birth weight (BW) was the dependent variable (Y) in the following model:

$$Y_{ijklmn} = \mu + y_i + s_j + d_k + x_l + b_m + e_{ijklmn}$$

where:

Y_{ijklmn} = dependent variable

μ = overall mean

y_i = the effect of the ith year

s_j = the effect of the jth sire

d_k = the effect of the kth age of dam

x_l = the effect of the lth sex

b_m = the effect of the mth blood type or blood type
combination

e_{ijklmn} = residual error

Blood type combinations that occurred in fewer than five animals were deleted from the analysis to reduce confounding. Age of dam was deleted as a main effect in some models which included the S blood group system, also to reduce confounding. Because of the inadequate typing of some systems, some analyses had fewer than 25 individual calves for analysis. Such analyses were deleted from this study because of extreme confounding. Age of calf was entered in these models and all other models as a covariate because the computer facili-

ties used permitted it and because this variable exhibits great variation in these herds. All other main effects were considered discrete variables. To reduce confounding associated with age of dam, all animals with ages greater than 11 years were deleted.

For the sex-linkage analysis, animals from both herds which were the progeny of parents that differed with respect to blood phenogroups within a system were observed. Sex-linkage is very easy to determine in the heterogametic sex, and, thus, most of the attention given to this analysis was directed to observing blood phenogroups inherited by male calves. Calves and their parents were studied. It is an easy matter to determine from which parent an allele was transmitted, for, as mentioned above, parents differed with respect to their phenogroup composition.

Linkage between the F-V and R'-S' systems was studied in the UT herd by observing progeny of test cross matings and matings involving double heterozygotes. Phenotypes of the resulting progeny were studied to ascertain whether random assortment of the alleles in question was occurring. A phenotypic ratio of 1:1:1:1 among the test cross progeny and a 9:3:3:1 phenotypic ratio of progeny from matings of double heterozygotes would be indicative of independent or random segregation.

To make comparisons between double heterozygotes and homozygotes of the F-V and R'-S' systems in the UT herd, analyses of variance were performed. The same models and variables previously explained were employed in the analyses. Each analysis was done twice, once with the

effect of sire included in the model and again with this effect excluded.

Snedecor and Cochran (1967) described a procedure utilizing a chi-square formula which was used in this study to test for homogeneity of blood phenogroup frequencies within blood group systems of cattle of the VPI herd. The chi-square formula employed was:

$$\chi^2 = [n_i(\bar{p}_i - \bar{p})^2 / \bar{p}\bar{q}]$$

where:

n_i = the total number of blood phenogroups present within a blood system in the i th year

$\bar{p}_i$ = the frequency of the blood phenogroup being tested in the i th year

$\bar{p}$ = the mean frequency (over nine years' time) of the blood group being tested

$\bar{q}$ = the mean frequency (over nine years' time) of all phenogroups within the system not being tested

Such chi-square values with eight degrees of freedom for each blood phenogroup represent a measure of the change in frequency of blood phenogroups over the nine-year period and were used as a measure of random drift of phenogroup frequencies within blood group systems.

The F-V system was chosen in the VPI herd to make a comparison of observed and expected heterozygosis. This system was chosen because, within it, homozygous and heterozygous individuals can readily be recognized. Gene frequencies were determined for each year and from these genotypic frequencies were determined. Frequencies of heterozygotes were adjusted (reduced) according to the average inbreeding by

year and then used to obtain expected numbers. Observed number and calculated expected number were used to derive chi-square values. The standard chi-square formula,

$$\chi^2 = \sum \frac{(O_i - E_i)^2}{E_i},$$

was employed to obtain these values. These chi-square values were based on only one degree of freedom because the expected values were derived from a gene frequency calculated from the blood type data.

CHAPTER IV

LINKAGE STUDIES OF BOVINE BLOOD SYSTEMS

1. SUMMARY

This investigation was conducted to determine whether genes responsible for ten bovine blood type systems and blood serum transferins are sex-linked and secondly to test for autosomal linkage of the F-V and R'-S' blood systems. Cattle from the University of Tennessee Cumberland Plateau Experiment Station and from Virginia Polytechnic Institute and State University Front Royal Herd provided the data for this study.

To determine sex linkage, bull calves were studied as to the transmittance and inheritance of their blood type phenogroups. Special attention was given to bull calves of parents that differed in blood phenogroups of a system.

Progeny of test cross matings and matings of double heterozygotes were studied to determine random assortment or linkage of alleles in the F-V and R'-S' blood systems.

Evidence was found which rules out the possibility of any of the blood and transferrin systems studied being located on the sex chromosome. No conclusion could be reached concerning the possibility of linkage between the F-V and R'-S' systems because of the small number of calves available.

2. INTRODUCTION

Because the number of genes comprising the inheritance in any individual far exceeds the number of chromosomes, it is inevitable that any one chromosome must carry many genes (Hutt, 1979).

Other than in chickens, very little is known concerning the linkage of genes in most livestock species. Due to shorter generation intervals and large numbers of progeny, much more is known of linkage groups in chickens than in all the mammalian species combined. Several investigators have reported on the linkage of blood groups in chickens. At the present time, no genes responsible for fowl blood groups are known to be sex-linked. However, several cases of autosomal linkage have been reported. It was determined by Briles et al. (1967) that the P blood group locus is linked to that for naked neck by 29.1 ± 1.4 map units and that the H blood group locus is linked by 22.1 ± 1.6 map units to the white skin locus. These investigators provided information that suggested linkages of the B, H, P, and J blood group loci. Schierman and Nordskog (1963) reported linkages involving the C and A blood systems. They found the C blood group locus to be linked to the gene for crest with a crossover percentage of 38.9. The A blood group locus was reported linked to the blue plumage color locus with a recombination percent of 33.8. Somes (1970) stated that efforts to confirm these two relationships have been unsuccessful. Briles (1968) found a very close linkage between the A and E blood group and reported a crossover percentage of $.49 \pm .09$.

As late as 1964, Hutt (1964) stated that not a single case of linkage had been incontrovertibly established in mammalian livestock species. However, a few cases had been reported before this time.

All reports of linkage groups in swine have involved blood group loci. Andresen and Baker (1964) determined the C and J blood group loci to be closely linked, having a recombination of 5.3 ± 1.1 percent. Andresen (1966) reported the K blood group locus to be linked with the locus for hematin binding globulins. The H blood group locus was reported to be linked to loci responsible for 6-PGD and the enzyme PHI (Andresen, 1970a; 1970b). Rasmusen (1982) found the H, C, and J blood group loci to be linked very closely. He reported recombination frequencies between H and C and H and J of $.424 \pm .030$ and $.417 \pm .035$, respectively.

In horses, Sandberg (1974) found linkage between the K blood group locus and the 6-PGD locus with an estimated recombination frequency of $.24 \pm .02$.

Few studies have dealt with the linkage of bovine blood group genes. Hines et al. (1981) using sequential probability tests, found evidence of linkage between the A blood group locus and the locus for hemoglobin and between the J blood group and the milk protein B-lactoglobulin loci. Neimann-Sorensen and Robertson (1961) found no evidence of linkage between blood group genes and genes affecting production characters.

Sex-linked genes have been reported in cattle. The gene responsible for streaked hairlessness was reported by Eldridge and Atkeson (1953) to be sex-linked. Based on only three observations

involving male calves, Drieux et al. (1950) concluded that the gene responsible for the syndrome congenital hypotrichosis with anadontia was located on the sex chromosome.

Selection for or against sex-linked genes is an easy matter in the heterogametic sex since a member of that sex carrying the gene will show the trait. If association can be proven to exist between blood types and quantitative production traits, selection for or against specific phenogroups will become important and easier if they are located on the x-chromosome.

Data from cattle in two herds, the University of Tennessee Cumberland Plateau Experiment Station Angus herd (UT herd) and the Virginia Polytechnic Institute and State University Front Royal herd (VPI herd) consisting of Angus, Shorthorn, and Hereford cattle, were used in this study. The first objective was to determine if genes responsible for the A, B, C, F-V, J, L, M, R'-S', S, Z, and transfer-rin blood systems are located on the sex chromosome. A second objective was to determine if the loci responsible for the F-V and R'-S' systems are linked. These two systems were chosen because, within them, heterozygotes are easily recognized. Due to the fact that the R'-S' system was not typed for in the VPI herd, only animals of the UT Angus herd were used in analyses involving this system.

3. EXPERIMENTAL PROCEDURES

Combining the data from both herds resulted in a total of 2464 animals available for the sex-linkage analysis. The procedure for finding evidence of sex-linkage centered around observing progeny

resulting from mating of individuals differing with respect to blood phenogroups. Such observation allowed for determination from which parent the allele or alleles found in the progeny came. If sex-linkage is evident, male calves would receive only one allele for a system, which would be transmitted by the dam to the male calf. Thus, sex-linked inheritance can easily be dismissed if two alleles are present in males, for this would indicate that the sire contributed an allele. Female calves, because they receive two x-chromosomes, carry two alleles whether sex-linkage exists or not.

Procedures for determining linkage between the F-V and R'-S' systems consisted of observing progeny resulting from test cross matings and of matings of double heterozygotes. Both observations relied upon determining if random assortment of the alleles in question was occurring. Test cross progeny, if found in a 1:1:1:1 phenotypic ratio, would indicate that loci responsible for the two systems are not located on the same chromosome or, if so, are so far apart that they segregate independently. A deviation from this ratio in favor of certain phenotypes would be indicative of linkage. Progeny of matings involving double heterozygotes indicate independent segregation at the two loci if the classical 9:3:3:1 phenotypic ratio is observed. It should be remembered that close linkage prevents random assortment because genes at closely linked loci cannot segregate independently of one another.

4. RESULTS AND DISCUSSION

No evidence of sex-linkage was found. Table 3, which contains only one example for each system, exemplifies the findings. It can be seen that bull calves as well as their sires do carry two phenogroups for each of the polymorphic systems. Furthermore, it can be seen that one allele was transmitted to the calf by the dam and one by the sire. From these results, it was concluded that genes responsible for cattle blood systems are not located on the sex chromosome.

After determining that blood type genes were not located on the sex chromosome, an attempt was made to determine if linkage exists between the F-V and R'-S' systems. These two systems lend themselves well to test crosses because of lack of complete dominance, within them homozygotes and heterozygotes being readily recognized.

Four test crosses were theoretically possible. However, due to incomplete typing of these two systems, only two of the possible crosses resulted in progeny for observation. Nine progeny resulted from the matings involving FFSS x FVRS individuals. Only one calf resulted from VVSS x FVRS matings. Thus a total of only ten animals were available for determining random assortment or linkage of loci.

As can be seen from Table 4 a 1:1:1:1 phenotypic ratio was not obtained from the mating of FFSS and FVRS animals as two phenotypes, FFRS and FVSS, predominated. However, reaching a conclusion based on such a small sample is difficult if not ill-advised. Thus, it was decided to approach the problem from another angle, to observe the progeny obtained from matings of double heterozygotes.

