A GENETIC HISTORY OF MODERN YORKSHIRE SWINE IN CANADA

I. INBREEDING AND INTER SE RELATIONSHIP

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TABLE OF CONTENTS

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INTRODUCTION

Livestock improvement was practised long before the development of a science of breeding. Primitive man in domesticating the wild animal, most likely retained the most docile. Naturally he made no distinction between the natural and acquired differences between these animals, believing that all characters were equally transmissible and that good management was a short cut to livestock improvement. Other beliefs such as those concerning the injurious effects of mating close relatives, maternal impressions, telegony, and so on, influenced the breeding methods employed. As man gained intelligence the great fact of heredity must have become apparent to him. The realization of inheritance no doubt led to more rapid improvement.

Intensive efforts to improve the local types of livestock began in England early in the eighteenth century. As improvement by selection became impossible, breeders, cautiously practised inbreeding within their own herds. Robert Bakewell, generally accredited with setting the pattern of modern animal breeding, began his constructive work in the year 1760. He demonstrated that close and continued inbreeding could be practised effectively to improve livestock. It was during his time that pedigree breeding became established. His breeding work was with the old Longhorn cattle, Leicester sheep, and Shire horses. The Colling brothers, founders of the Shorthorn breed of cattle, followed Bakewell's system of mating with great success. Thomas Bates, a student of the Colling brothers, practised considerable inbreeding and developed a highly inbred line of Shorthorns.

Later attempts to improve livestock using close breeding seemed to meet with such a degree of failure in the hands of less competent breeders that they discouraged the practice. However, the superior types of each region were maintained, and developed into the pure breeds as we know them today. To maintain the purity of these breeds or types, herd and flock books were established for the recording of pedigrees. The first such register was the Coates register of Shorthorns, first published in 1822. Livestock improvement since the establishment of the breeds has been slow and mostly through selection from within the pure breeds or from the grading up of common stock by the continued use of pure bred sires. It is essentially the system of livestock breeding being practised today.

What these breeders accomplished by their breeding programs is difficult to measure quantitatively. However, by the study of pedigrees we can discover how much inbreeding was practised and the degree of relationship which they maintained between animals within a herd or breed. It is of interest to study the breeding methods used since they reveal the progress in breed improvement. The studies which have been made portray a general picture which is surprisingly similar for all the breeds, with the exception of the early Shorthorns. Modern genetics has made it possible to express the breeding methods used, and what, in consequence, is the present genetic status of the various breeds.

REVIEW OF LITERATURE

Methods of Analyses

The modern theory of genetics has made it possible to produce measures of inbreeding and relationship, which are essential for the analysis of the breeding methods used by livestock breeders. Genetics itself may be defined as "the science which seeks to account for the resemblances and differences exhibited among organisms related by descent."

The first attempts to apply scientific study to the phenomena of variation in inheritance were made late in the nineteenth century by Francis Galton, in the field of human heredity. However, it was not until after the rediscovery of Mendel's laws in 1900 that a real science of animal breeding was established.

Pearl (1917) presented his coefficients of inbreeding and relationship. This coefficient of inbreeding is based on the fact that an inbred animal has fewer different ancestors than the maximum possible number. The coefficient of relationship is based on the number of ancestors two individuals have in common, as compared to the maximum number possible. A separate coefficient is obtained for each ancestral generation for both of these measures. These coefficients in many cases gave inconsistent results, as they did not take into account the different systems of mating, and are now mostly of historical interest.

It was not until Wright (1922,1923) gave us his coefficients (of inbreeding and relationship) that accurate measures of inbreeding and relationship were obtainable. Wright (1922) states: "An inbreeding coefficient to be of most value should measure as directly as possible the effects to be expected on the average from the system of mating in a given pedigree." The coefficient of inbreeding is a relative and not an absolute measure of the percentage of homozygosis obtained.

The sire and dam of an inbred individual are connected by lines of descent from a common ancestor or ancestors. The coefficient of inbreeding for the individual in question is obtained by a summation of the coefficients of every line by which the parents are connected. Each line is traced back from the sire to a common ancestor and then forward to the dam, without passing through any individual more than once within the given line. It has been shown theoretically that this coefficient gives the coefficient of correlation between the uniting egg and sperm producing the individual in question. This coefficient measures the percentage reduction of heterozygous factors that were present in the foundation stock. The formula is as follows:

$$Fx = \sum\left[(1/2)^{n + n' + 1}(1 + F_A)\right]$$

where Fx and F_A are the coefficients of the individual (X) and the common ancestor (A), respectively, and n and n' are the number of generations between the common ancestor and the sire and dam, respectively. The factor 1/2 considers the fact that the germ cells which unite to form the individual are each one half a generation from sire and dam.

The coefficient of relationship measures the degree of kinship, or duplication of genes, which exists between two individuals or groups of individuals related by descent. The measure, as in the inbreeding coefficient, is a relative and not an absolute one. The formula showing the coefficient of relationship between two individuals is as follows:

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

where x and y are the two individuals whose relationship we wish to measure; n and n' are the number of generations between the common ancestor and x and y, respectively; (A) is the common ancestor, and F_A, F_x, and F_y the coefficients of inbreeding of A, x, and y, respectively.

The formula for calculating the coefficient of relationship between sire and dam of the individual X is:

$$R_{sd} = \frac{2 F_x}{\sqrt{(1 + F_s)(1 + F_d)}}$$

The coefficient of relationship between sire and dam is twice the coefficient of inbreeding of the progeny unless the parents are themselves inbred, in which case a correction is to be made for that, as shown by the term under the square root sign.

Wright and McPhee (1925) developed an approximate (short) method by which much of the detail encountered by writing the complete pedigree and working out the complete coefficients of inbreeding and relationship may be avoided. It is based "on the tabulation of random samples of the pedigrees of sire and dam." The random sampling need be continued only until a tie occurs between the pedigrees, without considering the number of generations to the closest common ancestor. In a two column pedigree the inbreeding coefficient is either 50 per cent or 0, depending on whether a tie does or does not occur. The short method is of little value for the individual, but for a group it is almost as accurate as the long method.

Wright's system of designating inbreeding and relationship has been used in the genetic analysis of several breeds of cattle, two breeds of sheep, two breeds of swine, and several breeds of horses.

Breed Analyses

Wright (1925) himself conducted a genetic analysis of the Duchess family of Shorthorns as bred by Thomas Bates. He states that the Duchess family as established from Colling-bred stock was already 40 per cent inbred. Through his entire breeding career of about 40 years, eight generations, Bates maintained the same level of inbreeding by introducing just the right amount of "blood" to keep the percentage from rising above 40 per cent. The bulls were about 40 per cent inbred, whether bred by Bates or others. This level of inbreeding is approximately equal to two generations of straight brother-sister mating, a little higher than four generations of half brother-sister mating, and six generations of double first cousin mating.

Wright found that a 60 per cent relationship had been kept between the animals mated whether bred by Bates or others. This relationship is higher than that existing between the average brother and sister. A high relationship was maintained to Charles Colling's famous bull, Favorite. This fell gradually from 76 per cent to 57 per cent during the eight generations of breeding studied.

