

STUDIES ON THE
INHERITANCE OF MILKING CAPACITY
IN
DAIRY CATTLE.

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By

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I N T R O D U C T I O N

A. Present Knowledge of the genetic principles underlying milking capacity.

The art of Breeding is of ancient origin, but the science of Genetics is still in its infancy. Yet, in spite of its comparative newness, it has secured very considerable knowledge relating to small animals and to the more easily measured characters of larger ones. The science has, however, owing to the difficulties encountered, made but little progress in those branches which relate to the inheritance of productivity in the larger farm animals. In particular, there is one branch which has resisted all methods of investigation and experimentation, and that is the genetical aspect of milking capacity in cattle. For many years, even in the Pre-Mendelian period, this problem had attracted the attention of investigators of many nationalities, and from such points of view as the biological, statistical, cytological and purely economic. A study of the results of this work gives rise to much surprise. Although many assumptions and theories have been suggested, and attempts to prove them have been made, yet practically no definite conclusions have been reached as to the actual mode of inheritance of milking capacity. There are certain general principles which are widely accepted/

accepted - such as the factor, or factors, responsible for high milk yield being dominant over those for low milk yield, but theories as to the actual number and the mode of transmission of the hereditary factors involved are many and of great diversity. The review following makes some attempt to bring together for comparison, most of the theories which have been offered in the past as contribution towards the solution of the problem.

A comparison of the data provided by the official milk records over a period of years shows very clearly that improvement, as estimated by increased yield, has been disappointingly slow. An examination of Table I will show that over a twelve-year period, there has been an increase of only 98 gallons in the average yearly production per individual of the cows and heifers recorded by the English Milk Recording Societies. It may be assumed that these animals represent the best stocks in the country.

TABLE I/

TABLE I (296).

Increase in Average yearly milk production of all cows and heifers recorded under the Scheme of the Ministry of Agriculture.

Year Oct. 1. to Oct. 1.	No. of Cows and Heifers Recorded	Average per Cow or Heifer
1917-18	19,793	426 gallons
18-19	37,880	450
19-20	61,323	479
20-21	97,903	495
21-22	117,023	517
22-23	127,151	534
23-24	138,086	535
24-25	148,905	513
25-26	154,322	529
26-27	156,847	524
27-28	149,971	513
28-29	144,812	524

Before 1924-25 the average yield was calculated at the equivalent of $10\frac{1}{4}$ lbs. per gallon and subsequently at 10 lbs.

The increase of 98 gallons per annum is not principally due to improved breeding practices. During the last twelve years, feeding methods have received great attention and in all probability, the greater part of this increase is the result of better nutrition rather than the application of a knowledge of genetics.

