BREEDING METHODS USED IN THE DEVELOPMENT OF THE HERD OF HEREFORD CATTLE OWNED BY THE OKLAHOMA AGRICULTURAL AND MECHANICAL COLLEGE

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By

ROLLAND C. OUTHIER

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APPROVED:

Oliver S. Willham

In Charge of Thesis

H. M. Briggs

Member of the Thesis Committee

A. E. Darlow

Head of Department of Animal Husbandry

D. C. McIntosh

Dean of Graduate School

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TABLE OF CONTENTS

I. INTRODUCTION

Most of our livestock improvement of today is due to the use by breeders of the principles of livestock breeding evolved and practiced early in the history of the breeds. For around two hundred years the principles and effects of inbreeding, cross breeding, line breeding and outbreeding have been successfully employed to originate and improve the various pure breeds of livestock. A present day study of animal breeding must necessarily start with a study of the methods used in the development of the most successful of such herds and an expression, in terms of modern genetics, of what these methods accomplished. The dissemination of the methods which have given the best results will add much to the wide-spread improvement of livestock. The ultimate objective in animal husbandry is, according to Winters, 1945, (19) the economical production of meats, dairy produce, wool, furs, working power, and other animal products useful to man. The field of animal husbandry is divided into three parts: (1) breeding, (2) feeding and management, and (3) marketing and servicing for consumption.

Animal breeding is the first step in the production of livestock. The problems of reproduction and improvement are in reality the beginning; it is the first step with which the breeder of either market or breeding animals has to contend; it is, therefor, fundamental in livestock production. The general principle in livestock breeding that "like begets like" has been known to some practically as far back as the records of domestic herds are known. Just how early shepherds and herdsmen came to a realization of the great facts of heredity for the conscious molding of animal forms and functions toward their own needs is unknown. The first improvement of the wild types of animals which they domesticated was made long before the science of breeding had been discovered or worked out.

Winters, (19), states that the improvement of livestock by controlling the parentage undoubtedly goes back beyond the time of Prince Mehenwetre of Egypt, who reigned about 2100 B.C. In 1919 a chamber, previously overlooked, in the tomb of this prince was discovered and opened for the first time since it was closed by the Egyptians 4000 years before. This chamber contained models of Egyptian life, more nearly perfect than any that had up to that time been discovered. It was the Egyptians' custom to bury with the deceased his tools and weapons; and if he was wealthy they included many additional articles, including miniature models of the many and varied possessions of the deceased. In this particular chamber were found models of cattle, barns, a brewery, a bakery, an abattoir, and many other illustrations of their daily life.

The largest of these models showed the prince counting his cattle as they passed by. The census, which was found, disclosed that he owned 835 long-horned cattle, 220 polled cattle, 750 donkeys, 974 sheep, and 2,234 goats. Apparently the Egyptians took some note of the arts of animal breeding, as one of the models illustrated the difference in type between the wild animals and the improved ones. As mentioned above, polled cattle also existed at this early time, and it is also quite certain that there were different beef breeds, each of which had its partisans.

It is very likely that none of these early people was as efficient in either the art or the practical understanding of animal breeding as they have often been described. From the writings of the Roman, Columella, and the Greek, Aristotle, we find many evidences that they knew little of the principles of animal breeding. They thought brood-mares were conceived by the wind unless brought to the stallions in the breeding season only, that if rain falls after the act of intercourse it must be repeated, and that lambs are white or black according as the veins beneath the tongues of the rams are white or black.

From about 1800 B.C. we get from the Bible the story of Laban and Jacob as recorded in the 30th chapter of Genesis. Laban hired Jacob to manage his flocks and herds and as his hire agreed to give him all the spotted, striped, black, or ring-straked born in the flock. To increase his wage, Jacob mated the females of the species to males that showed these colors. This indicates some knowledge of heritability but we also read that Jacob took rods of green poplar, hazel and chestnut and pilled white strakes in them and then set these rods before the flocks in the watering troughs when the flocks came to drink, that they should conceive when they came to drink. The report is that the cattle so conceived came forth the desired colors. So we see that the Hebrews were much like some of our present day enlightened farmer-breeders who use late scientific principles but also plant in the proper phase of the moon to be safe.

During the several thousand years that animals were handled by the ancients, improvements in the animals' temperament and form were made gradually. It is very clear, however, that the amount of improvement made within any given period was rather small. The first rather definite step taken toward the improvement of animals was initiated by the British royalty. Henry VIII had laws enacted regarding horse breeding, imported horses and maintained a royal stud. James I established the race course and gave special attention to horse breeding. Charles I and Charles II gave it even more attention. This led to the establishment and development of the Thoroughbred horse. During this same period the earls and dukes of England were making some improvements in their cattle and sheep, mostly through crossing and selection.

The development of modern breeding, however, dates from 1760 A. D. when Robert Bakewell assumed the management of the estate on which both his father and grandfather had resided at Dishley Grange, in Leicestershire, England. He became known as the "Father of Livestock Husbandry" through his achievements as a breeder and improver of Shire horses, Longhorn cattle, and Leicester sheep. He gave more careful and serious study to livestock breeding and improvement than anyone who had preceded him and established certain principles and methods of breeding which became popular in England and paved the way for the development of most of our modern breeds of livestock. According to Vaughan, 1931, (16), Bakewell's success seems to revolve about the practice of mating close relatives. He inbred extensively and demonstrated that inbreeding accompanied by careful selection is a great power for good in livestock improvement.

It was not until the latter part of the nineteenth century - 1865, when Gregor Mendel, an Austrian monk, experimented with peas and discovered some definite principles of heredity, that a scientific basis for animal breeding was known. The Mendelian principles were ignored, however, until Correns of Germany, DeVries of Holland, and Tschermak of Austria, working independently, re-discovered the Mendelian principles and established them among scientists. The Mendelian principles may generally be accepted as the regular mode of inheritance of all characteristics in all organisms.

With accurate knowledge of heredity much new interest in the field of breeding was inspired. Extensive research in the fields of histology, cytology, physiology and other related sciences have added much information to that supplied by Mendel. Rather extensive experimental breeding, carried on primarily with smaller forms of life because of the time and expense elements involved, has added materially to the practical application of Mendelian principles.

The application of statistical methods to the Mendelian theory of closebreeding and crossbreeding has given a definite measuring stick for interpreting and evaluating the methods used in the development of the modern breeds and herds of livestock. Since there are a large number of herds of livestock of outstanding merit which can be studied statistically instead of experimentally, and the same kind of information can be obtained, it seems logical that more of this type of work should be done.

When studies of this kind are made and the proper conclusions obtained, the present day breeders can have a much more reliable basis upon which to base their breeding practices. It will then no longer be so much of an experimental method of breeding as has been the case in so many of the herds of the past. Much of the fascination in livestock breeding, however, is due to the fact that each breeders situation is slightly different and a different course of procedure is advisable in each man's case.

In this study, the Hereford cattle herd of the Oklahoma A. & M. College of Stillwater, Oklahoma was selected. This is not one of the nation's outstanding Hereford herds but it is one with which hundreds of our coming livestock men of the state are trained each year. It is important that these coming agricultural leaders become familiar with the genotype as well as the phenotype of the animals with which they are working.

The main objects of this study were: first, to find what breeding methods were used in the establishment of the herd; second, to determine whether the herd has evolved as the result of a continuous line of breeding or has been influenced by currently popular families; third, to find what part line breeding and inbreeding has played in its development; fourth, to see whether the herd was developed as a homogeneous unit of related animals or whether it is split into definite families or groups; fifth, to find which animals were most widely used in founding the herd; sixth, to see which sires have contributed most to the herd up to and including the calf crop of 1945.

II. REVIEW OF LITERATURE

A. Breeds and Herds That Have Been Analyzed.

The methods used in this study were developed by Wright and McPhee (23) and Wright (20). Table I gives a summary of the several breeds of livestock that have been analyzed by similar methods according to a compilation made by Click (3) with additions by the writer.

TABLE I

INBREEDING FOUND IN VARIOUS BREEDS AND HERDS (5),(7),(I),(17),(10) and (13).

Breed Studied	Interval Studied		Inbreeding Coefficient: Total Increase Percent	Inbreeding Coefficient: Increase per Generation
Shorthorn Cattle	1790 to 1810		16.6	3.57
in	1810 to 1825		3.3	.94
Great Britain	1825 to 1920		6.1	.27
	1790 to 1920		26.0	.86
British Dairy Shorthorn	1790 to 1925		27.5	.89
Clydesdale Horses in Scotland	1865 to 1925		6.2	.90
Rambouillet Sheep in the United States	1890 to 1926		6.0	.70
Holstein-Friesian Cattle in the United States	1881 to 1928		4.7	.47
Ayrshire Cattle in Scotland	1877 to 1927		4.3	.39
Brown Swiss Cattle in the United States	1884 to 1929		3.8	.47
Jersey Cattle in England	1876 to 1916		3.9	.44
Poland China Hogs in the United States	1900 to 1929		5.8	.48
Hereford Cattle	1870 to 1880		1.7	.92
	1880 to 1890		.5	.27
in the	1890 to 1900	drop	.7	- .38
	1900 to 1910		2.2	1.19
United States*	1910 to 1920	drop	.3	- .16
	1920 to 1930		3.5	1.89
	1860 to 1930		8.1	.61
Hereford Cattle in Gudgell & Simpson Herd	1904 to 1914		4.6	2.44
Hereford Cattle in the Hazlett Herd	1900 to 1936		7.3	1.15
Aberdeen-Angus Cattle in the Fullerton Herd	1920 to 1942		6.68	1.62

* The average length of each generation used here is 5.4 years.

B. The Duchess Family of Shorthorns as Bred by Thomas Bates.

The first and most complete analysis of a herd of livestock was made by Wright, 1923, (22) on the Duchess family of Shorthorns as bred by Thomas Bates. Thus it should be of value to review the history of the Bates herd and the results obtained by Wright in his genetic analysis of it. The foundation for the herd was laid by Charles Collings of Ketton farm, who had made a long study of Bakewell's methods at Dishley and in 1784 bought, among other cattle, a massive, short-legged, wide-backed cow named Duchess, who became the progenitress of the family we are to study. Meanwhile Robert Collings purchased the bull Hubback, the best Shorthorn bull of his time. One of his grandsons was the noted bull, Foljambe, with whom the Collings were so impressed that they started an intense inbreeding program to him. A daughter, Phoenix, was bred to a son, Bolingbroke, and produced in 1793 the great bull, Favourite. Favourite was 19.2 percent inbred, not only through Foljambe but through his granddams, one of which was the dam of the other. Mr. Collings was so satisfied with Favourite that he began breeding him to his daughters and granddaughters, in some cases for even five or six generations.

At the dispersion of the Charles Collings herd in 1810 (one year after the death of Favourite) one of the bidders was a young breeder, Thomas Bates, who had made a careful study of cattle pedigrees. He purchased a rather "shabby" cow called Young Duchess, largely it appears, on the strength of her pedigree, her top sires being Comet, Favourite, Daisy Bull (a son of Favourite), Favourite again, and Hubback. She was a descendant in the straight female line of the cow, Duchess, mentioned first in this article. Following the custom of naming families by the female line, Bates developed a Duchess family from this cow, which he renamed Duchess I. Up to the time of his death in 1849 he had bred sixty-three cows in the family which he named Duchess 2 to Duchess 64. Two other females are recorded as having died. Forty-five males are recorded as dropped by Duchess cows, twenty-nine of which were named. The family was not a prolific one. They won, however, an extraordinary reputation in both England and America.