McPhee and Wright (1925) made a rather complete genetic analysis of the Shorthorn breed of cattle as recorded in Coates' Herd Book. Using Wright's formula (1922) for inbreeding they report a rise from zero in 1790 to about 17 per cent inbreeding in 1810 and by 1825 the inbreeding had risen to 20 per cent. This figure had changed very little until 1920,when it was 26 per cent. The authors believe that the high figure for 1810 is probably due to the fact that in the first volume of the Coates' Herd Book,published in 1822,only the "best" bred animals were recorded. The sharp increase in inbreeding reached in the period 1810 to 1825,was no doubt due to the Colling brothers' herds. By 1850 the inbreeding had dropped to 18 per cent,revealing a diffusion of the "better" bred herds through the breed. The sudden rise from 18 per cent inbreeding in 1850 to 27.4 per cent inbreeding by 1875 indicated a renewed tendency toward family breeding. These families were based largely on Bates and Booth bred stock. A slight drop in inbreeding between the years 1875 and 1900 was probably due to the diffusion of the blood of Champion of England,owned by Amos Cruickshanks. Again the slight rise in inbreeding from 1900 to 1920 may also be credited to Champion of England, as his blood became more concentrated within the breed. The inbreeding coefficient of 26 per cent for the breed as a whole in 1920 means that the breed was 26 per cent more homozygous than the original stock, and almost the same as if the entire breed had descended from a single pair of animals chosen at random from the foundation stock.

The inter se relationship showed a steady rise from 22 per cent in 1810 to 39 per cent in 1920 with the most rapid rise occurring before 1850. This rise was in agreement with the rise in the coefficient of inbreeding. The high correlation (nearly .40) between random animals, the practical identity of the observed inbreeding and that due to random mating for 1900 and 1920, indicated that the breed was then a rather homogeneous unit.

McPhee and Wright reported that the two famous sires, Favorite and Champion of England, showed a relationship of 55 per cent and 46 per cent, respectively, to the Shorthorn breed as a whole.

The partial genetic analysis of the 20 leading American prize winning sires as taken from Malin (1923) further indicates the homogeneity of the Shorthorn breed. The differences between the coefficients of inbreeding and relationship of these sires and those for the entire breed were found to be insignificant. The average relationship between these sires and the breed of 1920 was 30 per cent, while the relationship of Champion of England and Favorite to these prize winning sires was found to be 47 per cent and 45 per cent, respectively.

McPhee and Wright (1926) made a Mendelian analysis of the British Dairy Shorthorns with the purpose of comparing the inbreeding of high-producing and average-producing cows, and their relationship to Champion of England and Favorite. They reported that the coefficients of inbreeding and relationship between these two groups and those for the entire breed in 1920 revealed an insignificant difference, indicating that there had been very little inbreeding practised among dairy Shorthorns. McPhee and Wright assume "that the dairy Shorthorn group is based on as great a diversity of blood lines as a random sample of the breed." Furthermore, these authors claim that due to the large probable error it would be unsafe to attach any significance to the differences between the relationship of Favorite and Champion of England as compared with their average relationship to the breed as a whole, in 1920.

Brockelbank and Winters (1931) made a study of the methods of breeding the so-called "elite" of the Shorthorns, comparing the Present Day Show Winners with Random Selected Individuals. The 100 Random Selected Individuals were chosen from the same volumes of the herd book in which the Present Day Show Winners were recorded. Brockelbank and Winters report that the Present Day Show Winners had an inbreeding coefficient of 2.064 per cent, while that of the Random Selected Individuals was 1.028 per cent. These authors state that the results of this study show a slight rise in inbreeding since

1920 which was similar to that for the entire breed since 1900, as reported by McPhee and Wright (1925). Inbreeding apparently has not been practised extensively in the production of the Present Day Show Winners. The junior author, in a similar study with Hereford sires, found the same general trend, indicating that inbreeding had not been a great factor in the production of recent leading Hereford sires.

According to this study the Present Day Show Winners are probably more homozygous for desirable characters than the Random Selected Individuals. In a comparison the former had 14 per cent more show winners in the first generation and slightly more than 10 per cent in the second generation. The margin gradually narrowed down to 1.37 per cent in the sixth generation.

In view of the results obtained, Brockelbank and Winters conclude that selection in the broad sense of the term, considering individuality, breeding performance, and pedigree, has been the tool used by Shorthorn breeders in the production of show winners. Furthermore, the higher coefficients of inbreeding revealed by the Present Day Show Winners as compared with their sires and dams, indicates that outcrossing has not been practised by breeders in the production of show winners. However, they state that this does not prove that inbreeding could not be used effectively for the production of breeding animals and outcrossing for the production of show animals. The study further indicated that the degree of inbreeding for the breed as a whole is increasing gradually.

Fowler (1932) in his genetic study of the Ayrshire Breed of cattle, found that the coefficient of inbreeding for the entire breed as calculated by Wright's "Approximate Method" showed a progressive increase from zero in 1877 to an average value of 5.3 per cent in 1927. No inbreeding was revealed until 1892. Fowler attributes the lack of inbreeding before this period to the very incomplete pedigrees, some tracing only to sire and dam. The author reports a distinct fall in 1917 and a corresponding rise in 1922 which he believes a possible result of the war period. A special register was kept for heifer calves during this period. These had to produce calves before being admitted into the later volumes. No difference in inbreeding was found between registered bulls and cows. A large proportion of the inbreeding was traced to two foundation sires, Burnhouses and Hover-a-Blink of Drumjoan. Using Wright's "Long Method" Fowler reports that the high producing cows had an inbreeding coefficient that was considerably lower than that for the breed average. However, inbreeding apparently had no harmful "effect on the milk yield when the coefficient of high milk yielding cows (over 1000 gallons) was compared with that of cows giving average yields (under 800 gallons)."

The foundation sire, Hover-a-Blink of Drumjoan, and the Drumjoan herd as a whole, had exerted an extreme influence on the genetic construction of the breed. Fowler reports that in 1923, 39 per cent of the inbreeding ties of high milk producing cows could be traced to the Drumjoan herd, as compared with the next highest of only 6.37 per cent. The Drumjoan herd contributed 18.36 per cent of the total coefficient of inbreeding, while that of the next highest herd was 8.35 per cent. Animals related to Hover-a-Blink of Drumjoan were responsible for almost 50 per cent of these ties.

Lush, Holbert, and Willham (1936) made a genetic study of the Holstein-Friesian cattle in the United States. They report a rise of a little over 4 per cent of inbreeding in the ten generations from 1881 to 1928 or 1931. The average inter se relationship had risen to 3.4 per cent during the same period. Had all the inbreeding resulted from random mating, considering the fact that all the members of the same breed are related to each other, the inter se relationship coefficient would have been nearly twice as large as the observed inbreeding coefficient. However, in all six samples the observed inbreeding coefficient came out more than twice as large as was to be expected from the average degree of relationship. The authors state that this is statistically significant showing a tendency toward family formation. Nevertheless, this separation into families is not carried far, presuming that the more popular families are soon used for top-crossing on other families. In this way the average relationship of the breed increases as the degree of inbreeding does. If, however, the degree of inbreeding increased without a corresponding increase in inter se relationship, the indication would be a distinct tendency toward family formation, showing that breeders were averse to making even mild outcrosses.

The high producers and the outstanding show specimens of the breed differed only slightly from the breed average in their inbreeding and relationship to remote ancestors. Lush et al further report that these special groups did show a higher relationship to a few recent ancestors, this being especially true of show winners. These results may stem as much from the fact that only a limited number of herds compete in the show ring as from any biological basis.

The cow, De Kol 2nd, is almost a great grandmother of the entire breed. She contributed about one-tenth of the genes of the breed today and exerted more influence on the breed than any other individual.

The average interval between generations was about four and one-half years.

Yoder and Lush (1937) in their genetic analysis of the Brown Swiss cattle in the United States found that there was only a slight difference between the inbreeding and relationship coefficients of the breed as a whole, and the Register of Production Class,and the Show Group. Using the Short Method as developed by Wright and McPhee (1925) they found the coefficients of inbreeding and relationship for the interval between 1909 and 1929. They report that the inbreeding coefficients of the entire breed for the three samples for the years 1909,1919, and 1929 came out 5.4 per cent, 4.0 per cent, and 3.8 per cent, respectively, while the inbreeding coefficient for the Register of Production sample was found to be 4.4 per cent,and that for the Show Group sample 4.7 per cent.