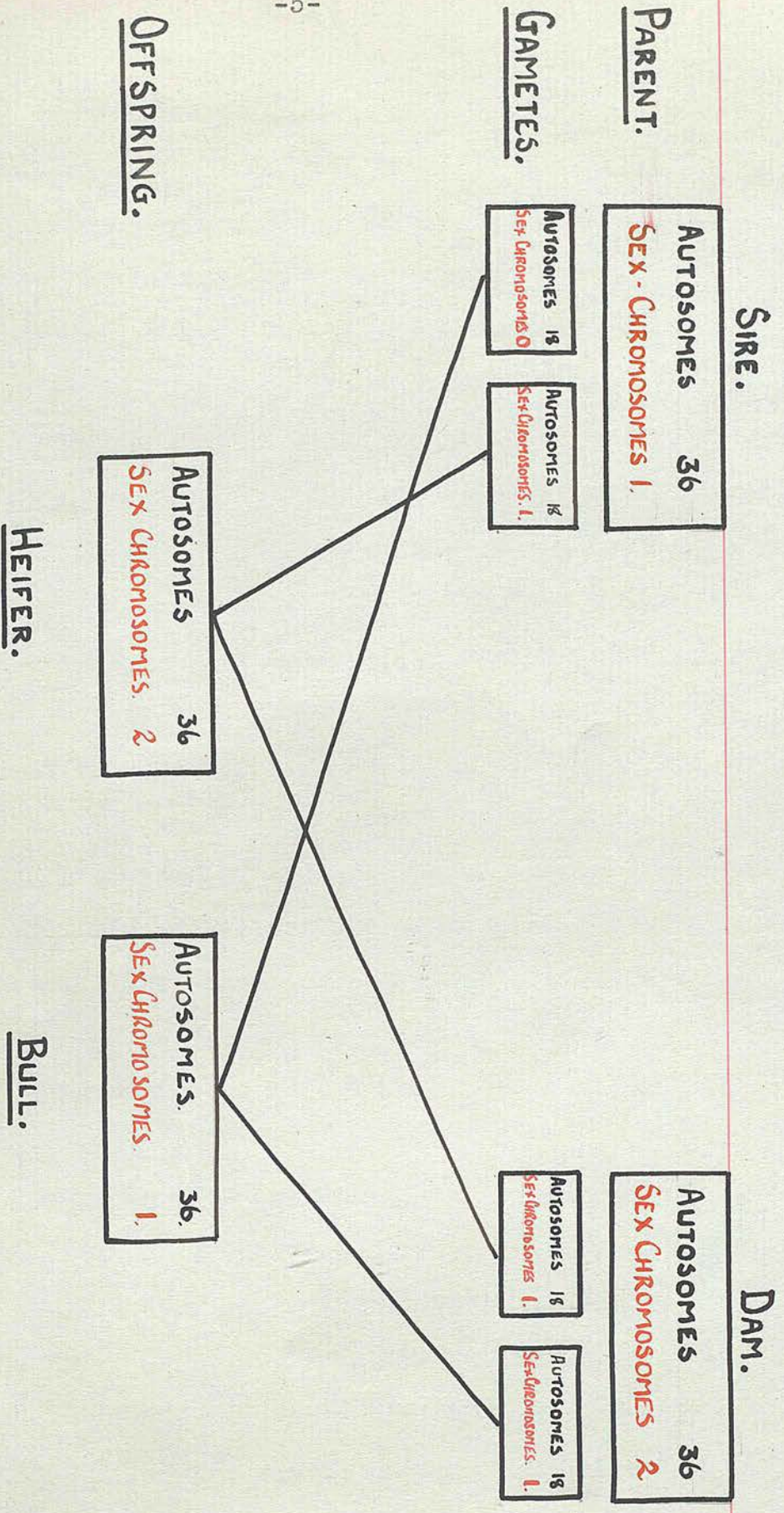
B. Cytological aspect of inheritance in dairy cattle.

At present little is known regarding the cytological basis of inheritance in dairy cattle. There is even controversy as to the number of chromosomes. Masui (285) found 33 chromosomes in the bull, and/

and Wodsedalek (293, 294) postulates 18 pairs of autosomes, plus one sex chromosome in the male and two sex chromosomes in the female. The position and relationship of the genes in the chromosomes responsible for the characters of milk production have not yet been ascertained. The chromosomes carry factors which cause the development of the characters of the new body. The characters inherited by the new organism from its parents are dependent on the distribution and recombination of these genes in the chromosomes. At fertilisation, each parent contributes, according to Wodsedalek, 18 single autosomes thus making a total of 18 pairs in the individual of^{the} next generation. Of the sex chromosomes, the female always contributes one, whilst the male may, or may not, make a like contribution. When both parents contribute a sex chromosome, the resulting animal is a female, whilst a male arises when the dam alone contributes a sex chromosome.