TABLE 3

EVIDENCE DISPROVING SEX LINKAGE OF GENES RESPONSIBLE FOR
BOVINE BLOOD SYSTEMS

Blood System	Sire Blood Type†		Dam Blood Type†		Male Calf Blood Type†	
	Allele A	Allele B	Allele A	Allele B	Allele A	Allele B
A	1	3	3	3	3	3
B	16	45	206	233	16	206
C	3	2	2	32	3	32
F-V	1	1	1	4	1	4
J	0	0	1	0	1	0
L	0	0	1	0	0	0
M	0	0	1	0	1	0
R'-S'	1	2	1	2	2	2
S	0	0	6	0	6	0
Z	1	0	0	0	1	0
Tf	2	2	1	1	1	2

† See Tables 1 and 2 (pages 28-31) for decodings of blood types.

TABLE 4

RESULTS OF FFSS X FVRS TEST CROSS TO DETERMINE SEX LINKAGE

Possible Phenotype	Number of Progeny	Frequency of Phenotypes
FFRS	4	.444
FFSS	1	.111
FVRS	0	.000
FVSS	4	.444

If independent segregation of alleles at the two loci occurs, a 9:3:3:1 phenotypic ratio of the progeny would be expected from the mating of double heterozygotes. The minimum number of progeny to make this test is 16. Unfortunately, in this study, only five calves resulting from such matings had been completely typed for both systems. Three of the five had the blood type VVSS, and the other two calves were typed FVRS and VVRS. Unfortunately, no conclusion can be drawn from these data. Thus, the question of linkage between the F-V and R'-S' system remains unanswered.

It is often asked why knowledge of linkage groups or relationships is important. The answer is, for the most part, academic in nature. Hines et al. (1981) stated that it is desirable to identify occurrences of chromosomal linkage or of other genetic interrelationships and to determine chromosomal arrangement of or the nature of genetic interaction because such determinations provide a better understanding of the genetic composition of cattle. Chromosomal linkages are especially important to those using genetic markers for parentage verification or estimation of phylogenetic relationships (Hines et al., 1981). Using Monte Carlo computer techniques, Gill and Glemmer (1966) studied the effects of linkage on the degree of inbreeding. They reported that all populations with linkage increased in mean level of inbreeding more rapidly than populations without linkage. These researchers concluded that linkage can cause considerable bias in estimates of the degree of inbreeding.

A practical use could be made of linkage if genes responsible for production traits are found to be closely linked with blood type genes. Knowledge of such linkage would be of some assistance in selection.

5. CONCLUSIONS

It can be concluded from the results of this study that the genes responsible for the A, B, C, F-V, J, L, M, R'-S', Z, and S bovine blood system and the transferrin system are not located on the sex chromosome. However, linkage or independent segregation of the alleles responsible for the F-V and R'-S' system could not be ascertained from the small number of calves available for study. Because so little is known of linkage groups in cattle, further work of this type is suggested and needed. For example, testing for possible linkage between genes responsible for coat color in Shorthorn cattle and blood systems could easily be completed. Unfortunately, information concerning coat colors of the VPI Shorthorns was not available for this study.

CHAPTER V

HETEROZYGOSITY OF THE F-V AND R'-S' BOVINE BLOOD SYSTEMS

1. SUMMARY

Cattle from the University of Tennessee Cumberland Plateau Experiment Station Angus herd were studied to determine differences between double homozygotes and heterozygotes at the F-V and R'-S' blood systems with respect to ten quantitative production traits and to ascertain the effects which confounding of sire effects and blood type effects had on results of analyses.

In almost every case heterozygotes had greater least-squares means of production traits than did homozygotes, which suggests that associations could exist between blood type heterozygosity and superiority in quantitative production variables. Evidence was found which indicates that extreme confounding of sire effects and blood type effects can and does exist. Statistical models excluding the effect of sire revealed numerous significant differences between blood type homozygosity and heterozygosity for production traits. Models including sire effect revealed far fewer significant differences, indicating that such confounding can greatly affect the outcome of such analyses.

2. INTRODUCTION

Numerous papers have been published on the subject of heterosis or, more commonly, hybrid vigor. Yet much remains to be learned in

order to understand and explain this phenomenon. W. E. Briles has written extensively on the heterozygosity of the B blood system of chickens. Briles et al. (1953) found in two of three inbred lines that male chicks heterozygous for the B blood group alleles were significantly heavier at nine weeks of age than homozygotes. Briles and Krueger (1955) reported significantly higher hatchability values for heterozygotes. Briles (1956), investigating hen-day production in two lines of inbred White Leghorns, reported that females heterozygous for the B blood group system consistently outlaid homozygous females.

Conneally (1962) investigating the Z blood system of cattle found Z/z heterozygotes to excel significantly homozygous z/z cows with respect to milk yield, fat yield, and percent butterfat. Sanders (1981) reported statistical differences between homozygous and heterozygous individuals in the S, Z, and M systems with respect to various production traits in Angus cattle. In all cases, heterozygotes had greater values than homozygotes. Hutt (1964) in discussing heterosis, stated that few examples are known in which heterozygosity at one locus increases vigor more than homozygosity at the locus.

This investigation tested for differences between combinations of double homozygotes and heterozygotes of the F-V and R'-S' bovine systems with respect to ten quantitative production variables and determined the extent of inherent confounding of sire effects and blood type effects. Cattle of the University of Tennessee Cumberland Plateau Experiment Station Angus herd provided the data for this study.

3. EXPERIMENTAL PROCEDURES

Analyses of variance, performed on the data to obtain least-squares means, were used to test for differences between combinations of double homozygotes and heterozygotes. The general linear models procedure of the Statistical Analysis System (SAS) was employed to analyze the data using appropriate models. Adjusted average daily gain (AADG), representing average daily gain from birth to weaning and adjusted for age of dam and sex of calf, and 205-day weaning weight (ACFWW) also adjusted for age of dam and sex of calf, were considered dependent variables (Y's) in the following model:

$$Y_{ijkl} = \mu + y_i + sy_{ij} + b_k + e_{ijkl}$$

where:

Y_{ijkl} = the dependent variable

μ = overall mean

y_i = the effect of the i th year

sy_{ij} = the effect of the j th sire in the i th year

b_k = the effect of the k th F-V, R'-S' blood group combination

e_{ijkl} = residual error

Postweaning average daily gain (PADG), lifetime average daily gain (LADG), heart girth measured at weaning (WHG), hip width at weaning (HIWTH), hip height measured at weaning (WHIHT), body length at weaning (WLENGTH) and shape ratio (SRATIO) were considered dependent variables (Y's) in the model:

$$Y_{ijklmno} = \mu + y_i + sy_{ij} + d_k + x_l + a_m + b_n + e_{ijklmno}$$

where:

$Y_{ijklmno}$ = dependent variable

μ = overall mean

y_i = the effect of the i th year

sy_{ij} = the effect of the j th sire in the i th year

d_k = the effect of the k th age of dam

x_l = the effect of the l th sex of calf

a_m = the effect of the m th age of calf

b_n = the effect of the n th F-V, R'-S' blood group combination

$e_{ijklmno}$ = residual error

Shape ratio was described by Dellmeier et al. (1979). Post-weaning average daily gain represents average daily gain from time of weaning until post weaning data collection. Lifetime average daily gain represents average daily gain to one year of age. Body length at weaning was measured as the distance from the midpoint of the scapula to a line connecting the posterior prominences of the pin bones.

Three-hundred-sixty-five-day adjusted weight (APWT) (adjusted for age of calf) was the dependent variable (Y) in the following model:

$$Y_{ijklmn} = \mu + y_i + sy_{ij} + d_k + x_l + b_m + e_{ijklmn}$$

where:

Y_{ijklmn} = the dependent variable

μ = overall mean

y_i = the effect of the i th year

sy_{ij} = the effect of the j th sire in the i th year

d_k = the effect of the k th age of dam

x_1 = the effect of the 1th sex of calf

b_n = the effect of the nth F-V, R'-S' blood type
combination

e_{ijklmn} = residual error

Age of calf was entered as a covariate; all other main effects were considered discrete variables. Each dependent variable was analyzed twice, once with sire effect in the model and once with the effect of sire deleted from the model. This was done to determine the effects of confounding of sire effect and blood type effect.

4. RESULTS AND DISCUSSION

It is interesting that Briles nowhere in his papers discussed the mathematical models used to perform his analyses. During personal communication with Dr. Robert Shrode, Professor of Animal Science at the University of Tennessee, who worked with Dr. Briles while at DeKalb, it was mentioned that Dr. Briles did not take into account the effect of sire in his models. Such an omission can produce erroneous conclusions because of extreme confounding as a consequence of unequal representation of the various blood types in sire progeny groups. As a result, it is conceivable that most of the effects Briles attributed to blood type may in reality be due to sire differences. By fitting each dependent variable to models with the effect of sire included and excluded it should be possible to demonstrate how such confounding can affect the results of the analyses.

Two possible homozygous combinations R1/R1/F1/F1 and R1/R1/F4/F4 were not available for analysis due to the inability to accurately

determine phenogroups present. Least-squares means and standard errors of the production traits studied are presented in Tables 5 and 6. It can be seen from these results that, in almost every case, higher values were associated with the heterozygous blood type. In the analyses with the effect of sire removed from the model, numerous significant differences exist between the least-squares means of homozygotes and heterozygotes. In the production traits SRATIO and WHG, heterozygotes significantly excelled both homozygotes. In SRATIO, significant differences ($P < .04$ and $P < .10$) were found between heterozygotes and R2/R2/F1/F1 and R2/R2/F4/F4 homozygotes, respectively. Heart girth measurements at weaning were significantly larger ($P < .05$) in heterozygotes than in either homozygote. Heterozygotes gained significantly more during the periods of time represented by PADG ($P < .007$), LADG ($P < .002$) and had greater ($P < .002$) APWT than R2/R2/F1/F1 homozygotes but did not differ significantly from the R2/R2/F4/F4 homozygotes.

Only one analysis which included sire effect in the model revealed heterozygotes to excel homozygotes significantly. In HIHT, heterozygotes were found to be significantly higher than R2/R2/F1/F1 ($P < .10$) and R2/R2/F4/F4 ($P < .09$) homozygotes.