Yoder and Lush state that the inbreeding found was equivalent to the loss of about one-half of one per cent of the remaining heterozygosis per generation which compares favourably with that found in other breeds of livestock.

The inter se relationship coefficients for the same years and samples or groups were found to be 3.6 per cent, 2.9 per cent, and 4.3 per cent, for the whole breed, respectively, and 2.2 per cent for the Register of Production sample, and 7.4 per cent for the Show Group. According to the inter se relationship found, the observed inbreeding shows a small but significant excess over what would have happened if the mating had been truly random with respect to relationship between mates. This would seem to indicate a slight tendency to family formation, which, however, rarely goes far.

Yoder and Lush further report that the Register of Production group does not reveal any tendency to be a distinct family within the breed as they are composed of relatively unrelated animals. However, the Show Group, being more closely interrelated, shows a slight tendency to be different from the breed average in its relationship to a few recent ancestors.

This study revealed that no one animal ever dominated the whole Brown Swiss breed in the United States. The Show Group showed the highest relationship coefficients between individual animals and whole groups. Sires had values as high as 14.9 per cent and 14.2 per cent, and cows had values of 13.5 per cent and 9.5 per cent. Single animals in the general breed samples showed relationship coefficients only as high as 9.2 per cent (William Tell in 1909), and 9.1 per cent (College Boy in 1929).

The average interval between generations was found to be 5.4 years.

Willham (1937) in a genetic study of the Hereford cattle in the United States used 1860 as the base date in sampling intervals of 10 years. He reports a rise in the inbreeding coefficient for the entire breed from 1.2 per cent in 1860 to 8.1 per cent in 1930 (12.9 generations). A slight decrease in 1900 and 1920 might be attributed to sampling errors alone except that this drop occurred just after prices had begun to rise and periods of profitable expansion were on the way. 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 periods of less active trade. Another factor responsible for the lower degree of inbreeding found in the 1920 sample might have been the increasing popularity of the Gudgell and Simpson cattle. Willham assumes that by 1920 many herds were in their first or second top-crossing stage with the Gudgell and Simpson cattle on foundation stock that had come from other families. The sharp increase in the degree of inbreeding from 1920 to 1930 had probably resulted from the increased popularity of the "straight-bred" breeding during that period. The special samples of Prize Winners and the Register of Merit animals revealed a higher degree of inbreeding than the corresponding random samples.

These special groups also showed a higher relationship to the famous sire, Anxiety 4th, and his descendants. The inbreeding and inter se relationship ratio was found to be similar to that found in the random samples, indicating the same slight tendency to family formation in the special groups.

The bulls in the regular samples showed a slightly higher, but insignificant, degree of inbreeding than the cows, except in 1880. However, the bulls in the Register of Merit revealed an inbreeding coefficient of 7.6 per cent, higher than that of the cows. Willham suggests that this might be an argument for the use of inbred sires, as this group is supposed to represent the very best breeding animals of the breed in recent years.

Willham states that the inbreeding coefficient of the Hereford breed in 1930 is higher than that found in the Holstein-Friesian, Ayrshire, Jersey, or Brown Swiss breeds, but that the base date for the Herefords was earlier. He suggests that had the base dates of the Herefords or Shorthorns been chosen to correspond to the base dates used in other cattle studies, the amount of inbreeding found might also have been very nearly the same.

The inter se relationship for the breed in 1930 was found to be 8.8 per cent. This would be responsible for only 4.6 per cent pf the 8.1 per cent of the inbreeding actually found, had random mating been practised in the group, indicating a tendency to the formation of separate families.

Anxiety 4th and his grandson Beau Brommel showed the highest relationship to the breed in 1930 (18.5 per cent and 24.6 per cent, respectively). Nearly all the animals showing exceptionally high relationships to the breed at the various periods were either ancestors, descendants, or mates of Anxiety 4th.

The average interval between generations in this study of Hereford cattle was found to be 5.4 years.

Stonaker (1943) in his study of the breeding structure of the Aberdeen-Angus breed in the United States found that the degree of inbreeding was equivalent to about one generation of half brother-sister mating. The average inbreeding percentages of the five samples of animals born in 1900, 1910, 1920, 1930, and 1939 were found to be 8.9, 12.7, 10.8, 14.2, and 11.3, respectively. Short time fluctuations in inbreeding revealed a similarity in the Angus, Hereford, and Holstein breeds. Suggestions have been made that these shifts reflect the effect of economic conditions on the population breeding structure. However, the causes of these shifts are not fully understood. Stonaker suggests that the slightly higher shift in inbreeding found in the Angus breed as compared with that found in any other breed of livestock yet studied (except the Shorthorns) might be partly due to the earlier base period used. Had the base date been 1860 instead of 1850 the inbreeding would have come out 9.8 per cent rather than 14.2 per cent in 1930. According to Stonaker this 9.8 per cent compares favourably with the 8.1 per cent in the Herefords in 1930, relative to their ancestors in 1860.

The fluctuations from sample to sample were found to be significant and parallel to the fluctuations in inter se relationship, as revealed by the inter se relationship in each of the five samples of 9.4, 16.3, 12.2, 6.1, and 13.3 per cent, respectively. The inter se relationship accounts for only 62 per cent of the inbreeding actually found, thus indicating a slight tendency for closer relationship between mates than if mating had been entirely random with respect to pedigree. Stonaker further states that about 10 per cent of the average 0.3 per cent rise in inbreeding per generation was apparently due to the partial isolation of herds on account of distance.

Black Prince of Tillyfour was found to be the most prominent ancestor of the breed. His relationship of 24.1 per cent to the breed is practically equivalent to having been a grandsire of the whole breed. Numerous less important ancestors could be mentioned. Stonaker suggests that over 60 per cent of the genes in the breed probably came through foundation animals bred in only five herds, of which the Hugh Watson herd was the most important.

The average interval between generations was nearly 5.4 years. This compares favourably with that found in other breeds studied. The apparent breeding systems used as a whole, for the Aberdeen-Angus breed in the United States were found to be very similar to those used in other breeds of cattle.

Dickson and Lush (1932) in their study of inbreeding and genetic history of the Rambouillet sheep in America, report that the inbreeding coefficient rose to 5.5 per cent in the 34 years (8 generations) ending in 1926. The coefficients of inbreeding for the years 1896, 1906, 1916, and 1926 were 2.2, 3.8, 3.7, 5.5 per cent, respectively. The inter se relationship coefficients for the same samples were found to be, 5.2, 1.5, 2.7, and 2.6 per cent, respectively. The degree of inbreeding found in 1896 was the same as it would have been had the mating been entirely at random. Dickson and Lush suggest that in view of the fact that the breed was relatively new in the United States, with only a small number of breeders and a few sheep, a considerable interchange of breeding stock must have taken place between breeders. All these factors would have a tendency to make the breed a unified group with all animals related to each other. The inter se relationship of 5.2 per cent in 1896 indicates that such a situation existed. Also the relationship between any two animals picked at random came out almost the same as that between animals having one grandparent in common and no other relationship. The sudden decline in inter se relationship after 1896 was believed to be due to the uneven distribution of the imported animals between the breeders. Some breeders sought anxiously for imported sheep while others were more interested in animals whose ancestors had been in the breed before 1896. Dickson and Lush state that the slight rise in the average inter se relationship since 1906 "is a natural consequence of the cessations of importations and of the fact that the different branches of the breed were not kept entirely isolated from each other." However, partial isolation is reported evident as the inter se relationship did not rise as fast as the inbreeding coefficient. Furthermore, the average relationship between any two lambs in 1926 was reported only half as close as the inter se relationship in 1896. This was concluded from the fact that the average relationship between any two lambs in 1926 was a little less than if one had been the grandson and the other the great grandson of the same ram but otherwise unrelated.