TABLE II/

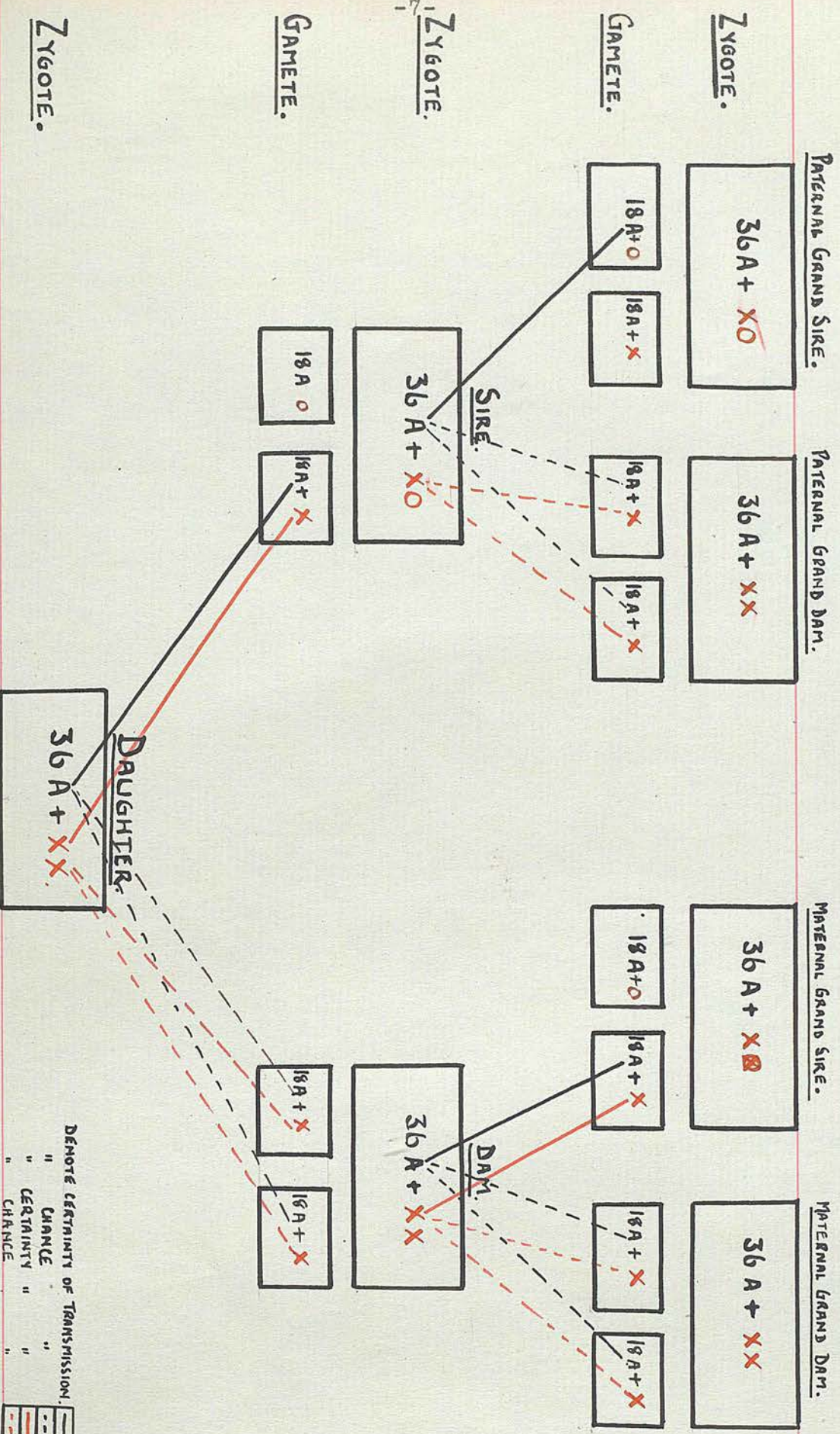
FORMATION OF MALE AND FEMALE IN CATTLE.