After Bates death, a line of Duchesses was maintained without outcrossing. They became the aristocrats of the cattle world. Never a prolific family, it became increasingly difficult to maintain as a pure strain. This lack of fertility enhanced their value due to their scarcity. The climax came in a sale of New York Mills in 1873. The "pure" lines of Duchesses had run out in England and all in America were owned by one man. This brought international competition for the pure Duchess. One cow sold for $40,600. The average of the eleven cows was $21,705, that for three bulls was $7,866.

In Wrights study all pedigrees have been traced to the beginning of the Coates herd books. It is shown that at the start the Duchess family came from Collings bred stock already about 40 percent inbred. During the eight generations which Bates bred them (about forty years) he maintained substantially the same level of inbreeding by constantly introducing just the right amount of fresh blood to keep the percentage from rising above 40 percent. He used bulls, whether of his own or other breeding, which averaged about 40 percent inbreeding. The general opinion is that Bates began his career with very intense inbreeding and on encountering deterioration was obliged to make outcrosses. Darwin states, "For thirteen years he bred most closely in-and-in; but during the next seventeen years, although he had the most exalted notion of his own stock, he thrice infused fresh blood into his herd; it is said he did this not to improve the form of the animals, but on account of their lessened fertility."

At the start Bates herd was 76 percent related to Favourite, but this had reached 57 percent at the end of eight generations. These figures can be compared to a coefficient of 50 percent between random bred brothers and sisters, or parent and offspring. This shows, that through eight generations, he maintained in his herd a closer resemblance to Favourite than exists between parent and offspring in random bred stock. Bates maintained from the beginning to the end of his breeding career a certain average degree of relationship between the animals he mated (about 60 percent), a degree distinctly higher than that between an ordinary brother and sister.

It is suggested that these levels of inbreeding and relationship yielded the proper balance between the extreme plasticity of the original heterogeneous Shorthorn stock and the more complete fixation of characters which would have resulted from any closer inbreeding, to enable Bates, with his great skill as a judge of cattle to maintain a high degree of vigor and to mold a new type according to his ideals on the basis of the type represented by Charles Collings bull, Favourite. It is interesting to note that his breeding practices throughout were very uniform. He did not concentrate the blood of one bull for a few generations and then turn wholly to a different line. Neither did he inbreed at the closest possible rate for a few generations and then make violent outcrosses. Of course he did not face the curse of modern breeders in having the temptation to change every few years to a currently popular new blood line as his Duchess family was the outstanding popular blood for the entire period.

TABLE II

A summary by generations (female line) of the coefficients of inbreeding and relationship for the 64 Duchesses, including Duchess I, bred by Charles Collings and purchased by Bates and the eight generations bred by Bates.

Generation from Duchess I	No. of Cows	Inbreeding: Individual	Inbreeding: Sire	Inbreeding: Dam	Relationship: Sire and Dam	Relationship: To Favourite Individual	Relationship: To Favourite Sire	Relationship: To Favourite Dam
0 (Duchess I)	1	40.8	47.1	31.5	58.7	76.3	80.5	72.7
1 (Bates)	4	43.5	21.6	40.8	54.0	68.6	62.5	76.3
2 "	10	47.1	43.4	37.1	67.0	69.2	72.1	69.4
3 "	14	42.4	38.0	43.9	60.2	67.9	67.8	68.7
4 "	7	38.3	38.6	43.7	54.7	66.8	64.9	67.3
5 "	9	36.7	41.9	42.5	51.8	67.3	64.7	67.4
6 "	10	43.4	35.5	33.9	64.4	62.0	61.7	66.2
7 "	7	36.4	33.2	34.9	54.3	56.7	56.7	57.9
8 "	2	42.8	32.1	41.7	62.6	57.4	56.7	60.5
Total	64	40.9	37.5	39.6	59.2	65.6	65.1	67.2

C. A Genetic Study of the British Shorthorn Breed.

The preceding paper presented the results of a detailed study of the breeding of a particular noted strain of Shorthorn cattle, Bates Duchess family, in terms interpretable on a Mendelian basis. It should be said, however, that while this family has been of great importance in the development of the breed, it should not be considered as typical. In order to get a proper perspective it is necessary to learn the situation in the breed as a whole.

This brief of the study made by McPhee and Wright, 1925, (12), gives in broad outline the history of the British Shorthorns with respect to the use of inbreeding, the influence of particular sires, and the degree of homogeneity of the breed. This Shorthorn study is made more accurate because the first herd book published in 1822 contains many pedigrees extending back through the forty years that the Collings had been carrying on their breeding program before the herdbook was published. All but about three percent of lines of ancestry of modern animals, chosen at random, can be traced back through this pre-herd book period.

The methods of analysis were essentially those described in the Duchess study. The practical difference in the two studies is elemental. The Duchess study was a complete tracing of the pedigree of each individual to the foundation animals and thus eliminated the vagaries of random sampling. The British Shorthorn study is an analysis of the breed rather than the individuals in it. Due to the very large number of animals involved it was impossible to consider all the animals of the breed and the analysis was confined to a strictly random sample. Samplings were made for the years of 1810, 1825, 1850, 1875, 1900 and

1920 with fifty cows and fifty bulls being used in each sampling with the exception of the first. The 1810 sample included seventy-five bulls and eighty-five cows and included all the registered bulls and cows of the years 1809, 1810 and 1811 since the number born in 1810 was too small for the purpose of the study.

Historically, the best products of the earlier, formative breeders of cattle which later formed the Shorthorn breed, seem to have been brought together in the herds of Charles and Robert Colling about 1780. Probably the greatest individual product of their breeding was the famous bull Favourite 252 dropped in 1793. His ancestry was given in section B., (The Duchess Family). The Collings bred him to his daughters generation after generation with notable success. Such families as the Duchesses were founded largely on his blood. Through the efforts of Thomas Bates (1775-1849), the Booths, and many others, his blood became diffused to such an extent that he may almost be said to have sired the entire breed.

What may be designated as a second period of breed improvement has been the development of the so-called Scotch type of Shorthorns, based in general on the herd of Amos Cruickshank (1808-1895) at Sittyton, Aberdeen, Scotland, and especially on his noted bull, Champion of England 17526, dropped in 1859. The herd had its origin in animals selected without regard to blood lines but with particular attention to vigor, early maturity, compactness, short legs and ability to lay on flesh rapidly. This contrasted with the earlier breeders, such as Bates, in which milk production was given considerable attention. The Scotch type predominates the Shorthorn breed today.

The widespread use of these two bulls and their inbred descendants accounts rather directly for the various changes in the coefficient of inbreeding of the breed in the various periods sampled. Prior to 1810 herds with an intense concentration of the blood of Favourite were built up by the Collings. Others followed this same policy to a lesser extent so that they raised the whole breed to such a point that there came to be a general resemblance to Favourite equal to that between parents and offspring in the foundation stock, and a correlation between random individuals as great as between half brothers in that stock. This brought by 1825 an elimination of 15 to 20 percent of the heterozygosis originally present. By 1850 the breed was a fairly homogeneous unit, with the blood of Favourite uniformly diffused. During this 25 year period there was even a slight drop in the inbreeding coefficient.

There then followed another period of inbreeding in particular lines, as the Bates and Booth stock. Meanwhile the blood of Champion of England, equal to the average of the breed in heredity and relationship to Favourite, but otherwise somewhat apart from the breed as a whole, was being concentrated by Cruickshank. His blood diffusion through the breed between 1875 and 1900, having slightly the effect of a cross, brought down the inbreeding. The homogeneity of the breed as measured by the relationship of random animals remained practically stationary as Champion of England blood, increasing in amount, gradually displaced Bates and Booth blood. The increase in relationship to Champion of England has gone on to the present, until in 1920, the coefficient of 46 percent is 20 percent greater than the original relationship to this bull and approaches the present relationship to Favourite of 55 percent. The relationship of random animals to each other, however, approaches 40 percent. The present coefficient of inbreeding of 26 percent indicates an elimination of more than one-fourth of the heterozygosis of the foundation stock.

The indications are that the breed is practically in equilibrium in all of these respects, an equilibrium which can only be disturbed by the formation and diffusion of the influence of a new, closely-bred family based on the excellence of a new Favourite or a new Champion of England. The increased size of the breed makes the difficulty of exerting an influence comparable to that of these earlier bulls enormously greater even than it was in Cruickshank's time.

Table III gives some interesting figures on the coefficients of inbreeding and relationship of the Shorthorn breed during the six indicated sampling periods.

TABLE III

Date	Observed Coefficient of Inbreeding	Coefficients of Relationship: Breed to Favourite	Breed to Champion of England	Breed Inter Se
1810	16.6	44.3	26.3	22.0
1825	19.9	51.3	29.9	26.8
1850	18.0	50.1	26.1	33.9
1875	27.4	57.6	32.9	37.8
1900	22.9	52.1	39.2	39.3
1920	26.0	55.2	45.5	39.5

D. The Aberdeen-Angus Cattle as Bred by S. C. Fullerton.

Mabry, 1946, (10) made a study of the herd of Aberdeen-Angus cattle bred by S. C. Fullerton of Miami, Oklahoma. This is the outstanding Angus herd of the state and one of the outstanding herds of the United States. Its study is included in order that we get an idea of some of the results obtained and methods used in all three of the leading beef breeds. This herd was established about 1920 and the base date used in the study is 1880. The study covers a period of 22 years until 1942.

The herd has been built around the noted Angus bull, Earl Marshall, and the blood of his descendants. Earl Marshall was born in 1913 and was in active service until some time in 1926, the year of his death.

Mr. Fullerton has operated through the 22 years of the study and up to the present time on a comprehensive, long-time breeding plan based on two points: first, to develop and maintain the highest possible relationship of the herd to Earl Marshall and consequently a fairly high Inter Se relationship in the herd; second, to avoid close inbreeding as much as possible and thus maintain the relationships indicated in item 1.

That he has been eminently successful in this plan is attested by the fact that the 1942 statistics shows the following: first, a relationship coefficient to Earl Marshall of 24.65 percent and a relationship coefficient of 11.37 percent to the bull, Black Peer of St. Albans; second, an inbreeding coefficient of 6.68 percent $\pm$ 1.03 percent as compared with an expected inbreeding coefficient of 7.57 percent; and third, an Inter Se relationship coefficient of 14.08 percent.

In addition to being successful in holding to his adopted breeding plan, Fullerton has proven it practical by the fact that his herd is one of the leading show herds of the nation in the various state, regional, and national exhibitions.

B. A Brief Genetic History of the Hereford Breed of Cattle in the United States.

Inasmuch as this study concerns an individual herd of Hereford cattle it is well to give here a brief review of the genetic history of Hereford cattle in the United States. Such a history was compiled in a study by Willham, 1937, (17) and is used in preference to an ordinary breed history because it is showing the breed in a genetic analysis. It also contains some regular historic background so that we may become reasonably familiar with this phase of the breeds' development.