No one animal, as reported, had ever dominated the entire breed. The highest relationship between any individual and the whole breed had not risen much above 14 per cent. The average interval from generation to generation was about 4.2 years.

Carter (1940) reported that the inbreeding coefficient for the Hampshire breed of sheep since it was brought to the United States had risen from 1.4 per cent in 1925 to

2.9 per cent in 1935. This loss of 0.7 to 0.9 per cent of the existing heterozygosis per generation during the period studied was much the same as that found in similar studies of other breeds of livestock.

The inter se relationship had risen from zero in 1925 to 0.5 per cent in 1935, which did not account for all the inbreeding found. The higher degree of inbreeding indicated that some separation into families had taken place. Carter suggests that such separation might have been from geographic location rather than a deliberate attempt of the breeders to keep families from interbreeding with each other.

This study revealed that no one animal or family had ever dominated the Hampshire breed of sheep. Only two animals showed a relationship of over 2 per cent to the entire breed.

The average interval between generations was 3.5 and 3.8 years in the two samples. Carter states that a shorter interval is to be expected in a rapidly expanding breed than that found in a breed relatively stable in numbers. Carter further suggests that the longer interval between generations (4.2 years) found in the Rambouillet sheep was probably due to the fact that it approached a numerical equilibrium at an earlier date than the Hampshire.

Steele (1944) made a genetic study of Thoroughbreds, Standardbreds, and American Saddle Horses in the United

States. In a comparison between stake winning (Stakes) and poor performing (Poors) Thoroughbreds, Steele reports inbreeding coefficients of 8.3 per cent for both, while the inbreeding coefficient for 50 leading money winners came out 10.2 per cent. A perfect sample of Standardbreds showed an inbreeding coefficient of 4.0 per cent. The inbreeding found in both, the Thoroughbreds and the Standardbreds, accounted for about a 0.6 per cent loss of heterozygosis per generation. The American Saddle Horses represented by one Show sample and two Random samples revealed average inbreeding coefficients of 4.0 per cent for the Show sample and 3.2 per cent for the Random samples. This showed an increase in inbreeding of 1.4 per cent and 1.1 per cent per generation, respectively.

The average inter se relationship for the "Stakes" and "Poors" were found to be 16.3 per cent and 14.1 per cent, respectively, while that of a sample of inter class of "Stakes-Poors" came out 16.8 per cent. The sample of Leading Money Winners had an inter se relationship of 13.9 per cent, the Show sample showed one of 14.1 per cent, while that of the average Random samples came out 6.0 per cent.

Steele states that the small difference in the average relationship between the "Stakes" and the "Poors" is statistically insignificant. Furthermore, comparisons between these two groups showed that they were as closely related as were individuals within the groups. The Leading

Money Winners revealed a similar degree of relationship as the other samples. Homogeneity in the Saddle Horses seems to be increasing more rapidly than in the other breeds.

In view of the inbreeding per generation in the samples studied, Steele suggests that the breeders of Saddle Horses made a slightly greater use of inbreeding than did the breeders of Thoroughbred and Standardbred. Inbreeding apparently has played a minor part in the modification of these Light Horses. Breeders seem to have depended more on selection in fixing the standards of these breeds. In this respect the breeding practices of all major breeds of livestock studied seem to be quite similar. Steele reports some tendency toward family formation and believes that geographical isolation is only a minor factor in Light Horses because of greater breed mobility, particularly in the Thoroughbreds and Standardbreds.

Of the ten famous remote ancestors, Steele reports that three sires were responsible for about one third of the genes of the modern American Thoroughbred. As for the American Saddle Horses only one sire out of nineteen famous ancestors contributed more than 10 per cent of the genes of the whole breed. Apparently no immediate ancestors have shown any great influence on the breeds.

Steele states that in similar studies of Scotch

Clydesdales, as carried out by Calder (1927), little inbreeding had been found in the formative period of the breed. However, the inbreeding had risen to about 6.5 per cent in a little over sixty years. Calder assumed, however, that the homozygosity of the Clydesdale was similar to that of other breeds showing more intense inbreeding.

Fletcher (1945) using complete four generation pedigrees, made a genetic study of the American Quarter Horse. The three representative samples of the breed designated, "Before 1930, "1935", and "1940-41", showed inbreeding coefficients of 0.86, 1.64, and 1.75 per cent, respectively. The select "Stallions" sample in spite of the high proportion of King-Ranch-Bred animals, differed only slightly from the breed average, revealing an inbreeding coefficient of 1.7 per cent. Fletcher believes that 1.7 per cent is probably the proper inbreeding coefficient for the breed. The lower figure of 0.86 per cent might be due to the relatively greater number of inbred lines in these pedigrees. With the exception of the "Before 1930" sample, the actual inbreeding is greater than the expected inbreeding. However, this difference is not significant enough to indicate any planned inbreeding. The inbreeding per generation compares favorably with that of other breeds.

The inter se relationship for the representative samples was found to range from 0.98 per cent to 3.02 per cent. The small amount of inter se relationship could not account for the inbreeding of the corresponding samples, indicating a slight tendency to family formation in the animals giving rise to the Stud Book of the Quarter Horse breed.

A sample of animals bred by the King Ranch showed an appreciable difference from the breed as a whole. Fletcher found an inbreeding coefficient of 4.89 per cent, and an inter se relationship coefficient of 20.11 per cent.

The sire, Peter McCue, was shown as the most frequently occurring ancestor in the samples as a whole. The average interval between generations was 8.99 years.

A comparison between the Holstein-Friesian cattle and the Quarter Horse indicated a more extensive use of a few sires in the Quarter Horse than has been the practice in Holstein-Friesian cattle.

Rhoad and Kleberg (1946) conducted a study of the Quarter Horse breeding at the King Ranch. Their studies were based on the pedigrees of 77 of Old Sorrel's inbred descendants of the 1941 and 1942 crop of foals scheduled to come up for registration as two year olds. After Old Sorrel had proved to be an outstanding sire, he had been mated repeatedly to Thoroughbreds, Quarter Horses, and to crossbred mares of these two breeds. Of the 77 pedigrees of this study, 41 trace back to foundation mares of these three types, bred to Old Sorrel, 35 pedigrees trace back to foundation mares of similar breeding which had been introduced into the line for the use on sons and grandsons of Old Sorrel, and one Arabian mare was reported as appearing in several of the pedigrees. Thoroughbred breeding had been kept at a high level by the use of sons of Old Sorrel out of Thoroughbred mares. The high percentage of inbreeding obtained was reported as being mainly due to four sires.

Rhoad and Kleberg report that since the beginning of this experiment, nearly twenty years ago, ten stallions and approximately 400 mares have been used. All of the stallions and about ten per cent of the mares were found to be descendants of Old Sorrel. The family of Old Sorrel is reported as having developed into a prepotent strain, made up of superior individuals in physique and intelligence to any other horses produced on the King Ranch.

Fletcher (1946) reports that the average inbreeding coefficients of the five samples of the Tennessee Walking Horse was found to be relatively low. The five samples consisting of, "Foundation" group, "1924-25", "1930","1935", and "1940" groups revealed inbreeding coefficients of 1.24, 1.39, 2.49, 3.14, and 3.62 per cent, respectively. Fletcher believes that much of the increase in the more recent entries is probably due to the more complete information regarding their ancestry. Hence he assumes that the inbreeding of 3.62 per cent for the 1940 group is probably fairly representative of the breed as a whole. Furthermore, Fletcher compares this figure with the slightly lower average inbreeding of 2.8 per cent reported by Steele for a selected group of 42 stake winning American Saddle Horses in 1940. Also, similarly selective samples of Thoroughbreds and Standardbreds, as reported by Steele, revealed materially lower coefficients of 1.4 per cent, and 1.6 per cent inbreeding, respectively.