These x, or sex-chromosomes, not only determine sex, but also carry other genes which are therefore, in their transmission, connected with the sex determining mechanism. The female possesses two x-chromosomes and always contributes one of these chromosomes to her offspring irrespective of sex. The female, as opposed to the male, can have in her genetic constitution a greater variety of these sex-linked factors upon which to draw. The sex of the offspring makes no difference to the transmission of sex-linked factors through the female. On the other hand, the male, if carrying sex-linked factors, must pass them to his daughter but cannot do so to his son as the son receives his single x-chromosome from his mother. Sex linked factors are therefore inherited in an alternate sex direction - that is from sire to daughter and thence with equal chances, to her son or daughter. Such factors cannot be transmitted from sire to son.

The result of this is that in three generations, and assuming the stock carries certain sex-linked factors, the granddaughter will have no sex-linked factors from her paternal grandsire but one sex chromosome must come from her paternal grandam while the other has equal chances of coming from either of the maternal grandparents.

MECHANISM OF INHERITANCE OF SEX LINKED FACTORS.



(No transmission of sex-linked factors from the paternal grand sire.)

Denote certainty of transmission.

" " CHANGE

" " CERTAINTY

" " CHANCE

	AUTOSOMES
	"
	SEX-CHARACTERISTICS
	"

It is not improbable that some of the factors responsible for the characters of milk yield may be resident in the sex chromosomes in which case some of these factors may be sex linked. In the late 19th century, the possibility of what is now termed sex-linked inheritance of milk yield was considered. In practice, in some herds, especially those of the Jersey Breed, and also in the grading up of native stock with British breeds, the possibility of sex linkage occurring in milk yield inheritance is recognised and breeding practices formulated accordingly.

I. REVIEW OF LITERATURE.

I. A Review of Literature on the Inheritance of Milk Yield and Butter Fat in Dairy Cattle.

The number of investigations and the amount of data concerned with the problem of the inheritance of milk and butter fat yield in dairy cattle are very considerable. This problem has been investigated from many and varied angles and the results of analyses published in various forms - from the popular article of the agricultural weekly to the scientific paper. Data have been described and re-interpreted. It would indeed be difficult to find another subject which lends itself so readily to this kind of treatment. The dissemination of undigested information and vague hypothesis is largely due to the acute desire by breeders throughout the world for any available knowledge on this subject.. In the first place, the results of an experiment, or of a statistical analysis, usually appear in a concise form in some purely scientific journal. Later the same work will be published in a semi-popular paper. Finally, after much simplification and the inclusion of many obvious remarks, it will end in a farmers' publication. It is granted that results of scientific work should be translated and elaborated for the benefit of those concerned with the practical application of research, but with the problem in question, this is somewhat overdone/

overdone-especially considering the lack of any real advance in knowledge of the underlying principles of the genetic constitution of dairy cattle.

The last remark calls to mind the second outstanding feature noticeable in the literature on milk inheritance. Many papers may be read and scoured for definite facts regarding the mode of inheritance, but all in vain. Paper after paper is written but the results are not conclusive because the assumption made by the authors cannot be proved, perhaps owing to insufficiency of data, and always to the intricate and elusive nature of the problem. Experiments are costly and of long duration, and statistical analyses require large quantities of first class data which are seldom obtainable.

Owing to the above two facts, the compilation of a bibliography on this subject is not easy. Also, many papers are written from the nutritional, or from the environmental, aspect of milk production with only a certain amount of inheritance data interwoven. This makes the process of elimination extremely difficult. However, the aim during the compilation of this bibliography has been to try to include all the outstanding work and as much as possible of the data of less importance, and lastly to avoid including material which does not bear upon the underlying/

underlying problem of inheritance.

Several possibilities as to the classification of this data presented themselves but it was decided that greater clarity could be obtained by making two main divisions, which are as follows:-

1. Examination and treatment of material.
2. Results of statistical and genetical analyses.

Between these two methods there is much overlapping and differentiation is not at all times easy to accomplish.

x x x x

Before dealing with the data falling under these two headings, mention should be made of the earlier views upon inheritance of milk yield. The breeding practices of earlier times are of extreme interest especially as many still prevail. It cannot be denied that those old time practices won for Britain her reputation as the "Stock farm of the world".