The number of cases of significant differences in the two separate groups of analyses is striking. The only difference between the two analyses was the presence or absence of the effect of sire. These results indicate that confounding of sire effects and blood group effects can be appreciable and should be considered in such analyses. To determine accurately the effect of blood type on quanti-

TABLE 5

LEAST-SQUARES MEANS AND STANDARD ERRORS OF PRODUCTION TRAITS IN UT
ANGUS HETEROZYGOTES AND HOMOZYGOTES IN THE F-V AND R'-S' BLOOD
GROUP SYSTEMS
(SIRE EFFECTS DELETED FROM ANALYSIS)

Traits°	Blood Types†		
	R2/R2/F1/F1	R2/R2/F4/F4	R1/R2/F1/F4
SRATIO	1450.568 ± 18.346	1425.025 ± 37.932	1491.155 ⁺⁺⁺ ± 22.231
WHG (cm)	137.238 ± .954	135.843 ± 1.669	139.066 ⁺⁺⁺ ± 1.081
WLENGTH (cm)	94.296 ± .679	93.702 ± 1.188	95.411 ⁺⁺ ± .769
HIWTH (cm)	36.301 ± .913	35.304 ± 1.598	36.450 ± 1.035
WHIHT (cm)	98.559 ± .472	97.631 ± .997	99.772 ± .573
PADG (kg)	.537 ± .025	.564 ± .044	.595 ⁺⁺ ± .028
LADG (kg)	.687 ± .015	.693 ± .026	.727 ⁺⁺ ± .017
AADG (kg)	.889 ± .021	.887 ± .066	.889 ± .028
ACFWW (kg)	202.635 ± 2.083	204.223 ± 6.547	200.547 ± 2.808

TABLE 5 (continued)

Traits [°]	Blood Types [†]		
	R2/R2/F1/F1	R2/R2/F4/F4	R1/R2/F1/F4
APWT (kg)	278.851 ± 5.678	280.122 ± 9.931	290.848 ⁺⁺ ± 6.389

⁺ Significantly different from the R2/R2/F1/F1 homozygous blood type

⁺⁺ Significantly different from both homozygous blood types

* P < .10

** P < .01

[°] For explanation of traits, see pages

[†] See Tables 1 and 2 (pages 28-31) for decodings of blood types.

TABLE 6

LEAST-SQUARES MEANS AND STANDARD ERRORS OF PRODUCTION TRAITS IN UT
ANGUS HETEROZYGOTES AND HOMOZYGOTES IN THE F-V AND R'-S' BLOOD
GROUP SYSTEMS
(SIRE EFFECTS INCLUDED IN ANALYSIS)

Traits°	BLOOD TYPEST		
	R2/R2/F1/F1	R2/R2/F4/F4	R1/R2/F1/F4
SRATIO	1486.592 + 20.342	1460.430 + 43.443	1495.531 + 24.044
WHG (cm)	138.021 + .835	136.571 + 1.795	138.407 + .991
WLENGTH (cm)	95.351 + .606	94.757 + 1.303	96.320 + .719
HIWTH (cm)	36.129 + .913	35.977 + 1.962	36.706 + 1.082
WHIHT (cm)	98.348 + .529	97.331 + 1.129	99.347 ^{++*} + .625
PADG (kg)	.566 + .023	.552 + .050	.608 + .028
LADG (kg)	.717 + .013	.704 + .028	.735 + .0155
AADG (kg)	.898 + .024	.895 + .071	.903 + .031
ACFWW (kg)	204.345 + 2.434	203.975 + 7.203	205.022 + 3.163

TABLE 6 (continued)

Traits [°]	BLOOD TYPES†		
	R2/R2/F1/F1	R2/R2/F4/F4	R1/R2/F1/F4
APWT (kg)	286.693	283.266	292.511
	<u>±</u> 5.069	<u>±</u> 10.845	<u>±</u> 5.954

++ Significantly different from both homozygous blood types

* $P < .10$

° For explanation of traits, see pages

† See Tables 1 and 2 (pages 28-31) for decodings of blood types.

tative production traits, sire effect must be included in the models because of this genetic confounding of sire effect and blood type effect.

It appears that heterozygotes are superior to homozygotes, for, in almost every case, heterozygosis was associated with higher values. Such findings are common and have been reported by many researchers. However, when effects of sire are included in the analysis, the majority of these differences are not statistically significant.

5. CONCLUSIONS

The results of this study indicate that double heterozygotes for the F-V and R'-S' blood systems combinations were superior to homozygotes even though most differences, when the effect of sire was included in the model, were not statistically significant. The findings also reveal the dangers of ignoring confounding of main effects.

CHAPTER VI

CHANGES IN FREQUENCY OF BOVINE BLOOD GROUP GENES:

A CASE OF RANDOM DRIFT

1. SUMMARY

Several instances of considerable random drift were observed in a population consisting of Angus, Shorthorn, and Hereford cattle. Chi-square tests for homogeneity among yearly frequencies of blood phenogroups of nine blood systems over a nine-year period revealed significant ($P < .05$ or $P < .01$) differences between years in gene frequencies in several phenogroups. A decreasing trend in the frequency of blood phenogroup Yl(I") and an increasing trend in the frequency of phenogroup J were observed in the Hereford segment of the population. Only one trend, one of reducing frequency of the phenogroup BYlEl'Y* was observed in the Shorthorn segment. No frequency trends were observed in the Angus portion of the population.

2. INTRODUCTION

Gene frequencies of blood type genes in cattle have become very important to breed associations. Many breed associations have enacted blood type rules excluding animals possessing nontraditional phenogroups. Hines (1978), in discussing such rules, pointed out that non-traditional blood phenogroups of a breed should be those having frequencies no greater than .0001.

Methods are now available for using gene frequency data to determine probable evolutionary histories of populations (Kidd et al., 1972). Blood groups of cattle and other species are well suited for such investigations.

Several researchers have reported on blood phenogroup frequencies in various cattle breeds (Dabczewski, 1969; Miller, 1966; Sanders, 1981). Such studies are important for the uses mentioned above.

Studies of blood type frequencies may be undertaken also by population geneticists. Random drift is a force known to affect gene frequencies, especially in small populations which lend themselves well to such genetic investigations. Gene frequencies can be of importance in demonstrating effects of inbreeding, outcrossing, etc.

This investigation was undertaken to determine gene frequencies by calf crop year in the Virginia Polytechnic Institute and State University Front Royal herd which consisted of Angus, Shorthorn, and Hereford cattle. Extreme changes from year to year probably resulted from random drift.

3. EXPERIMENTAL PROCEDURES

Gene frequencies in phenogroups of the A, B, C, F-V, J, L, M, S, and Z blood systems were determined for the years 1963-1971. To test for homogeneity among the frequencies over nine years' time, a chi-square procedure discussed by Snedecor and Cochran (1967) was used. The chi-square formula used was:

$$\chi^2 = \sum [n_i(\bar{p}_i - \bar{p})^2 / \bar{p}\bar{q}]$$

n_i = total number of blood phenogroups present within a blood group system in the i th year.

$\bar{p}_i$ = frequency of the blood phenogroups tested in the i th year

$\bar{p}$ = mean frequency of the blood group being tested over the nine years' time.

$\bar{q}$ = mean frequency of all blood phenogroups within a system not being tested over the nine years' time

The resulting chi-square values had eight degrees of freedom for each phenogroup frequency over the nine-year period. These values were used as a measure of random drift of the blood phenogroup frequencies over time.

4. RESULTS AND DISCUSSION

Presented in Tables A-1, A-2, and A-3 (Appendix), are the frequencies of blood type phenotypes over the nine-year period. It can be seen that random drift was more pronounced in the Angus and Shorthorns, with eleven and ten phenogroups, respectively, having significant chi-square values ($P < .05$ or $P < .01$). While erratic fluctuations occurred, a decreasing frequency of the phenogroup BYLEI'Y* was observed in the Shorthorn subpopulation. No increasing trends were obvious.

The reason the Hereford segment of the population had fewer significant changes in gene frequencies is not clear. It was originally thought that this segment of the herd would have as many if not more significant changes in phenogroup frequencies because Herefords made up the smallest portion of the population. The frequency of the

gene responsible for the phenogroup Yl(I'') was observed to be decreasing, and the gene eventually disappeared from this segment of the population while the phenogroup J appears to have increased in frequency.

Sanders (1981) reported numerous cases of random drift in an Angus herd over a ten-year period. Studying blood phenogroup frequencies, she reported significant chi-square values comparable to those calculated here for phenogroup frequencies in every system studied except the L system. She noticed a decreasing trend in the frequency of the S1 blood group of the S system. The present investigation, while not showing drastic changes in as many systems, nevertheless, illustrates once again that gene frequencies in small populations are subject to random drift.

In small populations, genes having low frequencies are especially affected by random drift. Such genes may more easily be deleted from the gene pool simply by not being transmitted to members of the next generation. In bovine blood systems, such situations may be encountered more often in the larger allelic blood systems. The large number of alleles makes for lower frequencies of individual alleles.

Selection can, of course, cause changes in gene frequencies. At present, blood phenogroups are not deliberately or consciously subjected to direct selection. However, their frequencies can be indirectly affected if they are linked or associated with the traits which are considered in the selection of breeding stock.

5. CONCLUSIONS

Fluctuations in blood phenogroup frequencies occurred in all blood systems studied. Significant chi-square values were found for eleven, ten, and three phenogroups within six of nine blood systems studied in Angus, Shorthorn, and Hereford, respectively. Only two decreasing trends and one increasing trend were observed in blood phenogroup frequencies. These findings illustrate that random drift can significantly change gene frequencies in small populations.

CHAPTER VII

ASSOCIATIONS BETWEEN PRODUCTION TRAITS AND BLOOD POLYMORPHISM
SYSTEMS AND TYPES IN THREE BEEF BREEDS

1. SUMMARY

This investigation sought to determine associations between production traits and blood system genes in beef cattle. Animals of the UT Angus herd and the VPI Front Royal herd of Shorthorns, Angus, and Herefords were used. Analyses of variance were performed to obtain least-squares means of production traits for comparisons among blood types.

Two approaches were taken in these analyses: (1) to analyze each system separately for association between production traits and blood phenogroups in the VPI herd and (2) to examine both the UT herd and VPI herd data for association between production traits and combinations of blood type systems. Analyses involving combinations of two blood type systems showed numerously more associations than analyses of systems separately. This is thought to be due to more blood type genes being present in these analyses for possible linkage with genes influencing production traits.

In the VPI herd data, the J and Z systems were found more often in associations than any of the other systems, with the phenotypes Z0/Z0 and J0/J1 occurring most frequently. The Transferrin system and the R'-S' and F-V blood systems were involved in the majority of associations in the UT herd.

2. INTRODUCTION

Numerous researchers have searched for relationships between blood types of livestock species and production traits (Rendel, 1961; Rausch et al., 1968; Brum et al., 1968; Sanders, 1981). The majority of this work has been with dairy breeds as investigators sought to determine associations of blood phenogroups with milk and butterfat production. Much of the research with dairy cattle has been concerned with the B system alleles BO_1Y_2D' , with conflicting results being reported. This one blood system phenogroup has been given more attention than any other in beef breeds as well.

The blood serum transferrin system also has been studied for possible associations with production traits (Brum et al., 1968; Kiddy et al., 1975; Makarechian and Howell, 1967).

If associations can be confirmed, whatever the basic cause of them, blood systems could become useful in selection to improve certain production traits. Another benefit to be gained from such studies is information concerning linkage of genes for blood systems and production traits. As genetic engineering is advanced in farm animal species, it will be important to know the location of various genes.

In this study, the relationships between blood types of the A, B, C, F-V, J, L, M, R'-S' and Z blood systems and the blood transferrin system were investigated. Data for this investigation were collected from two herds, the University of Tennessee Cumberland Plateau Experiment Station Angus herd (UT herd) from 1970 to 1979, and the

Virginia Polytechnic Institute and State University Front Royal herd (VPI herd), which consisted of three breeds, Angus, Shorthorn, and Hereford, from 1962 to 1969.

3. EXPERIMENTAL PROCEDURES

Blood systems typed in the VPI herd were the A, B, C, F-V, J, L, M, S, and Z systems. Analyses of data from this herd sought first to determine associations between cattle blood types within a blood group system and production traits and secondly to look for associations between double combinations of blood types in two blood group systems.