The Hereford breed originated in and around Herefordshire, England, from stock a part of which may have come from Holland. Herefordshire was given credit for having better than average cattle as early as 1627. The early breeders seemed to consider their systems of breeding as part of their trade secrets and very few records have been preserved. The Tomkins family, one of the earliest improvers of the breed, and their successor, Price, used inbreeding in their herds. Tomkins and Price together bred a closed herd for 70 years with no ill effects. Hewer, another early improver, kept five families or strains in his herd so that he could produce bulls for his own use and still not inbreed too much. Apparently when early breeders were unable to secure good bulls unrelated to their cows, they used inbreeding. It is likely that the early Hereford breeders used the contemporarily famous Bakewell system of breeding, but records are too fragmentary to measure the amount of inbreeding that actually took place then.

The first importation of Herefords to the United States was in 1817 and the first herd established about 1840 near Albany, New York. Some 200 animals were imported up to 1880 with about 3,500 imported from 1880 to 1886. No importations from 1886 to 1893 and 1,109 animals imported from then until 1918. The British herdbook was established in 1846 and the American Hereford Record in 1879. By January 1, 1935 the grand total of animals recorded in the Hereford Record was 2,328,895.

The most important early herd in the United States so far as effect on the breed is concerned was that of Gudgell and Simpson and we omit that part of Willham's review as it is covered in the next discussion in the present study.

In Willham's study samples were used at ten year intervals starting with 1870 and ending with 1930. Each sample except 1870 consisted of 250 cows and 250 bulls chosen from the recorded calves born in the year in question. In the 1870 sample all 65 recorded bulls born in 1870 were used and 65 cows born in the same year chosen at random. The base date to which pedigrees were to be traced was set at 1860. Two line random pedigrees were used in all the larger samples and complete pedigrees used in the 1870 sample. The average coefficients of inbreeding and inter se relationship found in the Hereford breed at the various periods are shown in Table IV at the end of this discussion. The coefficients of inbreeding in the table represent the percentage of those genes for which the breed was heterozygous in 1860 for which the breed would be expected to become homozygous since then because of the inbreeding practiced.

The coefficient of inbreeding increased gradually from 1860 to 1930 with the exception of slight decreases in 1900 and 1920. These slight decreases in inbreeding occurred just after prices had begun to rise and an era of profitable expansion was under way. It seems reasonable to assume that such an increase in exchange of breeding stock would have led to the intercrossing of families which had been beginning to separate from each other during the previous period of more stagnant trade. Moreover there was a large increase in popularity of the Gudgell and Simpson cattle from 1910 to 1920 and there must have been in 1920 a very large number of herds which were practically in the stage of making their first or second top cross with Gudgell and Simpson bulls on foundation stock which came from other families. Hence the lower inbreeding in 1900 and 1920, although not statistically important, seems logical in view of the general breed history.

The rise in the percentage of inbreeding from 1920 to 1930 was faster than during the other periods. This was no doubt the result of the increased popularity of the "straight-bred" breeding during the period. The 8.1 percent inbreeding for the breed in 1930 represents a decrease in heterozygosis of only 0.68 percent per generation during the period from 1860 to 1930. The extreme mildness of the 0.68 percent inbreeding per generation actually practiced may be made more vivid by contrasting it with the 19 percent loss of heterozygosis per generation to be expected under brother-sister mating or the 11 percent per generation to be expected in a herd entirely closed to outside blood and consisting of one male and many females in each generation.

There has been a gradual increase in the inter se relationship from 1860 to 1930. The inter se relationship is an estimate of the relationship that existed at the particular period between any two animals chosen at random from the sample. In Table IV are shown the coefficients of inbreeding which would be expected with random mating in a population with the average inter se relationship which was found in the particular sample. In every case the observed coefficient of inbreeding was more than the expected. This means that on the average there was a closer relationship between the sires and dams than between contemporary animals taken at random. The difference between the expected and the actual inbreeding was most pronounced in 1890, 1910 and 1930 and least pronounced in 1900 and 1920. Apparently the breed is always tending, at least a little, to separate into slightly related families. However the tendency toward family formation in the breed seems never to progress very far before the incipient families are used for top-crossing and are blended into the breed as a whole. The inter se relationship in the breed was 8.8 percent in 1930 as compared with an inbreeding coefficient of about 4.6 percent if random mating had been practiced.

Nearly all the animals which had unusually high relationships to the breed at the various periods were either the ancestors, descendants or mates of Anxiety 4th. The breed was 18.5 percent related to Anxiety 4th in 1930. Beau Brummel, a grandson of Anxiety 4th, had the highest relationship to the breed of any of the animals in the study. He was 24.6 percent related to the breed in 1930. Beau Brummel lived long and sired 186 bulls and 221 heifers which were recorded in the American Hereford Record. Don Carlos 33734, the sire of Beau Brummel, was nearly a grandsire to the breed in 1930. He was the most important son of Anxiety 4th and was used extensively in concentrating the blood of Anxiety 4th. The fact that Don Carlos had seven full brothers and sisters used extensively helped to increase his relationship to the breed which in 1930 was 22.6 percent. Other animals mentioned which had a high relationship to the breed included:- North Pole 8946, a contemporary of Anxiety 4th; Sir Thomas 20, who appears in the pedigrees of Anxiety 4th, North Pole, Dowager 6th, and many other subsequently important animals; Lamplighter 51834, a three-quarter brother of Beau Brummel;

Beau Donald 58996, a son of Beau Brummel out of a full sister to the sire of Beau Brummel; Dowager 6th 6932, approximately a grandmother to the breed in 1930 as dam of eight animals (all sired by Anxiety 4th) which included the bulls Don Carlos and Don Quixote and the cow, Donna; Belle 24629, dam of Beau Brummel; and Gayless 9905, dam of Anxiety 4th.

Other interesting genetic breed data included the following:-

The average interval between generation was 5.4 years which agrees well with the 5.3 years generation interval found by Lush and Lacy.

A special group of prize winners and the Register of Merit animals had higher coefficients of inbreeding and inter se relationship than the contemporary random samples and were also more highly related to Anxiety 4th and his descendants.

One hundred and two foundation animals were responsible for the ends of 84 percent of the ancestral lines in 1930.

Twenty English breeders were responsible for the breeding of the foundation animals in which ended over 80 percent of the random ancestral lines traced in Willham's study. Three of them bred 38 percent of the foundation animals (1930 sample).

TABLE IV

INBREEDING AND INTER SE RELATIONSHIP COEFFICIENTS

Year	Number of Pedigrees Sampled	Inbreeding Coefficients: Actually Found	Inbreeding Coefficients: Expected from Inter Se Relationship	Inter Se Relationship
1870	130	1.2	0.7	1.4
1880	500	2.9	1.1	2.1
1890	500	3.4	1.3	2.6
1900	500	2.7	2.6	5.2
1910	500	4.9	2.7	5.3
1920	500	4.6	3.7	7.1
1930	500	8.1	4.6	8.8

F. A Brief History of the Hereford Cattle as Bred by Gudgell and Simpson.

In 1877, the Gudgell and Simpson herd of Herefords was founded at Independence, Missouri. This was destined to be one of the greatest, if not the greatest, Hereford breeding establishments ever known in America. This herd, which continued until 1916, had, according to Willham (17), a more profound influence than any others on the breed, especially during the decade of 1920 to 1930 which terminated his study.

The beginning of this herd, according to Click, 1939, (3) consisted of the bull, Picture, bred by F. W. Stone, the great Canadian breeder, and sired by imported Portrait 3rd and out of imported Peach. With Picture he also secured eight selected females. He made other purchases about this time from Ohio breeders and in 1878 he returned to Stone and this time bought the excellent bull, Governor 4th and a number of females. Prior to 1880 Charles and James Gudgell had the herd but in that year formed the firm with T. A. Simpson. The new firm immediately began importation of breeding stock from England. In 1880 they brought in about sixty head, all but one of them being females. They went back in 1881 and brought about 100 head of which 75 were females for the breeding herd. In this importation came the two yearling bulls, Anxiety 4th 9904 and North Pole 8946, destined to revolutionize Hereford breeding in the states.

When Mr. Simpson was leaving for this second importation, Gudgell's parting instructions were that he find and buy a bull with thick, heavy hindquarters, a point in which the Hereford cattle of that day were noticeably deficient. Anxiety 4th was the bull he bought for this purpose. North Pole was of a different pattern, being somewhat upstanding and more stylish, but not so well quartered as Anxiety 4th. North Pole was particularly good in the heart girth, which was the weakest point in

Anxiety 4th. The heifers sired by North Pole were good but the bulls were too leggy. Both the bulls and heifers by Anxiety 4th were good ones, particularly the ones out of daughters of North Pole. The union of the blood of Anxiety 4th and North Pole proved to be one of the most successful "nicks" in American cattle history.

Of all the cattle imported by Gudgell and Simpson, Anxiety 4th was easily the outstanding animal. He was used extensively in the herd until his death, and after that date his sons and grandsons were at the head of the herd. For years the herd was the headquarters for Anxiety cattle and increased in size up to about 500 breeding cows.

Early American breeders, according to Vaughn, 1931, (16) did not favor the practice of inbreeding, and Gudgell and Simpson first tried various outcrosses with the Anxiety 4th blood. But these outcrosses resulted in lowering rather than raising the excellence of the herd, and it was therefor decided to pile up the blood of Anxiety 4th by inbreeding. Perhaps this decision was due to the fact that Anxiety 4th was himself the result of inbreeding. Both his sire and dam were out of cows sired by De Cote 2243, and both his sire and dam traced to granddams sired by Counsellor 2264. In other words the sire and dam of Anxiety 4th had over 75 percent of blood in common.

According to Hazelton, 1935 (6) Gudgell and Simpson selected a grand lot of matrons from the harems of Anxiety 4th and North Pole. They represented the best blood of the breed in England and America in the last quarter of the nineteenth century. They had plenty of size and scale but not at the expense of quality. Dowager 6th, dam of Don Carlos, Don Pedro and Don Quixote, and several important females, was imported by Gudgell and Simpson. She figures extensively in many of the present day pedigrees and was easily the outstanding female used in founding this great herd.

Fifteen sons of Anxiety 4th were used in the herd to a greater or less extent. The one that showed the best results, and the one through which the blood of his sire appeared to come with the greatest potency was Don Carlos 33734. Don Juan and Don Quixote were great sires of females and through their daughters, contributed much to the herd's greatness. Anxiety 4th was used constantly in the herd until his death in 1890. The herd book contains the names of 71 of his sons and 102 of his daughters.

From Don Carlos the blood of Anxiety 4th appears to have passed with greater potency to Beau Brummel 51817 than to any other of his grandsons. It received a fresh infusion of the blood of Sir David through the dam of Don Carlos. Lamplighter 51834, another great son of Don Carlos, was used extensively in the herd as were a number of his sons, chief of which was Paladin 126248. Beau Brummel was used more freely than any other bull and the herd book records 186 of his sons and 221 of his daughters. He was the sire of ten very important animals of which four were females.

Further proof that the Gudgell and Simpson herd of Herefords was one of the most outstanding in history is shown in the study made by Willham, (17). Of the twenty-four bulls which appeared most frequently in the study of the breed, seven of them were bred by Gudgell and Simpson, two were imported and used by them, and eight were ancestors of animals used by them. In the same study ten outstanding cows were listed and of these four were bred by Gudgell and Simpson, one was imported and used by them, and five were important ancestors of animals used by them.