At that period nothing definite was known concerning Heredity: it was mainly the question of breeding the best to the best. The conceptions of the old time breeders, such as Bakewell and Bates may be summarized under:-

1. Conception of the desired type.
2. Mating the best to the best.
3. Appreciation of Pedigree.
4. Use of the Progeny Test.

The/

The views of the Pre-Mendelian Period are described in detail by Von Patow (161) 1926, and therefore will be enumerated briefly. In this period there were three determinants of the methods of breeding of dairy cattle. Firstly, there was formalism, secondly, a conception of heredity based upon Galton's law of ancestral inheritance and finally, milking tests which dealt only with absolute yield.

Formalism (that is selection by form) even today bears far too much influence on the methods of selection and judging of dairy cattle. Pott (183) was one of the first to realise that performance, rather than selection of the ideal type, should be the first consideration. Schrewe (207) also realised that in addition to selection by form, performance of the female ancestors of the bull must be taken into consideration. However, it will be a long time before formalism takes the place of minor importance that it should. In practically all countries, except Denmark, type is one of the most influential factors in selection, although, with the development of milk recording schemes, the value of performance records as a slight indication of the possible genotype of an animal is being gradually recognised. The effect of formalism is lasting.

Many/

Many sires had, and still have, their reputation owing to prizewinning ancestors, these ancestors being judged purely by their appearance. That such a practice is dangerous to the improvement of production records is obvious.

Vogel (239) states that colour formalism no longer exists in Germany and he expresses doubt as to the fundamental soundness of the points considered in judging cattle. He advocates that conformation plus constitution be considered in helping to estimate innate ^{MILKING} capacity. He is also a supporter of the method of written judgments being given at shows. He considers many distinctions made are too fine especially for breeding animals. Lauprecht (283) 1930, is in disagreement with the above statement regarding colour as he states that the German Short-horn breeders never show a white cow.

Statistical Investigations.

Age and Origin of Data.

Some of the data examined statistically date back for many years. The records of von Patow go back as far as 1873, whilst those of Schrewe date from 1873 for milk yield and 1894 for fat content, and lastly those of von Lochow, to 1876. Following these records in chronological order came those of Fleischmann 1891, and Hittcher (1894-99). Work of this/

Work of this type in England is of comparatively recent origin. Speir (213) 1904, was the first British worker, but his studies on Ayrshire cows did not yield very conclusive results. From this period onwards the number of investigations has increased and there are none worthy of individual note.

The origin of data which have been statistically examined varies considerably. Formerly records were collected from individual herds which had been recorded for some time - such as those of von Patow and Schrewe, but these are limited in number. When such data are available and providing the records have been fully maintained throughout the period, they are of great value. Apart from the source of old records there are many other sources. Most common and numerous are the data from Advanced Registry Records and the Register of Merit. Those two sources have been used by Gowen, Turner, Ragsdale, Brody, Hooper and other American workers. Some few American investigators such as Copeland have used material from Jersey Cattle Clubs. In Britain, records analysed have usually been obtained from the English or Scottish Milk Recording Societies. Other sources of material are competition records of Breeding Centres as used by Funkquist, Blue Book data examined by Marshall, Swedish herd books by Richardsen, whilst many workers have used Breed Society or/

or private records. The drawback to many of the statistical studies for which published records provide the data is that these usually exclude the low yielding animals.

Measures of Comparison.

There are many opinions held as to the actual figure which should be taken as the measure of milking capacity in dairy cattle.

Various correction factors have been calculated and applied almost universally. Adjustment for length of lactation, dry period, service period, age etc., have all been made. These correction factors are obtained from great masses of data but, as would be expected, when applied to the individual, often fail. It would appear, therefore, that there is danger of defeating the very purpose of the study if too many correction factors are applied, for by their application, individuality is lost. Also, some of the variations may be due to genetic as well as to environmental and physical causes. Certainly, statistical data should, and usually do, deal with great numbers, yet surely greater accuracy would result from less material so selected that correction factors need be extremely limited in application.