Systems typed in the UT herd were the A, B, C, F-V, J, L, M, R'-S', S, and Z as well as the transferrin system. Analysis of data from this herd sought to determine if associations of production traits and combinations of blood types within two systems exist. Sanders (1981) had previously analyzed these data for associations between blood types within a particular system and production traits.

Analyses to test for associations consisted of analyses of variance performed on the data to obtain least-squares means. This was accomplished by fitting standard models using the general linear models procedure of the Statistical Analysis System (SAS). Analyses consisting of fewer than twenty-five observations were not completed due to extreme confounding. All blood types or blood type combinations occurring in fewer than five animals were deleted from the analysis, and all dams older than eleven years were deleted to reduce confounding. Production variables measured and the models used in

their analyses have been described previously and will not be repeated here.

4. RESULTS AND DISCUSSION

Because of the smaller numbers of Herefords in the VPI herd and the lack of complete or adequate typing of all blood systems, fewer of the systems were analyzed for associations with production traits. When systems were combined to form combinations of blood types in two systems, the number of individuals available for these tests was greatly reduced. This is due to the fact that cattle differ greatly in their blood type composition. Stormont (1967) estimated that nearly two trillion blood types are possible. Such severe reduction of numbers occurred in the Hereford data that no attempt to analyze for associations between production traits and double combinations of blood types was undertaken. Determination of associations between production traits and blood types within system will be discussed first.

Only three systems, the F, J, and Z, contained sufficient numbers of Herefords for analysis. No clear-cut cases of association were found. However, in the Z system, cases of approaches to significant association with production traits, BWT ($P < .11$); TADG ($P < .14$), ACFWW ($P < .14$) and AADG ($P < .19$) were found.

The Shorthorn data revealed associations of the Z and J systems with the production traits, ACFWW ($P < .03$) and AADG ($Z P < .03$; $J P < .02$). The Z system was found associated also with LADG ($P < .02$) and TADG ($P < .02$). The Z system, as previously mentioned, approached a

significant association with ACFWW, AADG, and TADG in the Hereford data. Interestingly, the Z system approached significant association also with ACFWW ($P < .20$) and AADG ($P < .16$) in the Angus data.

In the Angus data, the A system was found to have an association with PREADG ($P < .09$) and the B system with ACFWW ($P < .01$) and AADG ($P < .02$). The A system in Shorthorns was found not to be associated with these production traits; however, the B system approached a significant association with AADG ($P < .19$).

Ranges of least-squares means of these production traits and the blood type of the associated system having the highest value are presented in Table 7.

To the best of the author's knowledge, this study is the first to report on the effect of combinations of phenogroups of more than one system.

Blood systems found to have associations in analyses involving blood type combinations of two systems were generally the same as those reported previously in single system analyses. In the Angus data, the A, B, J, and Z systems were again found to be of importance (Table A-4, Appendix). The Shorthorn data revealed the J and Z systems to be included in all but one of the double-system combinations shown to have associations with production traits (Table A-5, Appendix). The J and Z systems' repeated significant association in these analyses is of great interest.

Other investigators have found associations of production traits with these two systems. Mishra et al. (1974) reported Indian cattle possessing the J gene to be superior in performance with respect to

TABLE 7

RANGES OF LEAST-SQUARES MEANS OF QUANTITATIVE PRODUCTION TRAITS IN THE
VPI HERD BY BLOOD SYSTEMS HAVING AN ASSOCIATION

Breed	Blood System	Trait ^o	Number of Animals	Range of L.S. Means	Blood Type† with Highest Value
A	A	PREADG	117	.7990-.8333 ⁺⁺	A1/A3
A	B	ACFWW	99	177.7427-245.9172 ^{**}	B0/B85
A	B	AADG	99	.7405-1.0328 ^{**}	B0/B85
S	J	ACFWW	212	191.5441-204.1137 [*]	J0/J1
S	J	AADG	212	.7753-.8390 [*]	J0/J1
S	Z	ACFWW	200	165.4527-195.4644 ^{**}	Z0/Z0
S	Z	AADG	200	.6534-.7947 ^{**}	Z0/Z0
S	Z	LADG	169	.8432-.9069 ⁺	Z0/Z0
S	Z	TADG	169	.9401-1.0227 ^{**}	Z0/Z0

Probability that highest L.S. mean = lowest L.S. mean

⁺ $P < .15$

⁺⁺ $P < .10$

^{*} $.01 < P < .05$

^{**} $P < .01$

^o These traits are measured in kilograms; for explanation of traits see page 26.

† See Tables 1 and 2 (pages 28-31) for decodings of blood types.

economic traits to those lacking it. Rendel (1961) found in Swedish cattle that the J1 allele had an effect of increasing milk fat percentage. Sanders (1981) reported significant differences among least-squares means of weaning length of calves of different types in the J system. J0/J1 animals were significantly longer than J0/J0 animals. These findings agree with the findings of the present study as the J0/J1 phenogroup was associated here with the highest least-square means of production traits. Significant differences were found by Sanders (1981) between blood types within the Z system with respect to adjusted weaning weight. She reported Z0/Z0 animals to weigh significantly less than Z1/Z0 cattle or Z1/Z1 cattle, which differs from the findings of the present study in which Z0/Z0 animals repeatedly had higher values for production traits.

It is often asked how so few genes as those carried by an animal for a blood system or even double combinations of systems can have an effect on quantitative production traits, for it is known that genetic variation in quantitative production traits results from segregation of genes at many loci. The most likely explanations for relationships between blood types and production traits are pleiotrophic gene action, somal linkage or the possibility that the antigenic substances occur also in tissues other than blood and have a physiological function (Oosterlee, 1964; Brum et al., 1968; Rausch et al., 1968). In discussing these possible explanations, Rausch et al. (1968) suggested that if the relationships were the result of pleiotrophy, they would probably occur whenever the gene is present in any breed. However, if the relationships are the result of linkage, it would not

necessarily be expected that the same relationships would be present in cattle of different genetic origin (Rausch et al., 1968).

Of these possible explanations for the associations, it seems to this investigator that the most plausible is that of linkage. A possible situation is that a blood system gene is closely linked to a linkage group of genes influencing a production trait.

Results in the UT Angus herd analyses are presented in Table A-6 (Appendix). The transferrin system was the system most frequently found in combinations of blood polymorphisms having associations with production traits. The transferrin system was followed in frequency by the R'-S' and F-V systems.

Transferrins have been investigated extensively in dairy cattle (Kiddy et al., 1975; Mather, 1977; Brum et al., 1968; Hargrove et al., 1980). Conflicting results have been obtained concerning relationships between transferrin types and production traits. Tf^A was reported by Mather (1977), Brum et al. (1968), and Young and Hunter (1966) to be superior to Tf^D with respect to apparent favorable influence on various production traits. On the other hand, Kiddy et al. (1975) found Tf^D to be superior to Tf^A in apparent favorable effect on milk yield in Holsteins. Ashton (1960) reported Tf^{DD} superior to Tf^{AA} so far as apparent favorable effect on milk production is concerned.

Working with feedlot Hereford steers, Markarechian and Howell (1967) studied feedlot gain and carcass trait association with transferrins. No significant associations were found. Tf^{DE} calves were found by Sanders (1981) to gain significantly less than Tf^{DD} animals and Tf^{AD} animals. In the present study, Tf^{EE} animals and Tf^{DD} animals

were the most prevalent transferrin types found in significant association with gains. The finding of Tf^{EE} in combinations of blood types with highest least-squares means of production traits is of interest because there seems to be general agreement among the studies reported above that Tf^E is the least preferred of the transferrin alleles.

Hargrove et al. (1980) found the F-V blood system associated with reproductive performance in Holstein cattle. Salerno (1964) reported finding significant differences in the F-V system with respect to weight gains in cattle from birth to two years of age weighed at six-month intervals.

To the best of the author's knowledge, this is the first study to report the R'-S' system to be found in blood and production trait associations. Sanders (1981) did not find this system to be associated with production traits in her study of the same UT Angus herd. It should be kept in mind, however, that her analyses were of differences among phenogroups of a particular system and that the findings reported here are concerned with combinations of blood types between two systems.

R1/R2 and R2/R2 phenotypes were about equally represented in associations discovered. It must be pointed out, however, that the phenotype R1/R1 had a lower frequency in this herd than R1/R2 and R2/R2 and that when this system was combined with others, this phenotype was deleted from most analyses.

From Tables 7, A-4, and A-5 (Appendix) it can be seen that in the VPI herd, more significant associations were found when systems were combined than when they were tested singly for association. This is

believed to be due to the fact that more genes are involved. If chromosomal linkage is partially responsible for such association, then it can be concluded logically that in systems-combinations studies, more genes are available to be linked to a gene or group of genes having an influence on production traits.

5. CONCLUSIONS

In the VPI herd, the J and Z systems were found in the majority of significant associations with production traits. Z0/Z0 and J0/J1 phenotypes were associated with more of the highest least-squares means of production traits than any other possible phenogroup combinations within either of the systems. When the two groups of analyses, within a system and combinations of two systems, were compared, many more significant associations were found in the analyses involving combinations of two systems.

The transferrin system and the R'-S' and F-V blood group systems were found in the majority of combinations of blood phenogroups found significantly associated with production traits in the UT herd.

These findings involving the R'-S' system are believed to be the first to reveal associations between production traits and this system.

CHAPTER VIII

COMPARISON OF OBSERVED AND EXPECTED HETEROZYGOSIS OF THE F-V BLOOD
TYPE SYSTEM IN A HERD CONSISTING OF THREE BEEF BREEDS

1. SUMMARY

Chi-square values were derived to identify significant differences between observed and expected values of heterozygosis in the three beef breeds of the VPI herd. The Angus portion of the herd had significantly different values ($P < .05$ or $P < .005$) in three of the seven years investigated, with observed values being higher than expected values. The Hereford portion had significantly different values ($P < .05$) in only one year as the expected value was significantly higher than the observed number. No significant differences were found in the Shorthorn segment of the population. It is believed that the amount of inbreeding in this herd was not sufficient to reduce heterozygosis appreciably.

2. INTRODUCTION

Inbreeding is known to reduce heterozygosis in allelic systems. Studies illustrating such effects on blood group genotypes have been reported by Larsen et al. (1974) and Briles et al. (1957). Larsen et al. (1974) reported that cattle isolated on the Isle of Jersey had a higher degree of homozygosity within the B and C blood systems than did their Danish descendants. Briles et al. (1957) found that the degree of inbreeding affects the number of B blood group alleles

present in chickens. These researchers found inbred lines of Leghorns having average inbreeding coefficients greater than .65 to possess uniformly two alleles while lines having average inbreeding coefficients of .65 or less possessed three to eight alleles.

This study was undertaken to make a comparison of observed and expected heterozygosis of the F-V blood system in cattle of the VPI herd from 1963 to 1969.