The superiority of this herd and the popularity it enjoyed can partially be appreciated by the fact that in 1930 Beau Brummel 51817 maintained a coefficient of relationship of nearly 25 percent to the Hereford breed and Anxiety 4th 9904 was still 18.5 percent related to the breed. Further indication of the general acceptance of the herd was the fact that a majority of the bulls bred by them were sold to the western range and they were a powerful influence in building up the great commercial herds of the west. That thousands of the descendants of the Gudgell and Simpson herd rendered good accounts of themselves on the open range in the hands of practical cattle growers is ample proof not only of their prepotency but is also convincing evidence that the inbreeding in this instance had not impaired the vitality of the Hereford.

Soon after the World War there developed in the Texas Panhandle a demand for "straight bred" Herefords which breeders defined as animals in which all the top lines of the pedigree traced to Anxiety 4th or North Pole. This movement was responsible for the further concentration of the blood of the Gudgell and Simpson herd which itself was the product of quite a bit of inbreeding.

The average coefficients of inbreeding and relationship for the Gudgell and Simpson for the two years in which samples were taken, according to Click (3) is shown in Table V.

TABLE V
INBREEDING AND INTER SE RELATIONSHIPS

Year	Pedigrees Sampled	Inbreeding Coefficients: Actually Found	Inbreeding Coefficients: Expected from Inter Se Relationship	Inbreeding Coefficients: Excess of Expected	Inter Se Relationship
1904	259	10.07	14.68	4.61	25.61
1914	277	14.59	19.45	4.86	32.57

If the average generation length of 5.4 years, Willham (17) can be applied to the Gudgell and Simpson herd, an increase of about 2.44 percent in the gene homozygosity of this herd would be indicated per generation for the period studied. The table also reveals that throughout the period studied the actual inbreeding found was considerably less than the expected inbreeding. This indicated that there was no appreciable segregation or grouping in the herd. It also showed a higher relationship between parents matched at random than between the actual sires and dams. This shows that they were avoiding inbreeding as much as possible through the use of a large number of sires.

Beau Brummel was nearly 36 percent related to all the animals of the herd born in 1914. This means he was almost half way between a sire and a grandsire to the herd at that time. Don Carlos was almost 28 percent directly related to the 1914 group of calves which means he was more than a grandsire to them. Anxiety 4th had a relationship of 24 percent, approximately that of a grandsire. North Pole was down to 15.5 percent or just a little closer than a great-grandsire. This study measured only the direct relationship between the herd and these important individuals. With the addition of collateral relationship these figures would increase. It is safe to say that the herd in 1914 was as much as 45 percent related to Beau Brummel, had the collateral relationship been considered, which is almost equivalent to that of a sire.

Gudgell and Simpson demonstrated in their herd that the concentration of the characters of outstanding sires by means of selection and line breeding combined is an excellent way to produce superior beef cattle.

G. A Brief History of the Hereford Cattle as Bred by Robert H. Hazlett.

Among the several men who have carried on the Gudgell and Simpson breeding, and probably the most prominent and successful, was Robert H. Hazlett of El Dorado, Kansas. (It is felt that a review of the breeding done by Gudgell and Simpson and by Hazlett is well included in this particular study since a later discussion will reveal a close connection between the herd to be studied and the above listed herds through the medium of the Turner Hereford Ranch of Sulphur, Oklahoma. The study of the Hazford Place Herefords made by Winchester, 1938, (18) contains the basic material of this review but a few other references will be included.) The herd was started in 1898 with the purchase of a small herd of Herefords bred by H. H. Grover near El Dorado.

Of the sixteen animals bought, fourteen were cows and heifers, the majority too young to breed. There were two bull calves both sired by Wild Beau 56099, by Beau Real, by Anxiety 4th. The dam of one of these calves, Major Beau Real, was Lou 2nd, then in the herd. She was by Stone Mason, by Beau Real, thus giving a strong concentration of Anxiety 4th blood in the calf, Major Beau Real. For two years Hazlett used the bulls, Major Beau Real, and Bernadotte 2nd, bred by Gudgell and Simpson. The latter bull, except for one grandsire, was of close Anxiety 4th breeding.

About this time he became influenced by older breeders that it would not be safe to continue such close line breeding further and that an out-cross was necessary. In the next two years he bought three different bulls (all straight out-crosses and good individuals of very popular breeding). All of these were used with very disappointing results. From all the heifers sired by the three bulls, only one was kept in the herd. Hazlett had by this time devoted a lot of thought and study to the science of breeding. The results of close breeding, as he had followed before trying the out-cross experiments, had been very satisfactory. He had a greater percent of good to outstanding calves. He then decided to go back to the Anxiety blood lines and use, so far as possible, nothing but sons of Beau Brummel for the near future, and follow that line of breeding indefinitely unless he learned, from experience, that close breeding would injure or destroy the usefulness of the herd.

In his private Herd Catalogue, Hazlett, 1925, (7) shows that he used after that Beau Brummel 10th, Beau Beauty, Printer and Beau Santos, all good sons of Beau Brummel. Following these sons of Beau Brummel, he used Caldo 2nd by Printer, Beau Baltimore by Beau Beauty, Paragon 12th who was a very close Anxiety 4th bred bull, and Publican by Paladin by Lamplighter by Don Carlos. As Beau Brummel was by Don Carlos, all the herd bulls he used, except Major Beau Real, trace to Don Carlos. Mr. Gudgell, of Gudgell and Simpson, always felt that Don Carlos did not receive his share of the credit for the excellence of their herd.

Mr. Hazlett felt that the matter of selection was as least as important as blood lines, whether a herd was composed of close bred cows, or cows promiscuously bred. He was always quite rigid in his policy of neither breeding or selling for breeding purposes any animal of any line of breeding which had any serious fault or weakness in conformation, quality or breed character. He continually practiced strict culling and these culls were always marketed as beef and not sold as second grade breeders. He believed that this was not only good business, but the right thing for the good of the breed. The value of Mr. Hazlett's system of breeding and rigid selection has been passed on by practically every prominent Hereford judge in America during his show ring career extending from 1915 to 1936. His long list of winnings cannot be given here but his top honor probably was the winning of the grand champion bull award at the International in Chicago four different years. The winners were Bocaldo 6th in 1916, Bocaldo Tone in 1926, Zato Rupert in 1933, and Hazford Rupert 81st in 1936. The 1936 International, which was his last, also saw a Hazlett cow, Bonita Zato, named grand champion female which was a fitting climax to an illustrious record.

In the Hereford Register of Merit (as of 1938) there are four bulls produced at Hazford Place. Of the eighty cows in this register, twelve of them were produced there. One, Izatone, is the highest ranking female in the entire register.

Following Mr. Hazlett's death in 1937 the entire herd was dispersed at auction. The chief buyer at this sale was the firm of Harper and Turner of Sulphur, Oklahoma. They bought ten head which were being fitted for the fall shows as well as 46 other animals. Among the latter were Hazford Tone 76th, one of the chief Hazford Place sires, and Hazford Tone 74th, formerly one of Hazlett's show bulls and later a popular sire.

The average coefficients of inbreeding and relationship for the Hazlett herd for the six years in which samples were taken is presented in Table VI, Winchester, (18).

TABLE VI
INBREEDING AND INTER SE RELATIONSHIPS

Year	Pedigrees Samples	Inbreeding Coefficients: Actually Found	Inbreeding Coefficients: Expected from Inter Se Relationship	Inbreeding Coefficients: Excess of Expected Over Actual	Inter Se Relationship	
1900	13	7.7 ± 1.6	30.4	22.7	46.1	± 2.9
1908	68	11.0 ± 0.8	13.5	2.5	23.5	± 3.3
1915	67	9.7 ± 0.8	19.9	10.2	32.8	± 3.8
1922	121	11.2 ± 0.6	17.1	5.9	28.9	± 2.7
1929	89	14.6 ± 0.8	18.9	4.3	31.5	± 4.0
1936	227	15.0 ± 0.5	17.2	2.2	29.1	± 2.0

The coefficient of inbreeding for the 1900 group was 7.7 percent which is about 5 percent greater than for the breed as a whole at that time. This means that the foundation animals of the Hazlett herd were approximately 5 percent less heterozygous than the average Herefords of the United States at that time.

There was an increase in the coefficient from 1900 to 1936 of 7.3 percent in the herd. This represents a decrease in heterozygosis of about 1.15 percent per generation when we apply the generation interval of 5.4 years. Willham,(17). The coefficient of inbreeding for the Hereford breed as a whole in 1900 was only 2.7 percent, and from 1900 to 1930 it increased to 8.1 percent representing about 1.0 percent decrease in heterozygosis per generation. Thus the rate of gene fixation which took place in the Hazlett herd was only slightly above that of the entire breed during those periods. The difference in the final percentage of inbreeding for the Hazlett herd and for the Hereford breed during that period is due primarily to the difference in the inbreeding of the foundation animals which he used.

The coefficient of inbreeding observed was well below that expected from the coefficient of inter se relationship which was maintained rather constantly at about 29 percent. This indicated that the herd was a somewhat homogenous unit of related animals rather than being divided into families or groups between which there was little relationship. The difference between the observed inbreeding and that expected indicated that inbreeding in general was avoided. We find that these same principles of breeding held true in the herd of Gudgell and Simpson from which it largely sprang. This is significant in that it represents almost a continuous herd with a continued constant breeding policy for a period of some sixty years because of the very close association of foundation stock, breeding policy and high ideals maintained successively by Gudgell and Simpson and by Robert H. Hazlett. It was also fortunate for the breed as a whole in thus maintaining a constant source of comparatively pure blood of Anxiety 4th.

The Hazlett herd in 1936 was about 25 percent directly related to Beau Brummel 51817 and to Bocaldo 6th 484626. In other words, they are a little more closely related to this group than grandsires. The herd in 1936 was a little more than 17 percent directly related to Hazford Tone 1093542, Don Carlos 33734 and Anxiety 4th 9904.

H. A Brief History of the Hereford Cattle as Bred by Oklahoma A. & M. College.

The Hereford herd at Oklahoma A. & M. College had its beginning sometime before May 4, 1900 as this is the date of calving of the first animal registered by the College in the American Hereford Record. In Herdbook No. 23 the College registered two bull calves which were bred by J. M. Curtice of Kansas City, Missouri. They were Gems Hesiod 114462 and College Hesiod 120049 with the former being calved May 4, 1900 and the latter July 14, 1900. The College purchased two cows, Gem Washington 72848 and Cherry Hesiod 80998, both of whom were with calf by the service of the bull, Hesiod 50th 76440. The results of these matings were the two bull calves mentioned above.

Mr. Curtice's bull, Hesiod 50th 76440, carried some exceptionally popular Hereford blood of the era. He was by Hesiod 2nd 40679, by the imported bull Hesiod 11925, by the great sire, The Grove 3rd 2490. Hesiod 50th was out of the cow, Fern 51625, whose sire was Don Carlos 33734 and whose dam was Petuna 3rd 27417 by Anxiety 4th 9904. We give his breeding because his son, Gems Hesiod 114462, was later used as a College herd bull.