The inter se relationship for the several samples was, 2.96, 3.12, 6.30, 6.45, and 5.80 per cent, respectively. Fletcher assumes that the relationship of 2.96 per cent as compared with that of 2.8 per cent reported by Steele for stake winning saddle horses of 1940, means that the Walking Horse like the other breeds studied has sprung from a relatively heterogeneous foundation as compared with the cattle breeds where inter se relationship coefficients of 8 per cent are reported. Fletcher further believes that, according to the 5.8 per cent relationship of the 1940 sample, the Walking Horse breed might be a somewhat closer knit unit than the other breeds of light horses.

The two most important ancestors of the breed were Allan F-1, and Roan Allen F-38. They showed a relationship of 16.48 per cent, and 19.44 per cent, respectively, to the 1940 group. The influence of the Standardbred had increased in the 1940 group, while that of the American Saddle Horses had decreased.

The average interval between generations of 10.02 years was almost the same as that reported by Fletcher (1945) for the Quarter Horse and slightly lower than that reported by Steele for the Thoroughbreds and Standardbreds. Fletcher doubts that any significance could be attached to these differences.

Lush and Anderson (1939) made a genetic study of the Poland-China breed of swine in the United States. They report that the average rate of inbreeding from 1886 to 1929 was enough to lose about six-tenths of one per cent of the existing heterozygosis per generation. The four samples of the years, 1900, 1910, 1920, and 1929 showed inbreeding coefficients of, 2.0 per cent, 5.6 per cent, 6.8 per cent, and 9.8 per cent, respectively, indicating little change in the average inbreeding rate, even though the inbreeding policies underwent wide changes at that time.

The average inter se relationship for the comparable samples was found to be 3.2 per cent, 6.4 per cent, 8.9 per cent, and 14.2 per cent, respectively. These relationship coefficients could not account for all the inbreeding found indicating some tendency toward distinct family formation.

Only three ancestors contributed more than 12 per cent of the genes of the breed, and one of these was the ancestor of the others. Lush and Anderson state that the principal breeding plan seems to have been selection and the extensive use of the sons and daughters and grandsons and granddaughters of currently most famous sires and dams. The spotlight of this current fame apparently shifted from one animal to another not very closely related to the reigning favorite that it displaced. The authors further report that most of the inbreeding was incidental to this. The interval from one generation to the next was about two and one-half years.

Lush and Anderson (1939) report that Malin in a similar study of the Poland-China breed of swine found similar results. However, he interpreted his findings as showing more inbreeding and also more distinct splitting into families. This, according to Lush and Anderson, is due to the fact that Malin used "percentage of blood" which is fairly accurate for expressing relationship between ancestor and descendant but makes the intensity of inbreeding seem higher than it actually is.

Lush and Anderson (1939) also show that the results obtained in a similar study of the Danish Landrace, as brought forward by Rottensten (1937), compare favorably with those found in the Poland-China. Rottensten, in his one sample of animals averaging 1930 for birth date, found that the inbreeding coefficient had risen to 6.9 $\pm$ .7 per cent from 1897 to 1930, showing a loss of about one-half per cent of the remaining heterozygosis per generation. This was even less than was expected from the average inter se relationship coefficient (16.0 $\pm$ 1.7 per cent), thus indicating the tendency of Danihh breeders to avoid even mild inbreeding.

The highest relationship of any one animal to the whole breed was 12 per cent. The average interval between generations was 2.2 years.

In the story of the origin and development of our present farm animals the evolution of the several breeds of swine are fairly well represented by the Yorkshire breed which was one of the first to be developed in Europe (Fig.1). According to the evolutionary tree the first differentiation of pig-like animals began in the late Eocene or early Oligocene period. Lydekker (1894) reports that these pig-like animals branched off into three families, the Pigs or Suidae, the Peccaries or Dicotylidae, and the Hippopotami or Hippopotamidae. The Pig family consists of three generic types of which only Sus, the true pig, is involved in the development of the modern hog. Two species, the European (Sus scrofa) and the Asiatic (Sus vittatus or sometimes called Sus indicus) being typical representatives of this genus, are mainly responsible for the domestic pig. Lydekker further states that the young of all the wild species are marked with longitudinal stripes. He also mentions the fact that if domesticated pigs are turned loose they will revert more or less completely to the wild type, some even producing striped young.

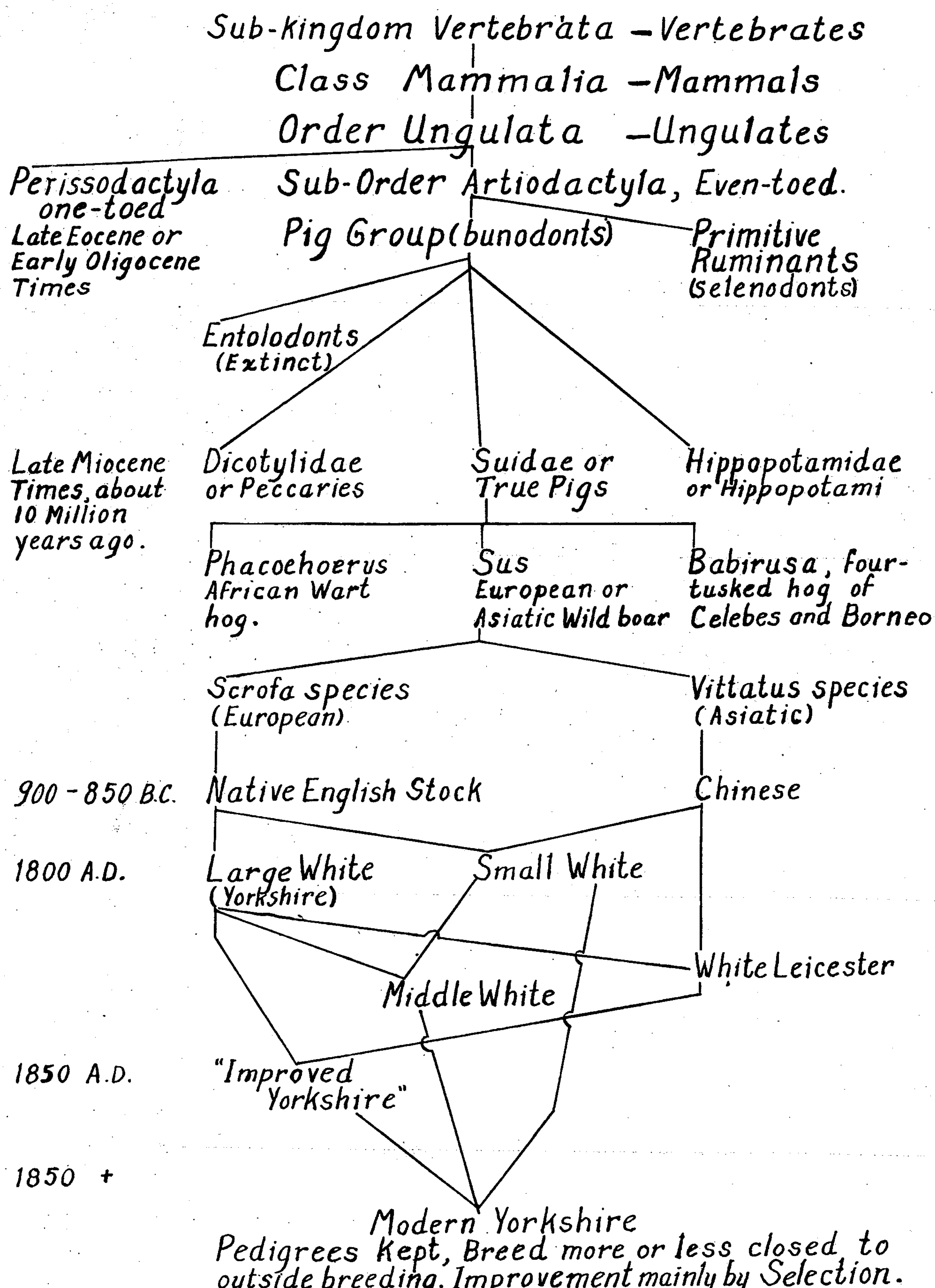
The earliest domestication of the pig probably took place in China as long ago as 3000 B.C. Domestication of pigs in Western Europe and more especially in the British Isles probably occurred at a later date and independent of of the Oriental achievement. The European wild pig, or wild boar, was formerly abundant throughout the British Isles and probably furnished the base stock from which most of the British breeds originated.