3. EXPERIMENTAL PROCEDURES

Gene frequencies within each of the three breeds were determined by year. Assuming random mating, heterozygosis was calculated from the gene frequencies. The heterozygosis was adjusted (reduced) by the mean inbreeding coefficient in each year and then used to obtain expected number of heterozygotes. Chi-square values were obtained using the standard formula and were based on only one degree of freedom as the expected numbers were obtained from a gene frequency calculated from the data.

4. RESULTS AND DISCUSSION

In the Angus segment of the herd, observed heterozygosis was greater than the expected value in every year. Significant differences were found between observed and expected values in 1966, 1967, and 1969 (Table 8). Interestingly, these were the years associated with the highest average inbreeding coefficients, .2139, .2062, and .3410, respectively. This may represent a situation in which heterozygotes are being favored by natural selection or possibly close

TABLE 8

COMPARISON OF OBSERVED AND EXPECTED NUMBERS OF HETEROZYGOTES IN THE
F-V BLOOD SYSTEM IN ANGUS, SHORTHORN, AND HEREFORD CATTLE FROM
1963 TO 1969

Breed	Year	Blood Type†	Observed	Expected	Chi-Square
A	1963	F2/F4	7	6.7148	.0121
S	1963	F2/F4	1	2.1869	.6442
H	1963	F2/F4	3	2.4869	.1059
A	1964	F2/F4	11	7.6751	1.4403
S	1964	F2/F4	4	2.9037	.4139
H	1964	F2/F4	1	5.9169	4.0859*
A	1965	F2/F4	10	9.6480	.0128
S	1965	F2/F4	3	3.2997	.0272
H	1965	F2/F4	1	2.3307	.7598
A	1966	F2/F4	25	14.1385	8.3440**
S	1966	F2/F4	0	0	0
H	1966	F2/F4	1	.6300	.2173
A	1967	F2/F4	20	12.3260	4.7777*
S	1967	F2/F4	1	.6278	.2207
H	1967	F2/F4	1	.6300	.2173
A	1968	F2/F4	32	31.5493	.0064
S	1968	F2/F4	8	6.9143	.1705
H	1968	F2/F4	22	21.2213	.0286
A	1969	F2/F4	21	9.5096	13.8838**
S	1969	F2/F4	4	2.6707	.6616
H	1969	F2/F4	1	.485	.5467

* $P < .05$

** $P < .005$

† See Tables 1 and 2 for decodings of blood types.

linkage of one or both of the phenogroups with genes influencing a production trait selected for by the animal breeder. However, the number of animals available for this study was very small, and conclusions, as a result, must be tentative.

In only one year, 1965, expected numbers exceeded observed numbers in the Shorthorn segment of the herd. No significant chi-square values were obtained.

Expected numbers were higher than observed numbers in 1964 and 1965 in Herefords. Significant difference ($P < .05$) was found between observed and expected values in 1964 (Table 8).

The major problem encountered in analyzing these results is that of such small numbers of animals for observation, permitting chance in sampling to have great influence.

5. CONCLUSIONS

In the majority of analyses, observed and expected numbers of heterozygotes did not differ significantly. However, in most cases, observed numbers were larger than expected numbers. Inbreeding in this herd was not intense as the highest inbreeding coefficient in any year was .3410. It appears that inbreeding was not intense enough to decrease heterozygosis noticeably in the herd. Other possible reasons for observed numbers being larger are that natural selection may favor heterozygotes or that both alleles of this system are linked with genes favored by the selection practiced by the breeder.

CHAPTER IX

SUMMARY

Data from two separate herds of cattle, the University of Tennessee Plateau Experiment Station Angus herd and the Angus, Shorthorn, and Hereford herd of the Virginia Polytechnic Institute and State University at Front Royal, Virginia, were used to investigate some of the genetic aspects of bovine blood type systems. Search for linkage relationships revealed that genes determining blood groups are not located on the sex-chromosome. Attempts to determine linkage between genes responsible for the F-V and R'-S' blood systems proved inconclusive because very few animals resulting from test crosses and from the matings of double heterozygotes were available. This resulted primarily because of inadequate blood typing. Studies in the UT Angus herd of combinations of double homozygotes and double heterozygotes between the F-V and R'-S' blood systems, showed double heterozygotes, in most cases, to have higher least-squares means of production traits than did double homozygotes. Several more significant differences ($.003 < P < .10$) were found between double homozygotes and double heterozygotes when sire effects were not included in models than when sire effects were included, indicating that confounding between blood type and sire is important. Comparison of annual gene frequency values indicated random drift to be causing fluctuations of blood type gene frequencies in the VPI herd. Several significant differences between years ($P < .05$ or $P < .01$) in gene frequencies were observed. Analyses of variance were performed on

various body and weight production traits to determine if associations existed between them and blood types within a system or combinations of blood types of two systems. The Z and J systems were found to be involved in the majority of the significant associations observed in the VPI herd. The phenotypes Z0/Z0 and J0/J1 occurred most frequently. Many more significant associations were found in the analyses involving combinations of blood types of two systems than in analyses dealing with blood systems separately. The transferrin system and the R'-S' and F-V blood systems were found in the majority of significant associations in the UT herd. In a comparison of observed and expected heterozygosis in the F-V blood type system in the VPI herd, significant differences ($P < .05$ or $P < .005$) were found in three of the seven years studied in Angus and in one of the seven years studied in Herefords. Expected values were almost always less than observed values, but the intensity of inbreeding was probably not sufficient to reduce appreciably the frequency of heterozygotes as compared to that expected in a random mating herd.

LITERATURE CITED

LITERATURE CITED

- Abbott, U. K., R. M. Craig and E. B. Bennett. 1970. Sex-linked coloboma in the chicken. *J. Heredity* 61:95.
- Andresen, E., N. Hojgaard, B. Jylling, B. Larsen, P. Moller, J. Moustgaard, and A. Neimann-Sorenson. 1959. Blood and serum group investigations on cattle, pig, and dog in Denmark. *Vith Intern. Blood-gr. Cong.*, (Munich), pg. 24.
- Andresen, E., and L. N. Baker. 1964. The C blood group system in pigs and the detection and estimation of linkage between the C and J systems. *Genetics* 49:379.
- Andresen, E. 1966. Linkage between the K blood group and the Hp locus for hematin-binding globulins in pigs. *Genetics* 54:805.
- Andresen, E. 1970a. Linkage between the H and the 6-PGD loci in pigs. *Acta Vet. Scand.* 11:136.
- Andresen, E. 1970b. Close linkage between the locus for phosphohexase isomerase (PHI) and the H blood group locus in pigs. *Anim. Blood Grps. Biochem. Genet.* 1:171.
- Ashton, G. C. 1960. Beta-globulin polymorphism and economic factors in dairy cattle. *J. Agri. Sci.* 54:321.
- Ashton, G. C., G. R. Fallon, and D. N. Sutherland. 1964. Transferrin (beta-globulin) type and milk and butterfat production in dairy cows. *J. Agri. Sci.* 62:27.
- Becon, L. D. and J. V. Craig. 1966. Evidence for histocompatibility locus on the W chromosome in chickens. *Poultry Sci.* 45:1066.
- Briles, W. E., L. W. Johnson and M. J. Garber. 1953. The effect of heterozygosity at the blood group locus B on weights at 9 weeks of age in related inbred lines of White Leghorns. *Poultry Sci.* 32:890.
- Briles, W. E. and W. F. Krueger. 1955. The effect of parental B blood group genotypes on hatchability and livability in Leghorn inbred lines. *Poultry Sci.* 34:1182.
- Briles, W. E. 1956. The relationship between B blood group genotypes and adult performance in two White Leghorn inbred lines. *Poultry Sci.* 35:1134.
- Briles, W. E., C. P. Allen, and T. W. Miller. 1957. The B blood group system of chickens. I. Heterozygosity in closed populations. *Genetics* 42:637.

- Briles, W. E., R. W. Briles, and R. N. Shoffner. 1967. Tests for linkage between ten blood group loci and the loci of seven morphological traits. *Poultry Sci.* 46:1238.
- Briles, W. E. 1968. New evidence for close linkage between the A and E blood group loci of the chicken. *Genetics* 60:164.
- Brum, E. W., W. H. Rausch, H. C. Hines, and T. M. Ludwick. 1968. Association between milk and blood polymorphism types and lactation traits of Holstein cattle. *J. Dairy Sci.* 51:1031.
- Conneally, P. M. 1962. Population genetics of cattle blood groups. Ph.D. Diss. Abs. 23:765.
- Conneally, P. M., and W. H. Stone. 1965. Association between a blood group and butterfat production in dairy cattle. *Nature* 206:115.
- Cooper, D. and J. Rendel. 1968. Incomplete family data selection and population studies of transferrins and blood groups in cattle. *Heredity* 23:49.
- Dabczewski, Z. S. 1969. Studies on hereditary blood properties in Kerry cattle. *Ir. J. Agric. Res.* 8:279.
- Dellemier, G. R., R. R. Shrode, and D. A. Shannon. 1979. Use of body measurements to select beef female replacements at weaning. *Tenn. Farm and Home Sci.* 111:33.
- Drieux, H. M. Priouzeau, G. Thiery, and M.-L. Priouzeau. 1950. Hypotrichase congenitale avec anodontie, acerie et macroglossie chez le veau. *Recueil de Med. Vet.* 126:385-99.
- Eldridge, F. E. and F. W. Atkeson. 1953. Streaked hairlessness in Holstein-Friesian cattle. *J. Heredity* 44:265.
- Gill, J. L. and B. A. Glemmer. 1966. Effects of selection and linkage on degree of inbreeding. *Aust. J. Biol. Sci.* 19:307.
- Hargrove, G. L., C. A. Kiddy, C. W. Young, A. G. Hunter, G. W. Trimberger and R. E. Mather. 1980. Genetic polymorphisms of blood and milk and reproduction in Holstein cattle. *J. Dairy Sci.* 63:1154.
- Hines, H. C. 1978. Cattle blood typing. *American Red Angus*, September, p. 27.
- Hines, H. C., J. P. Zikakis, G. F. W. Haenlein, C. A. Kiddy, and C. L. Trowbridge. 1981. Linkage relationships among loci of polymorphisms in blood and milk of cattle. *J. Dairy Sci.* 64:71.