The two cows, Gem Washington and Cherry Hesiod, were used for several years in the herd. Gem Washington 72848 traces back to Lord Wilton 5739 twice on her dams side in three and four generations respectively but otherwise her breeding is rather common. Cherry Hesiod 80998 was by Reliance 59154 by Hesiod 2nd 40679 by Hesiod 11925 by The Grove 3rd 2490 but otherwise shows no particular line of breeding. Each of these cows produced five calves registered by the College in the Hereford Herd books.

The five calves produced by Cherry Hesiod included four bull calves, none of whom are shown as used later in the college herd. However, the one daughter, College Cherry 142467, was used for a number of years in the herd and produced several calves which were registered by the college. The five calves produced by Gem Washington also included four bulls and one heifer. The heifer, Martha Washington 231334, was used in the herd with apparently good results for several years.

Gems Hesiod 114462, out of Gem Washington and the first registered Hereford calved on the College farms, was used later as a herd sire. He was mated with Cherry Hesiod 80998 and her daughter, College Cherry 142467. This line breeding resulted in a calf in the first case that was .03125 inbred to Hesiod 2nd 40679 and in the second case that was .015625 inbred to Hesiod 2nd 40679.

For a period of nine years no other females were brought into the herd and all the offspring were out of these two foundation cows and the two daughters mentioned. The two sires used almost exclusively were Gems Hesiod 114462 and Cadet 202174. Then in 1909 two more cows were purchased. One of these was Donna Anna 28th 303895 from the Gudgell and Simpson herd and bred to the famous Domino 264259. She bore a bull calf, Dominion 369038, who was kept for a herd sire. The other cow was Maxine 295540 purchased as a bred cow from Wm. Hutcheon of Bolchow, Missouri.

From 1909 until 1914 there was no particular activity indicated by the Hereford Record books. Then in 1914 the College went back to J. M. Curtice at Kansas City and purchased seven bred cows and practically all of these brought heifer calves. Three of these cows, Laura Perfect 322163, Miss Perfect 19th 246832, and Edna Champion 234053 were bred to Beau Perfect Jr 362129. The other four cows, Mascot 386363, Donna Perfect 5th 386509, Donna Perfect 4th 386508, and Gem Perfect 234054, were bred to Don Perfect 400000. All seven cows dropped calves during the months of June and July 1914.

From the beginning of the herd until the year 1917 it was maintained on a rather small scale as is indicated by the number of registrations made during the first sixteen years which totalled only twenty-five. This included all animals owned by the college at calving time of which a good number were actually bred by others. The year of 1917 saw the start of the establishment of a breeding herd of larger proportions and the records show that 16 animals were registered that year. Up to March 1929 there were one hundred fifty-three animals registered in the name of the college in the Hereford Record. Numbers for the last seventeen years are not available as no copies of the Record beyond Volume 76 are available in the College library.

In defense of the comparatively small number of animals registered annually we should state here that it has been the policy of the Department of Animal Husbandry at Oklahoma A. & M. College for many years to use the college Hereford herd primarily for the production of steers to be fitted later for competition as fat animals. For most of the forty-six years of its existance this practice has been followed very successfully as is shown by the consistent winnings of the College in the steer shows of the nation. This same policy has had a tendency to discourage much line breeding or continuity of breeding along the lines of any particular family.

Beginning with the period directly after the First World War and continuing to the present time we find the following succession of main herd sires:

Bras Repeater	935783	Beautys Bocaldo 17th	
Progress	1727750	Lassies Tone	1759101
WHR True Domino 6th	2080632	Hazford Tone 158th	2593856
T. Royal Rupert 23rd	3040702		

Of course a large number of other bulls were used but none of them to the extent that the above listed seven sires were used.

During the last ten years, particularly since the Hazlett dispersion sale and the establishment of the Turner Hereford herd in the state, there has been a rather pronounced trend to the use of animals with either Hazlett or Turner blood in the college Hereford herd. During that time all herd sires have been of this breeding and a considerable number of females of these blood lines have also been purchased. In addition it seems to have been the policy to keep for breeding animals almost exclusively the female progeny of cows of this breeding. This means that as a whole there is at present only a very small remnant of the blood lines that were established in the herd at its origin or infused into it during the first thirty years of its existance.

It is evident that the history of the college herd is essentially different from that of the herds of Gudgell and Simpson and of Robert H. Hazlett. In both of these herds, which were reviewed earlier, the history of the herd was in reality a picture of a long time breeding plan reflected directly in the composition of the breeding herd at every period of its life. In contrast, the history of the Oklahoma A. & M. College Hereford herd is simply a picture of the changes in the herd and only a small portion of the history is reflected in the present breeding herd of eighty-five animals which are the basis of this study.

III. THE INVESTIGATION

A. Method of Procedure

1. Coefficient of inbreeding.

The methods used in this study were developed by Wright, 1922, (20) and Wright and McPhee, 1925, (23).

The coefficient of inbreeding developed by Wright, 1922, (20), measures the approximate percentage of genes that have changed from a heterozygous state in the foundation stock to a homozygous state in the offspring as a result of inbreeding. Since it is based upon the statistical laws of probability, it is subject to the errors inherent therein. Therefor, it is not an absolute, but a relative measure of the inbreeding of an animal. It measures the probable similarity between the egg and sperm cells which unite to form the individual in question, relative to the similarity of random germ cells from the foundation stock.

A pedigree to show inbreeding must have the same animal appearing in one or more lines back of both the sire and the dam. The closer the animal responsible for the inbreeding is to the sire and dam the greater will be his contribution to the inbreeding of the animal. Likewise, greater will be the probability that the genes contributed through the sire and through the dam will be similar, thus establishing a state of homozygosity in the offspring for the characters in question. In the event the animal responsible for the inbreeding in a pedigree is himself inbred, even greater will be the probability that the genes he transmits to an offspring, through the sire and dam, will be similar. Thus, a method for computing inbreeding must attach a value to such a common ancestor which is proportionate to his degree of inbreeding.

The formula for computing the coefficient of inbreeding developed by Wright is as follows:

$$F_x = \sum \left[(\tfrac{1}{2})^{n + n' + 1} \; (1 + F_a) \right]$$

In this formula, F_x is the required coefficient, and F_a is a similar coefficient for any common ancestor that makes the closest connecting link between a line of ancestry tracing back from the sire and one tracing back from the dam. The factor $(1 + F_a)$ takes care of the contribution made by any common ancestor who is himself inbred. The Greek letter $\sum$ means "the sum of". The "n" is the number of generations back from the sire to the common ancestor, and the "n'" is the number of generations back from the dam to the common ancestor. A particular tie between the pedigrees of a sire and a dam contributes $(\tfrac{1}{2})^{n+n'+1}(1 + F_a)$. The factor $(\tfrac{1}{2})$ represents a 50-50 chance which occurs at each Mendelian segregation. In other words, the physiology of animal reproduction is that two sex cells are formed from one original, and the chances are even that any specific gene may be in either one or the other. Of course, the new individual formed is the product of only one sex cell from each parent. The $\tfrac{1}{2}$ is multiplied by n+n'+1 to take care of the comparative chance involved relative to n and n'. It is evident that every segregation or generation that a common ancestor is removed from the sire and dam, the probability that a particular gene will reach the offspring is halved. The total coefficient F_x is simply the sum of the contributions made by each common ancestor.

The coefficient of inbreeding is based on two major assemptions: first, that inheritance in Mendelian; and second, that the sire and dam contribute equally to the offspring. There is little question about the first, but the latter may be modified slightly by characters which are sex-linked. Only a slight discrepancy may be expected to arise from sex-linked characters in farm animals due to the large number of chromosomes which farm animals have, and the likelihood of only a few genes being sex-linked. The effects of sex-linked characters would tend to cancel since sires have no influence on their sons, but transmit these characters to their daughters as though they were homozygous. Inbreeding in a female's pedigree has no effect on her sex-linked genes when the line of descent is from sire to son, but when the line of descent is from sire to daughter, a higher degree of homozygosis for the sex-linked characters results. As the result of mother-son or father-daughter matings, there is expected a decrease of 29.3 percent in the heterozygosis in sex-linked genes, and 19.1 percent in autosomal genes.

2. Coefficient of relationship.

Closely related to the coefficient of inbreeding is the coefficient of relationship which measures the degree of correlation to be expected between two individuals in characters which are wholly genetic and without dominance. Since this coefficient is based on the assumption that correlation between parent and offspring or between brothers in a random stock is 50 percent, its interpretation, therefor, depends upon the genetic status of the foundation stock.

The following formula has been prepared by Wright, 1923, (21):

$$R_{xy} = \frac{\sum\left[\left(\frac{1}{2}\right)^{n+n'}(1+F_a)\right]}{\sqrt{(1+F_x)(1+F_y)}}$$

In this formula F_x and F_y are coefficients of inbreeding for the two animals in question. X and Y are used to represent the two animals being correlated. F_a is the inbreeding coefficient for the closest common ancestor connecting a pair of ancestral lines in their pedigrees. The factors n and n' are the number of generations from x and y to this common ancestor along the lines in question. R_{xy} is the required coefficient and may vary from 0 percent to 100 percent. This is a more accurate measure than would be obtained on the basis of the percentage of common blood in the two animals. Full brothers and sisters have 100 percent common blood. The percentage of common blood measures direct relationship where there is no inbreeding, but fails to measure collateral relationship such as exists between double cousins, for instance. Full brother and sister mating, according to the above formula, would yield a relationship of 50 percent. The factor $(1+F_a)$ weights the contribution made by a common ancestor. For further details of this formula the reader is referred to Wright, 1923, (21).

3. Approximate method of calculating coefficients of inbreeding and relationship from livestock pedigrees.

Wright and McPhee, 1925, (23) have developed an approximate method of calculating coefficients of inbreeding and relationship from livestock pedigrees. The approximate method depends on the tabulation of random lines back through the pedigrees of the sire and dam. The standard error involved can be calculated from the ordinary theory of sampling. A two-line random pedigree is therefor not at all complete as it consists of only a single line of ancestry back from each sire and dam. Even a four-line random pedigree is quite incomplete as it consists of only a single line of ancestry back from each grandsire and granddam. It is necessary that the sample lines be chosen wholly at random. Obviously, more of the common ancestors involved will be males, in livestock breeding, than females. Thus straight male or straight female lines can not give a fair basis for calculating the number of ties between either two-line or four-line pedigrees. Fairly accurate results can be obtained by alternating males and females but the accuracy of such a system can not be tested by the theory of sampling.

A truly random line of ancestry can be obtained by letting the sequence of sires and dams which are to be traced back in the herd-book be that of the heads and tails, respectively, in a coin tossing experiment. The same sequence should not, of course, be used frequently in the same study.

An example of this system is shown in Table III which is from a pedigree of Hazford Tone, 1093542, taken from the sample of sires used in this study.

TABLE III

HAZFORD TONE 1093542 CALVED SEPTEMBER 7, 1921

SIRE Bocaldo 6th 464826				DAM Tonette 2nd 722110			
GRANDSIRE Bocaldo 362186		GRANDDAM Buleen 372147		GRANDSIRE Publican 4th 429762		GRANDDAM Tonette 429765	
Sires	Dams	Sires	Dams	Sires	Dams	Sires	Dams
260444		192235			328056		121409
	155310	51817		260444		51817	
	93294	33734			155310	33734	
68061			6932		93294	9904	
20109					58939		
	4467			39258			
					9436		

Naturally, a second sample of the same pedigree would not show the same sequence of sires or dams. In this table note the tie between the two lines under the paternal granddam and the maternal granddam in which Beau Brummel 51817 becomes the common ancestor. In a second sampling of the same pedigree Beau Brummel might not even appear in any line, or he might appear in only one line, or he might appear in both lines of either the sire or the dam. In this case no inbreeding would be shown in Hazford Tone through Beau Brummel.