In the development of the modern hog, as represented in North America and the British Isles, the Asiatic as well as the European strains were used extensively. The ancestry of most modern breeds of swine trace back to both species. It is generally believed that the European influence predominates in the bacon breeds, while the Asiatic influence is stronger in the pigs, classified as pork, lard, or butcher type.

With the advent of the Industrial Revolution, modern breeding methods were developed with the purpose of producing farm animals that were better suited to satisfy the demands of the ever increasing numbers of industrial workers. The Yorkshire was one of the first breeds of swine to undergo intensive efforts toward improvement. According to Vaughan (1931) and Plumb (1920), the breed originated in Yorkshire and the adjoining counties in northern England, having descended almost directly from the large, coarse-boned, leggy white pigs native to northern England. Vaughan (1931) believes that these were later crossed with the Leicester white pigs which Robert Bakewell had improved by selective breeding. The Bakewell strain most likely originated from a cross between the White Chinese and Yorkshire bred pigs

Fig. 1.

Evolution of the Modern Yorkshire Hog.



and was used for refinement. Further improvement was made by selection and careful breeding. It is said that some Middle White and Small Yorkshire crosses were made to meet the demand for neater heads. The improvement of the breed has resulted in some reduction in size.

The most marked improvement in the Yorkshire pigs began about 1850, to meet economic needs. The exhibition of a sow at the Royal Agricultural Show in 1851 drew attention to the improved Yorkshire strain. Vaughan (1931) states that the National Pig Breeders' Association, which was organized for the promotion and registry of Large White swine in Great Britain, was founded in 1884. It was incorporated in 1886 and also registered Berkshires, Tamworths, Middle White, and Wessex Saddlebacks.

There seems to be some doubt as to when the first Yorkshire pigs were brought to Canada. However, according to MacEwan (1941) a certain John Miller (Scottish immigrant) brought a pair of pigs, so described to Canada (Markham, Ontario) in 1835, but the improved type did not appear until about 1886. In the early herdbooks of Canada the breed was known as the "Improved Yorkshire." In the United States the Yorkshires were known prior to 1840 but the improved type was not introduced until 1893, according to Vaughan (1931). The Yorkshire breed, however, has made greater progress in Canada than in the United States and is well represented in every province in Canada. Canada's bacon-export business with

England was responsible for putting the Yorkshire breed foremost among the breeds in Canada. Of the pure bred pigs recorded in the Canadian Swine Breeders' Record in 1949, about 88 per cent were Yorkshires.

OBJECTS OF THIS STUDY

The objects of this study were: (1) To find how much inbreeding has been used in the development of the Yorkshire breed of swine in Canada as it existed in the latest available issue of the herdbook (Volume 60). (2) To learn whether the breed has developed as a single homogeneous group of related animals, or whether there has been any tendency for the breed to be separated into distinct families.

METHODS USED

In the present study a representative sample of 171 animals (1 per cent) was selected systematically from volume 60 of the Canadian National Records for Swine. This sample consisted of 114 sows and 57 boars. The method of selecting the pedigrees was to determine the approximate sow-boar ratio of the herdbook. This ratio was obtained by taking several samples of twenty pages each,chosen at random. The sows and boars on each page were counted and the calculated ratio was found to be approximately 2 sows: 1 boar. To obtain the correct number of females and males the first listed animal of the correct sex on regularly spaced pages of the herdbook was chosen, with every third animal being a male. Complete five generation pedigrees were used. Slevinsky (1950) found that the average birth date of the sample animals was 1948,while the average birth date of the animals five generations back (considered foundation animals) was 1936.

The inbreeding was calculated after the formula developed by Wright (1922, 1923) and used by him in the genetic analysis of the Duchess family of Shorthorns as bred by Thomas Bates (1923). Calder (1927) applied them to the Clydesdale horse in Scotland, Smith (1926) to the Jersey cattle in England, Steele (1944) to the Thoroughbreds, Standardbreds, and American Saddle Horses in the United States, Fletcher (1945) to the American Quarter Horse, Fletcher (1946) to the Tennessee Walking Horse. Figure 2, and Table 1, shows an example of the application of the inbreeding formula to a sample pedigree.

The average inter se relationship is an estimate of the existing relationship between animals chosen at random from the breed. It is measured by matching a random line from one pedigree against a line from another pedigree to find the frequency with which common ancestors appear in a pair of such lines. Any random line is only used once in such matching. If mating were entirely random within a breed in which all the animals are related to each other, the inter se relationship would be nearly twice as large as the observed inbreeding coefficient. The formula for calculating the expected inbreeding (F) from the average inter se relationship (R) is, $F = R/(2 - R)$.

- Ranche Leader 81D 365606
  - Ranche Leader 130B 337254
    - Cadiuex G 4A 317580
      - Nichols 15Y 282997
        - Maska Mo Malm 17X 263109
          - Malm de la Parmentiere 224 217975
          - Modeste de l'Ecole 80R 192337
        - Nichols 15W 247567
          - Lennoxville Malm 43U 217459
          - Modeste de l'Ecole 29R 189984
      - Legace J P 10Z 297771
        - Ottowa Beau 238V 228762
          - Indian Head Beau 24 274200
          - Ottowa Lass 69U 219160
        - Ranche Queen 41W 244909
          - Ranche Duke 13T 202150
          - Ranche Queen 274T 215083
    - Ranche Bess 145Z 309385
      - Ranche Duke 33Y 290149
        - Ranche Duke 13T 202150
          - Ranche Sardis 9 167046
          - Ranche Queen 214R 193398
        - Ranche Queen 58X 277209
          - Lacombe Prince 178W 247383
          - Ranche Queen 274T 215083
      - Ranche Bess 124Y 291428
        - Lacombe Prince 178W 247383
          - Rockville York Lae 78T 204629
          - Lacombe Princess 113T 206651
        - Ranche Bess 238V 240665
          - Ranche Duke 13T 202150
          - Ranche Bess 234S 200450
  - Ranche Queen 55C 351847
    - Leitchcroft Chief 130A 334712
      - Oldhams Simcoe Chief 8W 248183
        - Doners York Major 40U 220158
          - O. A. C. 54T 205368
          - Willowdale Betty 61S 199947
        - Doners York Duchess 40U 219665
          - O. A. C. 242P 190667
          - Clearview Misabel 75P 189984
      - Locust Vale Sunbeam 25X 280178
        - Maple Lodge Marquis 29U 220103
          - Cedar Brook Marquis 45T 205922
          - Glenafton Empress 66S 196822
        - Glenquaich Sunbeam 5Y 223476
          - Galt Prince 2T 206167
          - Saugeen Valley Sun beam 56U 218301
    - Ranche Queen 51A 316476
      - Ranche Duke 33Y 290149
        - Ranche Duke 13T 202150
          - Ranche Sardis 9 167046
          - Ranche Queen 214R 193598
        - Ranche Queen 88X 277209
          - Lacombe Prince 178W 247383
          - Ranche Queen 274T 215083
      - Ranche Queen 131W 275204
        - Ranche Duke 13T 202150
          - Ranche Sardis 9 167046
          - Ranche Queen 214R 193598
        - Ranche Queen 274T 215083
          - Orchard Valley Sardis 41R 190017
          - Ranche Queen 215R 192778

Fig. 2. Pedigree of Ranche Leader 81D, an illustration of inbreeding and linebreeding.