- Hutt, F. B. and P. D. Sturkie. 1938. Genetics of the fowl: naked, a new sex-linked mutation. *J. Heredity*. 29:370.
- Hutt, F. B. 1953. Homologous sex-linked mutations in man and other mammals. *The American Naturalist* 87:160.
- Hutt, F. B. 1959. Sex-linked dwarfism in the fowl. *J. Heredity* 50:209.
- Hutt, F. B. 1964. *Animal Genetics*. New York: Ronald Press.
- Hutt, F. B. 1979. *Genetics for Dog Breeders*. W. H. Freeman and Co., San Francisco, CA.
- Juneja, R. K., B. Gahne, I. Edfors-Lilja and E. Andresen. 1983. Genetic variation at a pig serum locus, PO-2 and its assignment to the Phi, Hal, S, H, and Pgd linkage group. *Anim. Blood Grps. Biochem. Genet.* 14:27.
- Kaczmarek, A., H. Balbirz, Z. Darynek, M. Nikolajezuk, M. Switek, and T. Szalajka. 1972. Immunogenetic studies on cows of high and low butterfat production. 12th European Adnim. Blood Group Conference, p. 255.
- Kidd, K. K., L. A. Sgaramella-Zonta. 1972. Genetic relationships among cattle breeds. XIIth European Conf. Anim. Blood Groups, Biochem. Polymorph. p., 16
- Kiddy, C. A., R. H. Miller, C. Stormont, and F. N. Dickensen. 1975. Transferrin type and transmitting ability for production in dairy bulls. *J. Dairy Sci.* 58:152.
- Lancaster, G. M. 1968. Sex-linked winglessness in the fowl. *Heredity* 23:257.
- Landsteiner, K. 1901. Ueber agglutinationserscheinungen normalen menschlichen blutes, *Wiener Klinische Wochenschrift* 14:1132-4. Reprinted (in English) in S. H. Boyer, ed. 1963. *Papers on Human Genetics*. Prentice Hall, Englewood Cliffs, NJ.
- Larsen, B., C. L. Gruchy and J. Moustgaard. 1974. Studies on blood groups and polymorphic protein systems in Jersey cattle on the Isle of Jersey. *Acta. Agric. Scand.* 24:99.
- Makarechian, M. and W. E. Howell. 1967. Relationship between transferrin type and productive traits in beef steers. *J. Anim. Sci.* 26:27.
- Mather, R. E. 1977. Review of regional project NE 262: Relationships between genetic markers and performance in dairy cattle. *J. Dairy Sci.* 60:482.

- Miller, W. J. 1966. Blood groups in Longhorn cattle. *Genetics* 54:391.
- Mishra, R. R., H. K. Bhagi and S. S. Prabhu. 1974. Blood type J and production characteristics in cattle. *Indian J. Dairy Sci.* 27:188.
- Morrill, E. L. 1945. A new sex-linked defect in cattle. *J. Heredity* 36:81.
- Muller, C. D. and F. B. Hutt. 1941. Genetics of the fowl: sex-linked imperfect albinism. *J. Heredity* 32:71.
- Munro, S. S. 1946. A sex-linked true-breeding blue plumage color. *Poultry Sci.* 25:408.
- Nair, P. G. 1957. Studies on association between cellular antigens and butterfat percentage in dairy cattle. *Dairy Sci. Abstr.* 19:369.
- Neimann-Sorensen, A. and A. Robertson. 1961. The association between blood groups and several production characteristics in three Danish cattle breeds. *Acta. Agri. Scand.* 11:2.
- Oosterlee, C. C. 1964. Some aspects of studies on the relationship between blood groups and economic characteristics in farm animals. *World Rev. of Anim. Prod.* 1:21.
- Rasmusen, B. A., C. K. Beece and L. L. Christian. 1980. Halothane sensitivity and linkage of genes for H red blood cell antigens, phosphohexase isomerase (PHI), and 6-phosphogluconate dehydrogenase (6-PGD) variants in pigs. *Anim. Blood Grps. Biochem. Genet.* 11:93.
- Rasmusen, B. A. 1981. Linkage of genes for PHI, halothane sensitivity, A-O inhibition, H red blood cell antigens and 6-PGD variants in pigs. *Anim. Blood Grps. Biochem. Genet.* 12:207.
- Rasmusen, B. A. 1982. Linkage between genes at the H blood group locus and the loci for C and J blood groups in pigs. *Anim. Blood Groups and Biochem. Genet.* 13:285.
- Rausch, W. H., H. C. Hines and E. W. Brum. 1967. A blood type comparison in three beef breeds in America. *Immunogenetics Lett.* 2(5):43.
- Rausch, W. H., E. W. Brum, and T. W. Ludwick. 1968. Relationship between blood type and predicted differences in production of Holstein sires in artificial insemination. *J. Dairy Sci.* 51:445.

- Rendel, J. 1961. Relationship between blood groups and the fat percentage of the milk in cattle. *Nature* 189:408.
- Salerno, A. 1964. Relationships between blood groups and beef production in Chiana breed cattle. 9th European An. Blood Group Conference, p. 463.
- Sandberg, K. 1974. Linkage between the K blood group locus and the 6-PGD locus in horses. *Anim. Blood Grps. Biochem. Genet.* 5:137.
- Sanders, N. E. 1981. A study of blood type frequencies and association of blood types with other traits in an Angus herd. Unpublished M.S. Thesis, University of Tennessee. 56 pp.
- Schierman, L. W. and A. W. Nordskog. 1963. Linkage tests with blood group loci and morphological markers in poultry. *Immunogenetics Lett.* 3:54.
- Serebrovsky, A. S. and Wassina. 1922. Crossing over involving three sex-linked genes in chickens. *Amer. Naturalist.* 56:571.
- Shrode, R. R. and J. L. Lush. 1947. The genetics of cattle. In M. Demerec, ed. 1947. *Advances in Genetics Vol. 1*, Academic Press Inc., N.Y., NY.
- Smith, C. and P. R. Bampton. 1977. Inheritance of reaction to halothane anaesthesia in pigs. *Genetical Research* 29:287.
- Snedecor, G. W. and W. H. Cochran. 1967. *Statistical Methods*. The Iowa State University Press, Ames, IA.
- Somes, R. G., Jr. 1970. Congenital baldness, a sex-linked trait in the domestic fowl. *Poultry Sci.* 49:1440.
- Spillman, W. J. 1908. Spurious allelomorphism: results of some recent investigations. *Amer. Naturalist* 42:610.
- Spooner, R. L. 1967. Blood groups in animals and their practice application. *The Vet. Rec.* 81:699.
- Stormont, C. 1949. Acquisition of the J substance of cattle. I. Developmental and immogenetic studies. *J. Immunol.* 73:397.
- Stormont, C., R. D. Owen, and M. R. Irwin. 1951. The B and C systems of bovine blood groups. *Genetics* 36:134.
- Stormont, C. 1967. Contribution of blood typing to dairy science progress. *J. Dairy Sci.* 50:253.
- Stormont, C. 1978. The early history of cattle blood groups. *Immunogenetics* 6:1.

Sturtevant, A. H. 1912. An experiment dealing with sex-linkage in fowls. J. Expt. Zool. 12:499.

Trommerhausen-Smith, A. 1978. Linkage of tobiano coat spotting and albumin markers in a pony family. J. Heredity 69:214.

Young, C. W. and A. G. Hunter. 1966. Transferrin polymorphism studies in Holstein cattle. J. Dairy Sci. 49:735.

APPENDIX

TABLE A-1

CHANGE IN GENE FREQUENCY (PERCENTAGE) IN VPI ANGUS FROM 1963 TO 1971

Blood Pheno- group†	1963	1964	1965	1966	1967	1968	1969	1970	1971	Chi- Square
A1	26.923	25.000	34.146	16.667	23.214	35.556	25.000	28.440	25.989	9.8040
A2	3.846	3.125	-----	8.333	-----	2.222	-----	10.092	4.520	13.0181
A3	61.538	68.750	65.854	71.667	73.214	58.519	61.364	56.881	66.667	8.8711
A51	7.692	3.125	-----	3.333	3.571	3.704	13.636	4.587	2.825	12.0236
B0	19.231	29.730	29.730	20.000	23.077	24.823	41.071	18.852	22.034	13.3941
B16	3.846	8.108	8.108	5.000	17.308	5.674	3.571	4.918	5.650	13.9827
B22	7.692	5.405	5.405	3.333	-----	9.220	7.143	9.016	4.520	6.3830
B39	15.385	8.108	8.108	5.000	7.692	9.220	-----	3.279	2.825	14.7080
B45	26.923	16.216	16.216	31.667	25.000	17.021	14.286	16.393	19.209	17.3850*
B68	-----	-----	-----	1.667	1.923	1.418	-----	1.639	2.260	1.0938
B78	3.846	5.405	5.405	1.667	7.692	5.674	12.500	14.754	17.514	25.2380
B82	-----	-----	-----	1.667	-----	-----	-----	-----	-----	9.8325
B85	11.538	10.811	10.811	20.000	9.615	16.312	1.786	4.918	8.475	22.0215**
B89	-----	-----	-----	1.667	1.923	2.128	-----	0.820	0.565	2.9401
B90	-----	2.703	2.703	-----	1.923	0.709	-----	1.639	1.130	2.2177
B92	3.846	2.703	2.703	1.667	-----	-----	-----	1.639	0.565	5.7954
B96	3.846	-----	-----	-----	1.923	-----	-----	-----	2.825	7.5313
B111	-----	5.405	5.405	-----	1.923	0.709	1.786	0.820	1.130	6.6775
B144	3.846	5.405	5.405	6.667	-----	6.383	17.857	21.311	11.299	25.2859**
B239	-----	-----	-----	-----	-----	0.709	-----	-----	-----	3.1977
C0	54.167	25.926	35.484	36.000	36.170	41.026	29.545	44.660	31.757	10.6818
C1	29.167	44.444	35.484	16.000	23.404	25.641	38.636	32.039	40.541	17.6930*

TABLE A-1 (continued)

Blood Pheno- group†	1963	1964	1965	1966	1967	1968	1969	1970	1971	Chi- Square
C3	8.333	22.222	19.355	28.000	19.149	22.222	6.818	12.621	14.189	14.1352
C13	-----	-----	-----	-----	-----	0.855	-----	-----	1.351	2.3653
C16	-----	-----	-----	-----	-----	1.709	2.273	-----	-----	6.0603
C21	-----	-----	-----	4.000	6.383	1.709	-----	1.942	2.703	4.9133
C22	-----	-----	-----	-----	-----	-----	-----	-----	0.676	2.2475
C27	8.333	3.704	3.266	4.000	4.255	2.564	4.545	-----	-----	7.5071
C29	-----	-----	3.266	2.000	-----	0.855	4.545	0.971	0.676	6.1108
C32	-----	3.704	3.266	10.000	10.638	3.419	13.636	7.767	8.108	8.2480
F2	51.613	50.000	62.500	51.389	64.706	63.095	46.552	43.571	40.686	29.7417**
F4	48.387	50.000	37.500	48.611	35.294	36.905	53.448	56.429	59.314	29.7417**
J0	72.000	88.235	63.415	68.750	57.692	80.952	68.750	68.067	75.275	19.6649**
J1	28.000	11.765	36.585	31.250	42.308	19.048	31.250	31.933	24.725	19.6649*
L0	86.667	81.081	79.070	86.567	84.127	85.621	92.982	94.161	94.059	20.854**
L1	13.333	18.919	20.930	13.433	15.873	14.379	7.018	5.839	5.941	20.854**
M0	100.000	100.000	100.000	100.000	100.000	83.333	95.313	100.000	100.000	17.3188*
M1	-----	-----	-----	-----	-----	16.667	4.688	-----	-----	12.7346
S1	100.000	100.000	100.000	75.000	100.000	100.000	100.000	100.000	100.000	6.975
S2	-----	-----	-----	25.000	-----	-----	-----	-----	-----	6.075

TABLE A-1 (continued)

Blood Pheno- group†	1963	1964	1965	1966	1967	1968	1969	1970	1971	Chi- Square
Z0	68.750	84.211	64.583	80.556	79.412	73.457	81.034	76.259	82.353	12.35
Z1	31.250	15.789	35.417	19.444	20.588	26.543	18.966	23.741	17.647	12.35

* .01 < P < .05

** P < .01

† See Tables 1 and 2 for explanation of phenogroups.