An interesting example of what would occur had we used a straight male line for a sample rather than a truly random line is shown in Table IV, which is also from a pedigree of Hazford Tone, 1093542.

TABLE IV

HAZFORD TONE 1093542 CALVED SEPTEMBER 7, 1921

SIRE Bocaldo 6th 464826				DAM Tonette 2nd 722110			
GRANDSIRE Bocaldo 362186		GRANDDAM Buleen 372147		GRANDSIRE Publican 4th 429762		GRANDDAM Tonette 429765	
Sires	Dams	Sires	Dams	Sires	Dams	Sires	Dams
260444		192235		189221		323941	
66684		51817		126248		264259	
51817		33734		51834		189221	
33734		9904		33734		126248	
9904				9904		51834	
						33734	
						9904	

Table IV shows the closest tie through Don Carlos 33734 as the common ancestor in all four lines. He comes down to Hazford Tone through Beau Brummel in both lines from Bocaldo 6th, the sire of Hazford Tone. He comes down to Hazford Tone through another son, Lamplighter 51834, in both lines from Tonette 2nd, the dam of Hazford Tone.

A further check (which will not be shown in tabular form) reveals that every one of the eight great grandparents of Hazford Tone 1093542 traces in a straight male line directly to Don Carlos 33734 in from two to four generations, six times through the son, Beau Brummel, and two times through the son, Lamplighter. Thus it would be rather uncommon for a truly random line to fail to show some inbreeding in the pedigree of Hazford Tone. This is further emphasized when we find that in addition to all eight great-great grandsires tracing in a direct male line to Don Carlos, five of the eight great-great granddams trace in a direct male line to Don Carlos.

It is well to make clear that a single sample of this sort is practically worthless as an indication of the inbreeding of one individual. The average, however, obtained from a large group of pedigrees should not vary appreciably from the actual inbreeding of the group. Either the two-line or four-line samples of this kind fall at once into two classes: those which show an ancestral connection, as do those in Table III, and those which have no common ancestor. In the latter case the coefficient is zero so far as the particular sample is concerned. In the case of the four-line samples the tie must be between one of the two lines from the sire with one of the two lines from the dam in order to establish inbreeding on the part of the animal in question. Occurrence of a common ancestor in the two lines from the sire, for instance, would only indicate that the sire was inbred but would not indicate inbreeding on the part of the animal itself.

In the example given in Table III a contribution of $(\frac{1}{2})^{n+n'+1}(1+F_a)$ is indicated if the common ancestor is n generations back of the sire and n' generations back of the dam. In a complete pedigree, the number of ancestral lines doubles with each generation from the offspring. Thus, in a random sample pedigree, the chance of non-occurrence of a specific ancestor doubles with each generation from the offspring. The sire has 2^n ancestors in the nth generation and the dam 2n' ancestors in the n'th generation. The sample pair of lines is only one among the $2^{n+n'}$ possible pairs going back as far as the common ancestor. Therefor, if the sample pair of lines is a fair sample of the total, its contribution must be multiplied by $2^{n+n'}$ to obtain a fair estimate of the inbreeding of the whole pedigree.

On carrying out this multiplication, the n and n' disappear, and the coefficient takes the simple form of $\frac{1}{2}(1-F_a)$ in the two line sample pedigree and $\frac{1}{8}(1-F_a)$ in the four line sample pedigree. Therefor, it is not necessary, in calculating the inbreeding, to count the generations to the closest common ancestor or tie, but merely to note whether there is a tie and, if so, what animal is responsible for it. The coefficient of inbreeding for a group of animals is the sum of all such contributions divided by the number of animals in the group.

To secure a fairly dependable coefficient for the various common ancestors involved, it is necessary to resort to a more complete pedigree. A rather accurate figure can be obtained by the random method, however, providing that a number of such lines is tabulated from each pedigree. The more satisfactory method which is being used in this paper includes a complete pedigree for the first five generations and each of the lines then randomed to the foundation stock. A tie occurring in the random portion of the pedigree is worth approximately the same as one in the fifth generation, and may be considered so in computing the coefficient. The formula, $F_x = \sum \left[(\frac{1}{2})^{n+n'+1}(1+F_a)\right]$, has previously been explained in this paper. A coefficient of inbreeding that is rather highly reliable should be secured for those common ancestors responsible for the larger number of ties.

The standard error of the percentage of ties occurring can be calculated by the formula, $\frac{pq}{n}$, where n is the number of cases, p is the observed chance of the occurrence of a tie, and q, $(1-p)$, is the chance of non-occurrence. The standard error of $F_x = \sqrt{\frac{pq}{n}} \times \left(\frac{F_x}{p}\right)$. The factor $\frac{F_x}{p}$ is used to rate the standard error for the percentage of ties down so that it will apply to the coefficient of inbreeding.

The standard error for the percentage of ties measures the error which may result in sampling due to the use of incomplete pedigrees. The standard error of the coefficient of inbreeding does not measure the chance involved at the time of segregation.

The calculation of coefficients of relationship from random samples of pedigrees presents no additional complications of importance.

The presence of a tie between single random lines back of two animals considered, (x, y) indicates a coefficient of relationship equal to

$$\frac{1 + F_a}{\sqrt{(1 + F_x)\ (1 + F_y)}}$$

The standard error is calculated from the proportion of ties and is rated up by the ratio of the coefficient to this proportion as in the case of the inbreeding coefficient.

4. Analysis of the Oklahoma A. & M. College Herd.

In the present study the sample consisted of all the animals in the College Hereford breeding herd as of December 31, 1945 which numbered eighty-five individuals. These animals are all registered in the American Hereford Record. Since there has been no particular continuity of breeding lines during the forty-five years of the herd history it is felt that a study of the 1945 sample is more accurate and representative of the herd than the ordinary sampling which might include all the animals registered in certain years determined by regular intervals during its stage of activity.

Four line pedigrees were used. The date selected as the base to which all the pedigrees were to be traced was 1880 which was the birth year of Anxiety 4th 9904. This would include all the breeding activities of the College herd and would give a fair estimate of the foundation stocks used. In finding the coefficient of inbreeding for all animals responsible for a total of two or more ties, considering both inbreeding and inter se relationship, pedigrees were completed for five generations and then randomed to the base date. For animals responsible for only one tie a coefficient was ascribed which was equal to the average coefficient for the Hereford breed as a whole as determined by Willham, (17) at about that time.

The sequence of sires and dams which was used in the random lines was determined by the tossing of a coin. "Heads" was made to represent a male and "tails" to represent a female.

The same samples were used in determining the inter se relationship as were used in determining inbreeding.

The entire group of pedigrees was thoroughly mixed so that any two picked up together for matching represented pure random choice. A coin was tossed for each pedigree to determine whether the sires line or the dams line would be matched first and then another coin tossed to determine whether the sires line or dams line of the chosen animal would be matched first. The lines thus selected were compared and the ties marked. After the entire group was thus compared, they were again mixed. Again they were picked up in pairs as indicated in the coin tossing explained above with, of course, one line already eliminated by the previous comparison. This process was continued until every line on each pedigree had been compared with some line on some other pedigree. After all lines had been compared and all ties marked, a tabulation was then made of all ties according to the common ancestors.

In computing the coefficient of relationship between important sires and the 1945 sample, only direct relationship was considered. This was determined by tabulating from all the 1945 pedigrees the number of times each animal appeared in the random lines. The direct relationship equaled $\frac{\text{Total number of appearances}}{\text{Maximum possible appearances}}$.

No particular study was made of the foundation animals in the College herd. The original source of these animals was merely noted as herd history.

B. Results

1. Inbreeding and Inter Se Relationship.

The average coefficients of inbreeding and inter se relationship for the Oklahoma A. & M. College herd for the year of 1945 which was the year chosen for the sampling is presented in Table VI.

TABLE VI

INBREEDING AND INTER SE RELATIONSHIPS

Year	Pedigrees Sampled	Inbreeding Coefficients: Actually Found	Inbreeding Coefficients: Expected from Inter Se Relationship	Inbreeding Coefficients: Excess Over Expected	Inter Se Relationship
1945	85	16.63% ±1.32	4.18	12.45	8.04% ± 1.01

The coefficient of inbreeding measures the percentage of genes fixed for the particular year which were fixable but not yet fixed in the foundation animals of the herd. For example, the coefficient of inbreeding of 16.63%±1.32 found in the 1945 sample means that the average animal included in that sample was 16.63 percent less heterozygous than the average animal in the foundation stock of 1880.

The base date to which the pedigrees were traced was 1880. It is obvious, however, that all the lines would not end with an animal born exactly on that date. In this study the random lines were carried back either to an animal born in 1880 or, if the line did not end in an animal born in 1880, to the first animal in the line born immediately prior to 1880. Therefor the actual base date would be somewhere about 1877 or 1878. In this study the only sample taken was that of 1945 which included all the registered animals of the herd. College herd records did not include the listing of the individual members of the herd for any prior dates and since it has been primarily a steer producing herd a sampling of the registrations made at periodic intervals would not be in any way representative of the herd composition nor indicative of its breeding. Therefor, it is not possible to statistically determine the amount of this inbreeding which has occurred within the herd itself and that amount which was brought into the herd through purchase of breeding stock from outside herds. Likewise it is not possible to statistically determine whether this amount of inbreeding has been due to a gradual process of increase of inbreeding or to a rather abrupt rise in this respect due to the infusion at some particular time of rather highly inbred blood lines. For the same reasons, no attempt is made to determine the increase in inbreeding per generation. By a process of deduction we can get the probable answers to part of these questions as will be shown properly under the heading of "Discussion".

The coefficient of relationship, also shown in Table VI, is a measure of the approximate relationship existing between animals in the herd selected at random. The significance of these figures is dependent upon the inbreeding coefficient. McPhee and Wright, 1925, (11) have shown that the percentage of inbreeding expected from the purely random mating among the sires and dams of a group of any size may be calculated by the formula $F_x = \frac{R}{2-R}$ where F_x is the desired coefficient and R represents the coefficient of inter se relationship.

In column four of Table VI is presented the inbreeding coefficient of the sample which would be expected from purely random mating in this particular herd. This figure, in comparison with the coefficient of inbreeding observed, reveals at once whether the herd at the particular time tended to be divided into rather distinct groups or whether the members of the herd are rather highly interrelated. The higher the inter se relationship, the higher in proportion is the expected coefficient of inbreeding. For instance an inter se relationship of 50 percent would bring an expected inbreeding coefficient of 33 percent, while an inter se relationship of 10 percent brings only an expected inbreeding of 5.03 percent. In the present study, the amount of inbreeding observed was radically higher than that expected from the inter se relationship, indicating a very definite segregation into a considerable number of small groups. The fact that the observed inbreeding was materially higher than the expected inbreeding shows that there existed a much closer relationship between the various sires and dams than between parents of the herd matched at random.