Table 1. Deriving the Coefficient of Inbreeding of the Yorkshire Boar Ranche Leader 81D 365605

Individual	Common Ancestors of Sire and Dam	F_A	n	n'	$(1/2)^{n + n' + 1}(1+F_A)$
Ranche Leader	Ranche Duke	0	2	2	3.12
81D 365606	33Y 290149				
	Ranche Duke	0	3	3	0.78
	13T 202150	0	4	3	0.39
		0	4	3	0.39
		0	4	3	0.39
		0	4	3	0.39
	Ranche Queen	0	4	3	0.39
	274T 215083	0	4	3	0.39
		0	4	4	0.19
					6.43

ANALYSIS

Inbreeding

The inbreeding coefficient measures the similarity of the germ cells which united to produce the individual in question, "relative to the similarity of random germ cells from the foundation stock." Slevinsky (1950) found that the five generations studied covered a period from 1936 to 1948. During this period the average inbreeding coefficient had risen to 2.06 per cent, which represents a decrease in heterozygosis of about 0.51 per cent per generation. The decrease in heterozygosis per generation was calculated by dividing the total inbreeding coefficient by the number of generations less one. "The one generation was deducted since it is impossible among bi-sexual animals for any inbreeding to be visible in pedigrees traced only one generation."

Inter se Relationship

The average inter se relationship coefficient was 1.04 per cent. This would have produced an inbreeding coefficient of about 0.52 per cent, had mating been entirely at random. The observed inbreeding of 2.06 per cent is almost four times greater than this, indicating a tendency for the formation of distinct families. The small degree of inbreeding, however, indicates a reluctance to practise intense linebreeding.

DISCUSSION

Selection, inbreeding, and crossbreeding are the three tools with which the breeder may change the heredity of his animals. The purpose of selection and inbreeding is primarily to build up desirable genotypes, whereas crossbreeding is of particular use in the building of desirable phenotypes. Crossbreeding at first increases the uniformity of the breed but hampers further progress in breed improvement because it prevents the formation of separate and distinct families. Inbreeding and crossbreeding are generally accompanied by some degree of selection.

Selection is the simplest and most often used tool of the livestock breeders but its effects on genetic improvement are limited. It is most effective when the population is highly heterozygous and its effectiveness decreases proportionately as the undesirable genes become less frequent. Dominance, environment, and epistasis may cause the breeder to make mistakes, thus decreasing the progress that could have been made had he known the genotypes perfectly. Selection alone is unable to bring about complete fixation of desirable genes. As the undesirable gene becomes rare even slight mutation rates will offset the effectiveness of selection. Progress by selection alone is a rather slow process because most characters sought in animal breeding are affected by several factors. However, combining some inbreeding with selection will remedy some of the weaknesses of selection.

Inbreeding automatically promotes the purity of the stock produced by increasing the number of homozygous gene pairs. In the process of inbreeding many undesirable genes are uncovered which would otherwise be concealed by their dominant alleles. Since dominant genes, as a rule, promote vigor, the uncovering of these recessive genes would bring previously unrecognized and undesirable traits to light. Inbreeding in the absence of selection for vigor usually leads to some average decrease in vigor. The loss in vigor will vary according to the rate of inbreeding and the genetic constitution of the foundation stock. The purpose of an inbreeding program is to enable the breeder to purify lines or families for the more desirable genes.

Figure 3 shows some regular systems of inbreeding. It is of interest to note the differences between the most intense systems theoretically possible and some of the milder ones that might be practised more safely with farm animals. Even the milder inbreeding systems can bring the population to a high degree of homozygosis if continued long enough in an entirely closed population. The degree of homozygosis obtainable in terms of one breeder's lifetime can be seen by multiplying the number of generations by two and one-half years in the case of swine, four or five years in the case of cattle and sheep, and ten or more years in the case of horses.

Figure 4 shows the variation in relationship between full brothers under the same inbreeding systems. Inbreeding is apt to cause unrelated families to drift farther apart than they would under random mating. However, each separate and distinct family tends to become more uniform within itself. In a one-sire herd where no outside female blood is introduced and each new sire is unrelated to the herd the average relationship between herd mates will never rise above $33^{1}/_{3}$ per cent. By contrast a one-sire herd where no new blood is introduced and there is no overlapping of generations will reach an average relationship of 39 per cent between mates in the first generation and will pass 50 per cent in the next generation. This will make the herd more uniform than if all members were full sibs.

Lush (1934, 1949) describes and illustrates an actual example of a purebred Shorthorn herd in which the only new genetic material added in twenty years was from the purchase of a single sire. "In essence it was first almost a one-sire herd, then a two-sire herd, and then a one-sire herd again." To conserve the good qualities of the sire, Sultan Banner, his descendants were bred together without too much close inbreeding. After twenty years the relationship of the herd to this sire remained at 42 per cent, but was less than twenty per cent to any other foundation animal. The average inbreeding was only

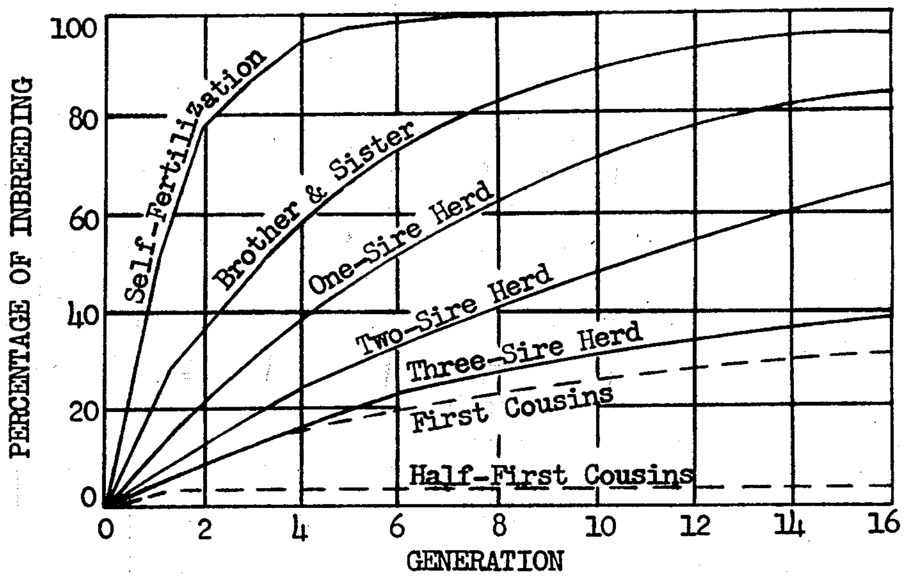


Fig. 3. The percentage of inbreeding under various systems of mating. (After Wright in Genetics, 6:172, and Lush in Animal Breeding Plans, p. 276.)