TABLE A-2
CHANGE IN GENE FREQUENCY (PERCENTAGE) IN VPI SHORTHORN FROM 1963 TO 1971

Blood Pheno- group†	1963	1964	1965	1966	1967	1968	1969	1970	1971	Chi Square
A1	50.000	44.828	40.000	43.750	51.351	37.815	34.848	28.689	29.932	3.3231
A2	4.167	---	---	---	---	---	---	1.638	---	10.0478
A3	45.833	55.172	57.500	56.250	45.946	61.345	65.152	68.852	68.707	13.5948
A51	---	---	2.500	---	2.703	0.840	---	0.820	1.361	2.3919
B0	25.000	32.143	38.636	28.571	57.143	44.762	39.655	39.806	42.857	10.7717
B3	---	---	---	---	---	---	3.448	---	---	15.9828
B16	---	---	---	---	---	0.852	---	---	---	3.6375
B22	37.500	35.714	31.818	46.429	26.190	38.095	37.931	40.777	35.714	4.5102
B65	4.167	3.571	2.273	---	---	2.857	---	---	---	7.9064
B89	20.833	17.857	15.909	14.286	14.286	12.381	17.241	12.621	15.000	2.1192
B92	---	---	2.273	---	---	---	---	---	---	11.0963
B92	4.167	3.571	4.545	3.571	2.381	---	---	0.971	4.286	5.1784
B93	4.167	---	4.545	---	---	0.952	1.724	0.971	2.143	4.3563
B96	---	---	---	---	---	---	---	1.942	---	7.4931
B144	---	---	---	---	---	---	---	1.942	---	7.4931
B235	---	3.571	---	---	---	---	---	0.971	---	9.4822
B268	4.167	3.571	---	3.571	---	---	---	---	---	16.0673*
B402	---	---	---	3.571	---	---	---	---	---	18.5099*
C0	---	---	---	---	---	---	---	2.381	---	6.1791
C1	6.250	5.263	8.333	5.000	7.407	8.108	9.091	2.381	0.990	8.8069
C3	93.750	84.211	83.333	95.000	74.074	82.432	63.636	53.381	73.267	34.0212**
C21	---	5.263	---	---	7.407	2.703	9.091	17.857	1.980	24.2130**
C27	---	---	4.167	---	3.704	5.405	6.818	7.143	5.941	1.2572

TABLE A-2 (continued)

Blood Pheno- group†	1963	1964	1965	1966	1967	1968	1969	1970	1971	Chi- Square
C31	-----	-----	-----	-----	-----	-----	-----	-----	1.980	4.6155
C32	-----	5.263	4.167	-----	7.407	1.351	11.364	17.857	15.842	17.3576*
F2	90.625	89.474	89.5830	100.000	98.077	93.151	94.872	96.324	96.988	12.8478
F4	9.375	10.526	10.417	-----	1.923	6.849	5.128	3.676	3.012	10.6310
J0	96.875	94.737	89.130	80.000	85.714	88.732	98.718	83.333	86.875	18.6641*
J1	3.125	5.263	10.870	20.000	14.286	11.268	1.282	16.667	13.125	18.6641*
L0	86.207	66.667	86.364	75.676	80.435	90.511	84.286	89.313	82.278	17.1343*
L1	13.793	33.333	13.636	24.324	19.565	9.489	15.714	10.687	17.722	17.1343*
M0	100.000	100.000	100.000	100.000	100.000	100.000	-----	93.548	100.000	13.5548
M1	-----	-----	-----	-----	-----	-----	-----	6.452	-----	8.4464
S1	100.000	100.000	100.000	100.000	100.000	100.000	100.000	100.000	100.000	0
Z0	77.419	77.143	76.744	80.488	89.362	82.979	75.676	88.971	87.952	13.5641
Z1	22.581	22.857	23.256	19.512	10.638	17.021	24.324	11.129	12.048	13.5641

* .01 < P < .05

** P < .01

† See Tables 1 and 2 (pages 28-31) for explanation of phenogroups.

TABLE A-3
CHANGE IN GENE FREQUENCY (PERCENTAGE) IN VPI HEREFORDS FROM 1963 TO 1971

Blood Pheno- group†	1963	1964	1965	1966	1967	1968	1969	1970	1971	Chi- Square
A1	43.750	22.222	26.667	33.333	66.667	16.000	---	12.500	---	12.7137
A3	56.250	77.778	66.667	66.667	33.333	76.000	100.000	87.500	100.000	10.6687
A8	---	---	---	---	---	1.000	---	---	---	0.4358
A51	---	---	6.667	---	---	7.000	---	---	---	2.1993
B0	14.286	13.333	33.333	---	50.000	17.284	---	---	---	10.2491
B22	---	---	---	---	---	---	100.000	---	---	150.0000**
B24	---	6.667	---	---	---	2.469	---	---	---	1.7840
B45	---	6.667	---	---	50.000	3.704	---	---	---	14.1840
B80	---	6.667	---	---	---	---	---	---	---	8.2200
B81	42.857	40.000	66.667	100.000	---	27.160	---	30.435	100.000	13.9400
B82	---	---	---	---	---	4.938	---	---	---	1.6460
B89	14.286	---	---	---	---	14.815	---	4.348	---	3.2550
B92	14.286	13.333	---	---	---	22.222	---	4.348	---	1.6670
B104	---	---	---	---	---	1.235	---	17.391	---	0.4030
B164	---	---	---	---	---	6.173	---	---	---	2.0720
B239	14.286	13.333	---	---	---	---	---	---	---	13.9910
C0	16.667	---	18.182	---	---	17.910	---	---	---	2.2087
C1	41.667	27.273	27.273	50.000	---	22.388	---	19.048	---	3.2200
C3	8.333	9.091	9.091	50.000	---	22.388	100.000	---	---	10.5770
C6	33.333	54.545	45.455	---	100.000	35.821	---	66.667	100.000	9.8875
C10	---	---	---	---	---	1.493	---	---	---	0.4264

TABLE A-3 (continued)

Blood Pheno- group†	1963	1964	1965	1966	1967	1968	1969	1970	1971	Chi- Square
C13	-----	9.091	-----	-----	-----	-----	-----	-----	-----	9.7085
C32	-----	-----	-----	-----	-----	-----	-----	14.286	-----	12.9447
F2	86.364	68.182	85.000	75.000	25.000	72.131	50.000	77.778	100.000	10.2533
F4	13.636	31.818	15.000	25.000	75.000	27.869	50.000	22.222	-----	9.5636
J0	65.455	90.476	88.889	100.000	100.000	100.000	100.000	66.667	50.000	46.7387**
J1	4.545	9.524	11.111	-----	-----	-----	-----	33.333	50.000	37.1735**
L0	16.667	16.667	18.182	33.333	-----	15.152	100.000	-----	-----	12.3109
L1	83.333	83.333	81.818	66.667	100.000	84.848	-----	100.000	100.000	4.6369
M0	100.000	100.000	-----	-----	-----	-----	-----	100.000	100.000	-----
Z0	81.818	90.909	75.000	100.000	75.000	78.992	-----	86.111	50.000	5.0693
Z1	18.182	9.091	25.000	-----	25.000	21.008	100.000	13.889	50.000	8.3503

* .01 < P < .05

** P < .01

† See Tables 1 and 2 (pages 28-31) for explanation of phenogroups.

TABLE A-4

RANGES OF LEAST-SQUARES MEANS OF QUANTITATIVE PRODUCTION TRAITS BY TWO-SYSTEM COMBINATIONS HAVING AN ASSOCIATION IN THE ANGUS PORTION OF THE VPI HERD

Blood Systems in Combinations	Trait	Number of Animals	Range of L-S Means	Blood Type† with Highest Value
C/L	PREADG (kg)	44	.7238-1.0739*	C0/C0/J1/J0
C/J	BWT (kg)	30	30.7592-38.9411	C0/C0/J0/J0
J/L	BWT (kg)	146	25.7696-31.0024*	J0/J0/L1/L0
B/Z	ACFW (kg)	59	186.3390-233.5910*	B0/B0/Z0/Z0
B/Z	AADG (kg)	59	.7671-.9783*	B0/B0/Z0/Z0
C/Z	ACFW (kg)	51	161.6891-252.7799*	C10/C0/Z0/Z0
C/Z	PREADG (kg)	44	.6832-1.2205**	C10/C0/Z1/Z0
B/J	LADG (kg)	38	.7581-1.0342**	B0/B0/J1/J0
B/J	BWT (kg)	43	24.4906-36.5058*	B0/B0/J1/J0
F/B	PREADG (kg)	63	.6684-.9595†	F2/F4/B22/B144
A/B	ACFW (kg)	56	162.4185-214.6281*	A3/A3/B0/B0
A/B	LADG (kg)	48	.7288-.9102**	A1/A3/B0/B0
A/B	TADG (kg)	48	.7614-1.0300**	A3/A3/B45/B0
A/L	LADG (kg)	100	.7685-.8189*	A1/A3/L0/L0

TABLE A-4 (continued)

Blood Systems in Combinations	Trait	Number of Animals	Range of L-S Means	Blood Type† with Highest Value
A/M	SRATIO	44	1435.5707-1658.2070*	A0/A1/M1/M3
A/M	WHG (cm)	45	136.7161-145.9160*	A0/A1/M1/M3
A/M	AWW (kg)	46	187.5109-218.4385*	A0/A1/M1/M3
A/M	ACFWW (kg)	46	196.4046-222.2513*	A0/A1/M1/M3
A/M	APWT (kg)	45	275.5825-309.4916†	A0/A1/M1/M3
A/Z	WHIETH (cm)	165	35.1504-37.0510*	A3/A3/Z0/Z1
J/B	PADG (kg)	564	.3373-.6575	J1/J1/B1/B233
J/C	AADG (kg)	42	.7742-.9811†	J0/J1/C0/C2
J/F-V	SRATIO	178	1319.0315-1536.1422*	J0/J1/F1/F1
J/F-V	WHG (cm)	218	132.1841-140.9505*	J0/J1/F1/F1
J/F-V	WHIETH (cm)	218	90.2176-96.2927*	J0/J1/F1/F1
J/F-V	LADG (kg)	220	.6240-.7353*	J0/J1/F1/F1
J/F-V	APWT (kg)	220	252.2981-292.5212*	J0/J1/F1/F1
J/S	AADG (kg)	25	.7784-.9693**	J0/J1/S0/S6
J/S	ACFWW (kg)	25	167.3071-220.9838*	J0/J1/S0/S6
B/F-V	APWT (kg)	799	262.9766-307.1504*	B45/B111/F1/F1
C/F-V	APWT (kg)	273	270.6548-316.6954*	C1/C32/F1/F4

TABLE A-4 (continued)

Blood Systems in Combinations	Trait	Number of Animals	Range of L-S Means	Blood Type† with Highest Value
Z/F-V	WHG (cm)	252	135.7494-143.8028*	Z1/Z1/F1/F4
Z/F-V	WLENGTH (cm)	252	91.0877-97.9961*	Z1/Z1/F1/F4
Z/F-V	WHIWH (cm)	252	35.0418-37.2162*	Z0/Z1/F1/F1

Probability that highest L.S. mean = lowest L.S. mean

+ P < .15

++ P < .10

*.01 < P < .05

** P < .01

† See Tables 1 and 2 (pages 28-31) for decodings of blood types.