The very low inter se relationship of the 1945 herd is partially due to the fact that the eighty-five animals are sired by twenty-nine different bulls, with only five bulls siring more than five different animals in the herd. Eighteen bulls were found to have sired only one animal each of the present herd.

2. Animals Used as Foundation Stock.

The foundation animals of the Oklahoma A. & M. College herd as they relate to this study will be dealt with later in the discussion. Briefly, the foundation stock of the present herd came from rather close bred herds which were line bred to Anxiety 4th 9904. With the exception of a few individuals, the foundation animals of the present herd came from the Turner Hereford herd at Sulphur, Oklahoma. Previous studies, reviewed briefly in this study, reveal that his foundation animals largely originated in the Robert H. Hazlett herd and the foundation animals of the Hazlett herd largely originated from the Gudgell and Simpson herd.

3. Sires Contributing Most to the Herd.

Table VII gives the most important sires with relation to this herd, their coefficients of inbreeding and their percentage of relationship to the present herd. The percentage of inbreeding shown in column six of the table is important in that it is a measure of the prepotency of this group of the most widely contributing sires. Column five in the table shows the percentage of direct relationship existing between these sires and the 1945 herd. This indicates the concentration of the blood of these sires within the herd at the present time. The date each sire was calved is shown as an indication of the period of years through which this relationship has existed. Beau Brummel 51817 has direct relationship of 31.5 percent to the herd, Don Carlos 33734 a direct relationship of 23.8 percent, while Hazford Tone 1093542, North Pole 8946, Anxiety 4th 9904, and Bocaldo 6th 464826 have direct relationships ranging downward in the order named from 20.3 percent to 17.0 percent.

TABLE VII

COEFFICIENTS OF INBREEDING AND RELATIONSHIP OF IMPORTANT SIRES

Name	Registry Number	Date Calved	Number of Appearances	% Related to 1945 Herd	Coefficient of Inbreeding
Hazford Rupert 81st	2348825	1-12-'35	32	9.41	.0334
Prince Rupert	2247105	6- 8-'34	23	6.76	.0133
Hazford Tone 76th	2127388	1-10-'33	30	8.83	.1111
Hazford Rupert 25th	1209734	2-19-'23	38	11.17	.0320
Hazford Tone	1093542	7- 9-'21	69	20.29	.0692
Hazford Rupert	634535	1-24-'17	30	8.83	.0254
Prince Domino	499611	9-13-'14	30	8.83	.1826
Bocaldo 6th	464826	3-20-'14	58	17.06	.1571
Publican 4th	429762	4-24-'13	39	11.47	.0712
Bocaldo	362186	1- 4-'11	34	10.00	.0494
Domino	264259	9-17-'05	23	6.76	.1810
Caldo 2nd	260444	11-23-'06	39	11.47	.0353
Beau Beauty	192235	6- 5-'03	33	9.71	.1206
Publican	189221	1- 3-'04	31	9.12	.1168
Printer	66684	11-11-'95	25	7.35	.0730
Lamplighter	51834	10-11-'91	27	7.94	.0039
Beau Brummel	51817	10- 5-'90	107	31.47	.0127
Don Carlos	33734	11-18-'86	81	23.82	.0117
Anxiety 4th	9904	5-23-'80	63	18.53	.1582
North Pole	8946	6-17-'80	65	19.12	.0000

Possible Appearance 340

TABLE VIII

SIRES OF PRESENT COLLEGE HERD

Name of Sire	Sires Number	Number Animals Sired
Tone T 75th	3742977	10
T. Rupert Mixer	3675308	1
Pontotoc Tone	3555555	1
Commando Rupert	3555000	1
Beau Zento 54th	3510744	1
Hazford Rupert 139th	3101784	2
T. Royal Rupert 23rd	3040702	11
T. Tone Again	3029016	1
Tone of Windsor	3013030	1
Tone T. 44th	2893337	4
T. Royal Rupert 8th	2893325	1
H. T. Royal Rupert	2797963	1
T. Bocaldo Tone 2nd	2719029	1
Windsor Tone	2714434	1
Hazford Tone 158th	2593856	5
H. T. Tone	2442887	7
Hazford Rupert 81st	2343825	9
College Tone 16th	2305028	1
Prince Rupert	2247105	9
Bocaldo Tone 19th	2207431	1
Mischief Aster 25th	2188720	1
Hazford Tone 76th	2127388	4
Hazford Tone 74th	2127386	3
WHR True Domino 6th	2080632	1
WHR Royal Domino 4th	2030595	1
Dandy Domino 90th	1836512	1
Lassie Tone	1759101	3
Bocaldo Tone 3rd	1733232	1
Progress	1727750	1

Total Animals in Sample 85

TABLE IX

Breeder of Individual Animals in Present Herd. (By Year of Calving)

Breeder	'45	'44	'43	'42	'41	'40	'39	'38	'37	'36	'35	'34	Total
Oklahoma A. & M. Stillwater, Okla.	21	4	4	1	2	1	2		2		1	1	39
Turner Ranch Sulphur, Okla.	3	6	1	3	3	7	7	2	3				35
Duncan Ranch Mill Creek, Okla.											1		1
Essar Ranch San Antonio, Texas				1									1
R. H. Hazlett El Dorado, Kansas									1	2			3
C. C. Buxton Oklahoma City, Okla.				1									1
W. E. Harvey Ada, Okla.					1								1
Walter Bones Minneapolis, Minn.										1			1
Fred C. DeBerard Kremling, Colo.									1				1
H. N. Arnold Buffalo, Okla.						1							1
W. C. Windsor Boonville, Mo.				1									1
Annual Total	24	10	5	7	6	9	9	2	7	3	2	1	85

Table IX gives some indication of the reason for the comparatively low coefficient of relationship existing in the herd at present. If the 1945 calf crop is disregarded, only nineteen of the animals in the herd were bred by the College as compared with thirty-two bred by the Turner Ranch of Sulphur, Oklahoma.

A study of the sires of the 39 animals bred by the College revealed that every one of the sires was bred either by the Turner Ranch or by R. H. Hazlett of El Dorado, Kansas, in the case of the older animals.

Table X gives further indication of the breeding trend of the present herd by listing the breeders of the dams of the 39 animals in the herd which were bred by the College.

TABLE X

Breeder of the Dams of College Bred Animals in Present Herd
(By Year of Calving)

Breeder	'45	'44	'43	'42	'41	'40	'39	'38	'37	'36	'35	'34	Total
Oklahoma A. & M. Sire Turner or Hazlett Bred	6	2	2		2	1			2			1	16
Oklahoma A. & M. Grandsire Hazlett Bred							1				1		2
Turner Ranch Sulphur, Okla.	12	1	2	1			1						17
Essar Ranch San Antonio, Texas	1												1
C. C. Buxton Oklahoma City, Okla.	1												1
Fred DeBerard Kremling, Colo.	1												1
W. E. Harvey Ada, Oklahoma		1											1
Annual Total	21	4	4	1	2	1	2	0	2	0	1	1	39

Tables VIII, IX and X clearly indicate that the current breeding policy of the College herd has been definitely to Anxiety 4th 9904 blood lines as brought down through Gudgell and Simpson, Robert H. Hazlett, and the Turner Hereford Ranch. This accounts to a large degree for the intensity of inbreeding. On the other hand the fact that 29 different sires were used to produce 85 offspring helps to account for the low percent of relationship existing in the herd.

IV. DISCUSSION

The Oklahoma A. & M. College Hereford herd was established early in 1900. At that time, Willham, 1937, (17), found that the coefficient of inbreeding of the Hereford breed as a whole was nearly three percent, that is, three percent less heterozygous than it was in 1860. In 1900, Winchester, 1938, (18) found that the Hazlett herd was about 7.7 percent inbred which was more than twice the inbreeding found in the breed as a whole. Although little was determined as to the amount of inbreeding existing in the foundation cows of the College herd it can be assumed from the casual observation that the inbreeding was probably closer to the breed average than to that of Hazlett's herd which had the benefit of the line breeding program carried on for so many years by Gudgell and Simpson. The original foundation stock largely came in the form of bred cows purchased from J. M. Curtice of Independence, Missouri. Mr. Curtice operated a Hereford breeding farm from 1897 till his death in 1916. Apparently Mr. Curtice did not at first practice very much inbreeding according to Hazelton, 1935, (6) who shows his foundation stock to have been purchased about equally from three northern breeders and his first four herd bulls to have a variety of blood lines. Two showed Anxiety 4th 9904 blood coming down through Don Carlos and Lamplighter, and one traced back to Anxiety 4th 2947, a half brother of 9904.

The above breeding was evidently what the College secured in the first cows purchased from Curtice. However, later Curtice used a son and a grandson of Beau Brummel 51817 and a son of Prince Rupert 8th as sires in building his herd to its greatest popularity. As the College got several of their animals at the Curtice dispersion sale it is rather probable they then got stock with a higher inbreeding coefficient.

As indicated in the history of the herd given earlier in this study no attempt was again made to increase materially the number of animals in the herd until the early twenties when an effort was made to build up the quality of the herd. At the International sale in 1922 a young bull was purchased that had just placed second as a junior yearling in the International Show. This bull was Brae Repeater 986783 who came from the herd of Hott Brothers of Wonewoc, Wisconsin. He was an extremely good type bull and sired wonderful steers one of which, Rupert B, was Grand Champion steer at the 1926 International, and another, College Ideal, was Grand Champion steer at the 1929 American Royal.

Brae Repeater spent all but two of the fifteen years of his life in active use in the College herd and did much to popularize the Hereford breed in the state because of his ability to sire good steers. However, he leaves very little imprint on the herd today. In the 340 random lines of this study he appeared only twice as compared with 69 appearances of Hazford Tone 1093542, who was also calved in 1921. A complete pedigree of Brae Repeater for five generations back failed to reveal any inbreeding which means that any slight inbreeding he might have possessed would have been through animals calved prior to 1900.

Thus it can be seen that whatever decrease in heterozygosis had been accomplished prior to 1922 was largely lost during the probable generation and a half in which Brae Repeater was the chief herd sire.

After the Brae Repeater era came the beginning of the transition period in which the Hazlett and later the Turner blood lines gradually replaced the former varied blood lines in the herd. Herd sires used to head the herd for the last ten years of this study include: Progress 1727750, Lassie Tone 1759101, Beauty's Bocaldo 17th, WHR True Domino 6th 2080632, Hazford Tone 158th 2593856 and T Royal Rupert 23rd 3040702. These sires with one exception were either Hazlett or Turner bred and rich in the blood of Anxiety 4th 9904. This has also been a period of frequent purchases of females of the same general blood lines and in fact since 1934 very few animals have been brought into the herd which did not carry this blood and almost all of the older animals which did carry other breeding have either been disposed of or their line allowed to die out when they reached the end of their breeding usefulness.

The coefficient of inbreeding of the Hereford breed as a whole in 1930, quoting Willham, (17), was 8.1 percent which represented in his coverage of 60 years an average increase in homozygosis of about .7 percent per generation. This would mean that, approximately three generations having elapsed from 1930 to 1945, the present coefficient of inbreeding of the Hereford breed as a whole would be between 10 and 11 percent. In 1936 it would have been approximately 9 percent.