Another outstanding feature is the expression of butter fat in terms of both yield and percentage or content/

content. Many investigators, especially in America, base their work on fat expressed as a percentage. Percentage **per** lactation is often calculated by taking the average of the butter fat tests which are taken during the lactation period. These tests are expressed as a percentage. Therefore the final average percentage is not a true indication of the fat content of the milk as it is not based upon the total quantity of fat in the total quantity of milk but upon the average of several percentages. Löwe (137) draws attention to this point by explaining that although he used fat percentage, the percentage was calculated by $\frac{\text{Fat Yield} \times 100}{\text{Milk Yield}}$. Secondly, fat percentage is influenced by quantity of milk and quantity of fat. If milk quantity increases without a proportionate increase in fat yield, the percentage will fall indicating less fat which is not necessarily true, as the cow may have secreted the same quantity of fat but of greater dilution as there is more milk. External influences affecting the yield of milk will be reflected on the butter fat percentage, although the yield may still be about the same. Von Patow (161) 1926, rightly states, "The use of fat-content for the testing and calculation of the correlation between milk and fat yield is entirely out of place.

In/

In the first ~~instance~~, one does not yet know whether there is any relation between the two, but when one performance is expressed from the beginning in the percentage of the other, such a relation is assumed beforehand". Later on, von Patow proves that the amount of fat must be the actual expression of fat production.

Formerly, only the absolute yield was used. Although Schrewe (207) examined his data with great care and realised the importance of non-hereditary factors, yet he used absolute yield. Other workers of this period were Fleischmann and Hittcher, whom, von Patow states, calculated milk yield for 500 kgs. of body weight and 300 days of lactation, abnormal lactations being eliminated. This calculation is interesting as there appears to be no other mention of employing body weight in estimating corrected yield.

The next outstanding measure is that first introduced by Peters, but latterly used by many German workers. Peters wished to introduce a method which would eliminate, as far as possible, the effect of environment and so for this purpose he compared individual yields with the average of the byre. For correcting to the "byre average" the herd average was taken as being 8 Kgs. of milk and 300 gr. of fat per day, and the following formulae applied:-

$$\text{Byre Average (for milk yield)} = \frac{8 \text{ (absolute performance)}}{\text{Byre Average}}$$

$$\text{" " (for fat yield)} = \frac{300 \text{ (absolute performance)}}{\text{Byre Average}}$$

By using this calculated yield, the effect of weather, feeding etc., are common to both individuals and the herd as a whole and therefore they are eliminated. There are two objections to this measure - the herd might be too small (Peters, 1924, places the limit at twenty) and secondly, the genetical composition of a herd may vary within a year.

The "Byre Average" has been largely used by von Patow. The method followed by Rinecker (194) is somewhat similar. He compared the yield of individual animals with that of their stable companions of the same age and year (if possible). All first lactations were disregarded and ^{LIKEWISE} those animals with only two or three lactations. Dettinger (31), working on data from cattle of the lower Rhine district also used a modification of the "Byre Average". Bonnier (12) employed an original method. First he calculated the individual correlation of every cow of the 79 Swedish Ayrshires. This was obtained by correlating the figures for butter fat percentage and milk/

milk yield per animal throughout the test period. Having obtained this correlation, he calculated the coefficient of correlation between these correlations and the average butter fat percentage.

For ordinary dam and daughter comparisons, Pearl formerly used the difference between the average performance of daughters and that of the dams in order to test the transmitting ability of the sire. This measure was also used by Driehaus, Löwe, Hayden, ~~and~~ Carroll, and to a certain extent by Feige. However approves of this system provided a sufficient number of pairs can be obtained. A modification of this was devised by Hansson and used by Terho (219) can be expressed as:- the average performance of daughters plus (average performance of daughters, minus average performance of dams).