TABLE A-5

RANGES OF LEAST-SQUARES MEANS OF QUANTITATIVE PRODUCTION TRAITS BY TWO-SYSTEM COMBINATIONS HAVING AN ASSOCIATION IN THE SHORTHORN PORTION OF THE VPI HERD

Blood Systems in Combinations	Trait	Number of Animals	Range of L-S Means	Blood Type† with Highest Value
F-V/B	AADG (kg)	75	.7314-.8638*	F2/F2/B0/B89
F-V/J	ACFWW (kg)	166	183.9216-207.3299*	F2/F2/J1/J0
F-V/J	AADG (kg)	166	.7289-.8529*	F2/F2/J1/J0
B/J	ACFWW (kg)	84	176.9362-234.1401*	B0/B89/J1/J0
A/Z	TADG (kg)	88	.9584-1.239	A3/A3/Z1/Z1
F-V/Z	ACFWW (kg)	129	167.7114-200.1035*	F2/F2/Z0/Z0
F-V/Z	AADG (kg)	129	.6552-.8175*	F2/F2/Z0/Z0
F-V/Z	LADG (kg)	110	.8406-.9082†	F2/F2/Z0/Z0
F-V/Z	TADG (kg)	110	.9082-.9960**	F2/F2/Z0/Z0
J/Z	ACFWW (kg)	184	169.1231-208.03502*	J1/J0/Z0/Z0
J/Z	AADG (kg)	184	.6711-.8576**	J1/J0/Z0/Z0
J/Z	LADG (kg)	156	.8564-.9232**	J1/J0/Z0/Z0
J/Z	TADG (kg)	156	.9347-1.0387**	J1/J0/Z0/Z0
L/Z	AADG (kg)	155	.6561-.8710*	L1/L0/Z1/Z0
L/Z	TADG (kg)	125	.9457-1.0856*	L1/L0/Z0/Z0

TABLE A-5 (continued)

Blood Systems in Combinations	Trait	Number of Animals	Range of L-S Means	Blood Type† with Highest Value
J/L	ACFWW (kg)	166	193.4585-208.1659*	J1/J0/L0/L0
J/L	AADG (kg)	166	.7661-.8552*	J1/J0/L0/L0

Probability that highest L.S. mean = lowest L.S. mean

+ $p < .15$

++ $p < .10$

* $.01 < p < .05$

** $p < .01$

† See Tables 1 and 2 (pages 28-31) for decodings of blood types.

TABLE A-6

LEAST-SQUARES MEANS OF QUANTITATIVE PRODUCTION TRAITS ASSOCIATED WITH DOUBLE COMBINATIONS OF BLOOD PHENOGROUPS AMONG TWO-SYSTEM COMBINATIONS IN THE UT ANGUS HERD

Blood Systems in Combinations	Trait	Number of Animals	Range of L-S Means	Blood Type† with Highest Value
Tf/A	AADG (kg)	829	.8600-.9676 ⁺⁺	Tf1/Tf1/A2/A3
Tf/A	ACFW (kg)	828	184.0851-208.4194 ⁺⁺	Tf1/Tf3/A2/A3
Tf/B	WLENGTH (cm)	630	91.1276-102.3934	Tf2/Tf2/B45/B89
Tf/B	PADG (kg)	639	.3540-.7506	Tf1/Tf1/B89/B233
Tf/C	WLENGTH (cm)	232	90.9296-99.9841 [*]	A3/A3/C0/C232
Tf/F-V	APWT (kg)	1231	253.1377-313.7372 ^{**}	Tf2/Tf3/F4/F4
Tf/F-V	SRATIO	1045	1299.6170-1570.0263 ^{**}	Tf3/Tf3/F1/F4
Tf/F-V	HIHT (cm)	1045	96.2051-101.6055	Tf3/Tf3/F1/F4
Tf/F-V	WHG (cm)	1214	133.3964-143.0905 ^{**}	Tf3/Tf3/F1/F4
Tf/F-V	WLENGTH (cm)	1214	90.1045-98.7951 ^{**}	Tf3/Tf3/F1/F4
Tf/F-V	LADG (kg)	1231	.6298-.7892 ^{**}	Tf3/Tf3/F1/F4
Tf/F-V	AADG (kg)	1237	.7570-.9655 ^{**}	Tf3/Tf3/F1/F4
Tf/F-V	ACFW (kg)	1236	177.6054-229.0438 ^{**}	Tf3/Tf3/F1/F4
Tf/S	PADG (kg)	139	.2963-.7984 [*]	Tf3/Tf3/S4/S6
Tf/S	LADG (kg)	139	.5841-.8606 ^{**}	Tf2/Tf3/S0/S6
Tf/S	APWT (kg)	139	238.4785-341.6744 ^{**}	Tf2/Tf3/S0/S6
Tf/R'-S'	SRATIO	437	1462.6803-1583.0224 ^{**}	Tf2/Tf2/R2/R2
Tf/R'-S'	WHG (cm)	451	137.0916-142.3704 ^{**}	Tf2/Tf2/R2/R2

TABLE A-6 (continued)

Blood Systems in Combinations	Trait	Number of Animals	Range of L-S Means	Blood Type† with Highest Value
TF/R'-S'	WLENGTH (cm)	451	94.6175-97.7625**	TF2/TF2/R2/R2
TF/R'-S'	LADG (kg)	456	.6922-.7716**	TF2/TF2/R2/R2
TF/R'-S'	AADG (kg)	458	.8414-.9493**	TF2/TF2/R2/R2
TF/R'-S'	ACFWW (kg)	458	194.1677-212.8947**	TF2/TF2/R2/R2
TF/R'-S'	APWT (kg)	456	276.4619-306.9273**	TF2/TF2/R2/R2
R'-S'/A	SRATIO	315	1466.7210-1651.4142*	R1/R2/A2/A3
R'-S'/A	WHG (cm)	325	137.1909-145.0142*	R1/R2/A2/A3
R'-S'/A	AADG (kg)	330	.8612-.9805**	R1/R2/A2/A3
R'-S'/A	ACFWW (kg)	330	195.4514-216.4862+	R1/R2/A2/A3
R'-S'/J	WHG (cm)	88	123.0310-140.6103*	R1/R0/J2/J2
R'-S'/L	HIHT (cm)	45	97.5944-102.2874+	R1/R2/L0/L1
R'-S'/M	SRATIO	34	1456.2175-1816.8985**	R1/R2/M1/M2
R'-S'/M	WHG (cm)	34	136.5339-153.1769*	R1/R2/M1/M2
R'-S'/M	WLENGTH (cm)	34	92.2384-105.6989	R1/R2/M1/M2
R'-S'/M	HIHT (cm)	34	94.5745-109.6528*	R1/R2/M1/M2
R'-S'/M	AADG (kg)	35	.7753-1.0936*	R1/R2/M1/M2
R'-S'/M	ACFWW (kg)	35	180.4289-262.5987**	R1/R2/M1/M2
R'-S'/M	APWT (kg)	34	273.0179-387.4056*	R1/R2/M1/M2
R'-S'/S	ACFWW (kg)	63	184.5213-218.1610**	R2/R2/S4/S6
A/B	ACFWW (kg)	465	177.5245-235.9614**	A3/A3/B111/B233

TABLE A-6 (continued)

Blood Systems in Combinations	Trait	Number of Animals	Range of L-S Means	Blood Type† with Highest Value
A/J	PADG (kg)	163	.2606-.6138*	A0/A1/J2/J3
A/L	PADG (kg)	67	.5158-.6421+	A0/A1/L1/L3
A/M	SRATIO	44	1435.5707-1658.2070*	A0/A1/M1/M3
A/M	WHG (cm)	45	136.7161-145.9160*	A0/A1/M1/M3
A/M	AWW (kg)	46	187.5109-218.4385*	A0/A1/M1/M3
A/M	ACFWW (kg)	46	196.4046-222.2513*	A0/A1/M1/M3
A/M	APWT (kg)	45	275.5825-309.4916+	A0/A1/M1/M3
A/Z	WHIETH (cm)	165	35.1504-37.0510*	A3/A3/Z0/Z1
J/B	PADG (kg)	564	.3373-.6575	J1/J1/B1/B233
J/C	AADG (kg)	42	.7742-.9811+	J0/J1/C0/C2
J/F-V	SRATIO	178	1319.0315-1536.1422*	J0/J1/F1/F1
J/F-V	WHG (cm)	218	132.1841-140.9505*	J0/J1/F1/F1
J/F-V	WHIETH (cm)	218	90.2176-96.2927*	J0/J1/F1/F1
J/F-V	LADG (kg)	220	.6240-.7353*	J0/J1/F1/F1
J/F-V	APWT (kg)	220	252.2981-292.5212*	J0/J1/F1/F1
J/S	AADG (kg)	25	.7784-.9693**	J0/J1/S0/S6
J/S	ACFWW (kg)	25	167.3071-220.9838*	J0/J1/S0/S6

TABLE A-6 (continued)

Blood Systems in Combinations	Trait	Number of Animals	Range of L-S Means	Blood Type† with Highest Value
B/F-V	APWT (kg)	799	262.9766-307.1504*	B45/B111/F1/F1
C/F-V	APWT (kg)	273	270.6548-316.6954*	C1/C32/F1/F4
Z/F-V	WHG (cm)	252	135.7494-143.8028*	Z1/Z1/F1/F4
Z/F-V	WLENGTH (cm)	252	91.0877-97.9961*	Z1/Z1/F1/F4
Z/F-V	WHIETH (cm)	252	35.0418-37.2162*	Z0/Z1/F1/F1

Probability that highest L.S. mean = lowest L.S. mean

+ $p < .15$

++ $p < .10$

* $.01 < p < .05$

** $p < .01$

† See Tables 1 and 2 (pages 28-31) for decodings of blood types.

VITA

Johnny E. Copeland was born February 8, 1950, in Mayland, Tennessee, to Mr. and Mrs. Turley M. Copeland. He was reared in Putnam County, Indiana, and Roane County, Tennessee, where he attended public schools. He was graduated from Roane County High School in June of 1969.

In September of 1969, he entered Tennessee Technological University at Cookeville and received a Bachelor of Science degree in Wildlife Management in June of 1973. He entered Graduate School at Tennessee Technological University in 1974 and received the Master of Science degree in Biology in June of 1976.

In March, 1976, he married Mary Jane Dagley of Oak Ridge, Tennessee. On October 4, 1977, their first child, Lydia Erin, was born. Their second child, Lucas Edward, was born October 25, 1979.

He entered The University of Tennessee in September 1981, to work toward the Ph.D. degree in Animal Science. He held an assistant professorship at Lincoln Memorial University during his study at The University of Tennessee. He is a member of Gamma Sigma Delta, National Association of Colleges and Teachers of Agriculture, The Wildlife Society, and the Tennessee Academy of Science.