The coefficient of inbreeding of the R. H. Hazlett herd in 1936, according to Winchester (18), was 15 percent and had been increasing on the average about 1.15 percent per generation. Had Hazlett been able to continue his breeding program until 1945 we might reasonably expect the coefficient of inbreeding to be around 17 percent. Since Turner started his herd largely from Hazlett breeding and has continued to concentrate on the same blood lines it is again reasonable to assume that his herd now has an inbreeding coefficient of between 16 and 17 percent. Table VI of this study shows that the Oklahoma A. & M. College herd as of 1945 has an inbreeding coefficient of 16.63 percent ± 1.32. When we refer to Tables VIII, IX and X and find that the composition of the present herd is essentially that of an offshoot of the Turner herd with almost no animal more than two generations away from Turner breeding. Thus it follows in all reason that the inbreeding coefficient of the College herd should be almost identical with that of the Turner herd. The above comparison of the prolongation of the Winchester (18) study and the present study reveals that this is exactly what did occur and is a verification of the accuracy of this particular study. It can be seen that the present high inbreeding coefficient of the college herd is not the result of a long accumulation and pyramiding of one line of blood here at the institution but the result of a transfer in toto during the past ten years of the end products of the breeding programs of R. M. Hazlett and Roy Turner. By this we do not mean to belittle the breeding program at the college as it is exactly the same thing, on a smaller scale, as was done by Turner and by Hazlett before him in establishing their herds. There is no way of determining through this study whether a comprehensive breeding program has been established for the college herd which can take advantage of this concentration of good blood. To do this would mean the use of fewer but better quality sires, establishment of a policy of breeding within the herd rather than unlimited purchase of highly inbred but slightly unrelated breeding stock, and strict adherence to a rather rigid line breeding program. From the composition of the 1945 calf crop as shown by Table IX it would seem that progress is being made in these directions but of course one year's results do not constitute a very sound basis for drawing conclusions.

One of the most disturbing elements of the study is that of the coefficient of inter se relationship in the herd which was found to be 8.04 percent. This figure is slightly smaller even than the relationship for the Hereford breed as a whole in 1930 by Willham (17). Add to that the fact that his figures show that the entire Hereford breed has increased its relationship steadily since 1910 when it was slightly above 5.2 percent until 1930 when it was slightly over 8.5 percent. This should mean, if the progression continued, a breed relationship of at least 10.0 percent. Even if we allow for a leveling off such as Willham found for the period of 1900 to 1910, it would still mean that that random bred Herefords of the breed as a whole with a relationship of 8.5 percent are more closely related to each other than are the present members of the College herd with a relationship of 8.04 percent. And this in spite of only a probable inbreeding coefficient of around 10 or 11 percent for random bred animals as compared with the 16.63 percent of the college herd. We attribute the low coefficient of relationship to the fact, as shown by Table VIII, that the eighty-five animals of the herd are sired by 29 different bulls only five of whom sired more than five members of the herd and that eighteen of the sires were responsible for only one offspring each. However, these facts should only tend to bring the inter se relationship down to a level with that of the entire breed rather than to a point below the breed average.

Table VII shows the relationship of twenty of the most important sires to the herd. It can be seen that the herd in 1945 bore a direct relationship of 31.47 percent to Beau Brummel 51817, 23.82 percent to Don Carlos 33734, 20.29 percent to Hazford Tone, 19.12 percent to North Pole 8946, and 18.53 percent to Anxiety 4th 9904. The figure on relationship to Beau Brummel can be compared with a 25.11 percent relationship of this bull to the Hazlett herd in 1936 and with a relationship of about 25.0 percent of the same bull to the Hereford breed as a whole in 1930. The relationship of Beau Brummel to the college herd is close to half way between that of a grandsire and a sire.

This study measured only the direct relationship existing between the herd and the particular sires, but one can readily see that the addition of collateral relationship would increase these figures. Winchester (18) estimates that the addition of collateral relationship to direct would raise the relationship of Beau Brummel to the Hazlett herd from 25.11 percent to around 33 percent. Applying the same principle to the relationship of Beau Brummel to the college herd should raise the figure from its present 31.47 to very close to 40 percent. The figure for Beau Brummel takes on added significance when one considers that he was born 55 years before the study was made.

It is interesting to note that the relationship of the herd to Anxiety 4th 9904 and to North Pole 8946 was practically identical with even a slight balance in favor of North Pole. Of course this is mostly accounted for by the fact that between the years of 1892 and 1905 most of the blood now found in the herd came down through Beau Brummel, Lamplighter 51834 and Printer 66684. Beau Brummel and Lamplighter were both grandsons of Anxiety 4th through Don Carlos 33734 and both were grandsons of North Pole through different dams. Printer was a son of Beau Brummel. Thus the random lines running back through these animals would tend to go equally to Anxiety 4th and North Pole.

A number of outstanding females of the breed also are rather closely related to the herd. These include Dowager 6th 6932, dam of Don Carlos, Don Pedro and Don Quixote, with relationship of 16.18 percent; Belle 24629, dam of Beau Brummel, with 15.88 percent; Beauty 403192, dam of Beauty's Bocaldo, Hazford Tone 8th and Hazford Rupert, with

11.47 percent; Tonette 2nd 722110, dam of Hazford Tone, with 10.59 percent; and Buleen 372147, dam of Bocaldo 6th, with 8.82 percent.

In order to work out a successful breeding program it is essential that maximum use be made of both line breeding and selection. Neither can be successful without the other for any considerable period of time. Each must be used with discretion because if either is practiced too closely the expense will be prohibitive and the user will be ruined. The more common practice with the average livestock breeder has been to select a sire not related to the majority of his females, use him until the first, second or third crop of calves become of breeding age, and then discard him in favor of another sire also practically unrelated to his females. Such a system of livestock improvement depends on the effectiveness of the selection employed and has at least four faults.

In the first place, the selection applied to non-related or remotely related animals is less effective than is possible among individuals of a more homogeneous group. Especially is this true when the factors involved are readily modified within the individual by environment or accidents of development. Secondly, the effect of any sire starts being diminished as soon as his use is discontinued. His contribution would be diluted one-half the first generation by the use of an unrelated sire. He would be responsible for only one-fourth of the genes in the second generation, one-eighth in the third, one-sixteenth in the fourth, etc. Third, depending upon superior individuality in out-cross males is a conservative breeding practice, but it is also a slower route to blood concentration or the fixation of characters.

In fact, it is very doubtful if any fixation at all can be achieved through selection alone as practically all the characteristics sought are the results of multiplicity of genes the individual identity of which cannot possibly be made by means of any of our present methods of selection. A fourth inadequacy of the system is encountered as the successful breeders begin to approach their goal, for it is impossible to achieve as complete fixation through selection as through linebreeding or inbreeding. Thus, further increase in the prepotency of the individual is halted; the attainment of maximum uniformity in the herd is limited; and the problem of securing sires which will 'nick' advantageously with the cows becomes increasingly difficult or impossible.

If the foregoing statements are true, it follows that breeders who are depending solely upon culling within the herd and the selection of unrelated sires for their improvement could make more rapid and positive progress by securing and maintaining a rather high degree of relationship between the breeding herd and their most outstanding sires. This high degree of relationship can be secured by the retention of superior sires until their blood has been rather highly concentrated within the herd. The maintenance of the effect of a superior sire can be accomplished through the concentrated use of relatives of the outstanding sire.

In combined inbreeding and selection there are several methods which may logically be followed, depending on the genetic complexity of the characters, the importance of environment and such factors as the extent of the operations and the risk to be involved.

The first step in any case should be the selection of a vigorous foundation, approaching as closely as possible to the desired type. Knowing that most lines will inevitably deteriorate greatly, one could not expect to continuously practice very close matings. By crossing lines within a herd one may reasonably hope to recover more than the original vigor and retain those characteristics which had been fixed. For the individual breeder, theory as well as practice indicates that a most constructive improvement program would be a combination of blood concentration and selection. The closeness of the breeding which should be practiced depends, naturally, on the homogeneity of the foundation animals and the breeder's skill as a judge of livestock. This apparently is the conclusion reached by Dickson and Lush, 1933. (4) at the conclusion of a genetic study of Rambouillet sheep.

Work to determine how closely one can inbreed and the best methods of establishing safe and yet efficient inbreeding programs is the responsibility of the institutions financed by public funds in that the heavy experimental cost and risk can be spread out and divided rather than be assumed by the individual breeder.

V. SUMMARY AND CONCLUSIONS

The breeding methods used by the Oklahoma A. & M. College in developing its herd of Hereford cattle are analyzed.

An approximate method of calculating coefficients of inbreeding and relationship from livestock pedigrees developed by Wright and McPhee was used in this study. Four-line random sample pedigrees were used. The sample included all the animals in the breeding herd of Oklahoma A. & M. College at the end of the year of 1945. These numbered eighty-five animals registered in the American Hereford Record. The base date used for this study was 1880.

The herd was established in 1900 but during the period of 1935 to 1945 its entire composition was radically changed and new breeding was substituted for the old which has now practically disappeared from the herd. For this reason, the only sampling which would accurately reflect the composition of the present herd and its breeding system is a study of the individuals composing the herd at present. Sampling made at periodic intervals during the history of the herd would reveal radical changes but would in no way reflect the breeding of the present herd and would only cause confusion and misunderstanding.

The coefficient of inbreeding for the 1945 group was 16.63 percent. This compares with an inbreeding coefficient of 15.0 percent for the Hazlett herd when dispersed in 1936. The inbreeding of the Hazlett herd had been increasing about 1.15 percent per generation and had it been continued it would in 1945 have been about the same as that of the present college herd. This comparison is made because the college herd is now primarily of the breeding of Robert H. Hazlett and later of Roy Turner, who carried on rather closely with his better animals and breeding system. This compares also with a probable inbreeding coefficient of approximately 10.0 percent for the Hereford breed as a whole.

The coefficient of inbreeding for the herd was radically higher than would be expected from the coefficient of inter se relationship which was found to be 8.04 percent. The low inter se relationship is partially due to the fact that the 85 animals in the 1945 herd were sired by 29 different bulls, with only five bulls siring more than five different animals in the herd. Eighteen bulls were found to have sired only one animal each of the present herd. This inter se relationship coefficient of 8.04 percent compares with an inter se relationship of around 8.5 percent for the Hereford breed as a whole in 1930. Thus random bred animals of the breed are apparently more closely related than are the animals of the college herd in 1945.

Most of the foundation animals for the herd from 1900 to 1916 were furnished by J. M. Curtice of Independence, Missouri. Most of the animals responsible for the present herd came from the Roy Turner herd or that of R. H. Hazlett.

It was found that the 1945 herd bore a direct relationship of 31.47 percent to Beau Brummel 51817, 23.82 percent to Don Carlos 33734, 20.29 percent to Hazford Tone, 19.12 percent to North Pole 8946, and 18.53 percent to Anxiety 4th 9904. The relationship of Beau Brummel to the college herd is about half way between that of a grandsire and a sire, while his relationship to the Hereford breed as a whole is 25 percent or that of a grandsire.

For most of the period of its existence the herd has been used for the production of steers for exhibition purpose. This program has been very successful but has resulted in a breeding improvement program that differs from that of the leading breeding herds of the period. The trend of the last several years and especially the last three indicates a revision of policy already being activated.

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Typist--Mrs. Grace Lewis