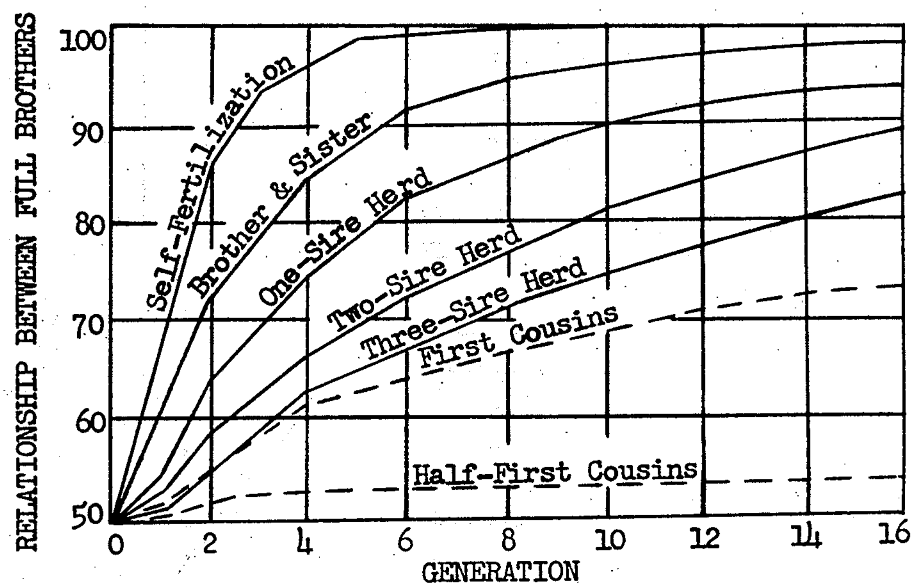


Fig. 4. The relationship between full brothers under various systems of mating. (After Wright in Genetics, 6:170, and Lush in Animal Breeding Plans, p. 277.)

16.9 per cent, while the maximum inbreeding for any individual was 31.5 per cent. Genetically, the whole herd was nearly as like each other as full sisters and still maintained a reasonable high average of individual merit.

The Yorkshire breed of swine may be considered as a closed population as the herdbook is entirely closed to the registration of any but purebred Yorkshires. Some probably believe that this fact and the small number of foundation stock might account for the inbreeding and relationship found. Wright (1931) gives the following approximate formula for calculating the amount of heterozygosis lost per generation for a closed population mating at random:

$1/8Nm + 1/8Nf$, where Nm is the effective number of breeding males and Nf is the effective number of breeding females in each generation. In animal breeding Nf is usually so much larger than Nm that the term involving Nf may be omitted without much error. The use of 24 sires within the Yorkshire breed of swine would have produced an inbreeding coefficient of 0.51 per cent per generation, as found in the Yorkshire, if random mating had prevailed within the breed. The inter se relationship, however, shows that some separation into families has taken place. The inter se relationship of 1.04 per cent would have resulted from an Nm of about 96, with random mating for five generations, in a closed populations Calculating the expected inbreeding from the inter se relationship of 1.04 per cent by applying the formula, $F = R/(2 - R)$, gives an inbreeding coefficient of 0.52 per cent. Substituting the inbreeding of 0.13 per cent (0.0013) per generation in the formula $1/8Nm$, results in an effective number of 96 males reaching breeding age in each generation.

A study of the pedigrees shows that there are far more than 96 boars in breeding use per generation, but most of these have no sons or daughters that are used in purebred herds, and therefore their influence on the breed is quickly diluted. By contrast, some are of noted merit or are used in prominent herds and they have several sons and daughters that go to purebred herds, which brings about a certain amount of inbreeding. This indication of mild linebreeding is verified in the study by Slevinsky (1950). He found that ten ancestors were responsible for approximately 27 per cent of the genes of the breed today, with no one individual showing a relationship much above 4 per cent to the breed as a whole. Figure 2 shows an example of one of the more intensive systems of linebreeding. Deliberate and intensive inbreeding has been practised only rarely. Out of the 171 pedigrees used in this study only 94 showed any inbreeding, and only one revealed an inbreeding coefficient as high as 25 per cent, which was the result of one generation of brother-sister mating. There is always a little more perpetuation of a few currently prominent sires by using their sons, than the term "random breeding" implies.

The decrease in heterozygosis of approximately 0.51 per cent per generation in the Yorkshire breed of swine is very much the same as that found in similar studies in other breeds of livestock. In the Danish Landrace (1937) and the Poland-China (1939) breeds, the only other two breeds of swine studied, the decrease in heterozygosis was about 0.5 per cent, and 0.6 per cent, respectively.

Winters et al (1943) suggest a certain procedure which should bring about improvement much faster than present breeding methods. These authors report that in five Poland-China lines the inbreeding coefficient was increased about 30 per cent in four or five generations without loss of vigor and with some possible increase in performance. These results indicate that more definite inbreeding might be used to advantage in breed improvement. Several such herds producing breeding stock to head other herds should advance the improvement of the breed considerably. It is difficult to say just how much inbreeding is required in livestock. In deciding the proper amount of inbreeding to employ much depends upon the goal, the genetic material being used, and the breeders ability to recognize and prevent the fixation of undesirable genes in his stock. There is also a probability that different lines will show considerable variation in their optimum coefficients of inbreeding. Winters (1948) reports that lines developed from other inbred lines seem to be able to withstand a faster rate of inbreeding. Furthermore, crossing studies in livestock "indicate that superior inbred lines and superior individuals on the average produce the best crossbreds." These indications are supported in studies of corn by Hayes and Johnson (1939) and Johnson and Hayes (1940). However, as inbreeding is generally accompanied by loss of vigor it is well to keep its level at the minimum necessary, coupled with persistent selection, to fix the genetic characteristics desired. The more effective selection is, the more inbreeding can be practised with some degree of safety.

The amount of inbreeding or linebreeding practised in the Yorkshire breed of swine was enough to bring about a fixation of approximately 0.51 per cent, of the remaining heterozygous gene pairs, per generation. This progress is extremely mild as compared with the inbreeding coefficients per generation, for inbreeding systems commonly found as shown in Table 2. At the present rate of fixation only about 20 per cent of the remaining heterozygosis would be lost in another hundred years. Evidence, Lush (1948), Lush (1934), Winters et al (1943), and Wright (1923), indicates that the present rate of fixation could be accomplished in a much shorter time without any real risk of fixing undesirable traits in the whole breed.

Table 2. Inbreeding or Line Breeding Matings Commonly Found (After Lush, Jay L. Iowa Expt.Sta.Bul.301:348)

Kinds of Matings	Per Cent: Relation of mates to each other	Per Cent: Inbreeding of offspring
Full brother and sister (first generation)	50.00	25.00
Full brother and sister (second generation)	60.00	37.50
Full brother and sister (third generation)	73.00	50.00
Parent and offspring (first generation)	50.00	25.00
Parent and offspring (second generation)	67.00	37.50
Half brother and sister Grandparent and grandson or granddaughter Double first cousins (4 grandparents in common) Full uncle and niece Full aunt and nephew	25.00	12.50
"Full brother and sister in blood" (i.e. by the same sire and out of full sisters	37.50	18.75
"Three quarter brother and sister in blood" (i.e. by the same sire and out of half sisters)	31.25	15.625
First cousins (two grandparents in common) Half uncle and niece Half aunt and nephew	12.50	6.25
Half first cousins (one grandparent in common)	6.25	3.125

SUMMARY

The recent genetic status of the Yorkshire swine in Canada was studied by the use of one sample derived from volume 60 of the Canadian National Records for Swine. Complete five generation pedigrees were used. The findings, using the formulae for inbreeding and relationship as developed by Wright (1922, 1923) are summarized as follows:

1. The average coefficient of inbreeding for the breed has risen to 2.06 per cent, in the five generations from 1936 to 1948. This was enough to lose approximately 0.51 per cent, of the remaining heretozygosis, per generation.

2. In the same period the average coefficient of inter se relationship has risen to 1.04 per cent. This accounts for about one-quarter of the inbreeding found, indicating a tendency for the formation of separate and distinct families.

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