The ordinary dam daughter difference method of estimating a sire's transmitting ability is criticised by Yapp (260) on the grounds that (1) No allowance is made for the widely varying transmitting ability of cows, (2) Physiological limits of production are determined by total produce rather than pounds of milk and (3) No definite value is set for the transmitting ability of a sire regardless of ^{the} reproductive capacity of the cow to which he is mated. Added to this is the disregard of the yield of the dam; if a sire is able/

able even to maintain in the yield of his offspring the high yields of their dams, he must be good.

Yapp attempts to overcome some of these difficulties by using the following formula for his bull index:

$$x = 2a - b$$

x = transmitting ability of sire, expressed in terms of milk of 4 percent butter fat, a = yield of milk of daughters and b = yield of milk of dams (both yields being reduced to a 4 percent butter fat equivalent).

Goodale (59) does not attempt to standardize the product but uses the formula:-

When daughter's average yield is greater than dam's

$$\text{Bull Index} = \text{Av. D.} + 1.4 (\text{Dr} - \text{D})$$

When dam's average yield is greater than daughter's

$$\text{Bull Index} = \text{Av. D.} - 3.3 (\text{D} - \text{Dr})$$

D = Dam's average yield Dr = Daughter's average yield

This method penalises the sire whose daughters are lower yielders than their dams.

Another objector to Pearl's method is Walther (243) who points out that the difference between dam and daughter should be compared with that of the dam and maximum yield of the breed - this comparison being expressed in a percentage form. Further, he is regretful that attempts at a practical explanation of the mode of inheritance should be outweighed by a scientific explanation. Turner (231) (and his colleagues/

colleagues, Ragsdale, Gifford and Elting) also bring forward certain objections to the dam and daughter comparison method as a measure of sire's transmitting ability. He holds the sire's influence constant by comparing progeny with small variations - that is grouping data according to 50 lbs. fat classes. Turner points out that Gowen does not hold the sires constant. Having grouped his material as above he next proceeds to determine the partial correlation.

Latterly the method devised by Pearl and used by Pearl, Gowen and Miner (167) involved dividing the population into four equal parts and designating values to the amount of milk (1) above the third quartile line (2) between medium and third (3) between first and medium and (4) below first. Each dam and daughter under consideration can then be given a value of A, B, C or D. From the relative proportion of daughters and dams in higher classes the sire was evaluated.

The problem of devising a true "Bull Index" requires further investigation but it is not the purpose of this paper to evaluate the different methods as this would make a study in itself.

Many opinions are held as to the best measure of innate milking capacity in cattle. One of the most generally/

generally used measures is the lactation yield; normal and probably corrected for age of animal but discarded if of too long duration and the cow non-pregnant. The number of lactations considered necessary in order to obtain a true lactation average varies. Löwe (137) holds that three lactations are essential whilst Johansson (114) takes the mean of the three best normal years in sequence. Terho's (218) measure is similar with the exception of discarding calving intervals of more than fifteen months duration. He is also responsible for an index which expresses the performance of the best five months as a percentage of the total performance. Rinecker (194) discards the first lactation and only takes data from animals having at least two or three. Driehaus also refrains from using the first and any abnormal lactation but apart from this, uses the absolute yield. Peters (177) discards five of the best and five of the poorest animals from each herd (over twenty animals) and then has three years of undisturbed performance. Per Tuff (221) is somewhat original in using the first lactation to standardize conditions (although he realises that it is useless as an indicator for life performance), the second lactation as an indicator and finally the average of the two. There appears to be some objection to this method/

method in that the first lactation carries half the weight in the mean if only two lactations are used. In other investigations, ^{PER TUFF} together with Langmark (220) ~~he~~ uses material having only the first lactation. They consider that the combined lactation plus dry period - that is the calving interval, is the true measure as it automatically allows for the drop in yield due to pregnancy. They also suggest the maximum yield as a suitable measure, for by this means the effect of environment is eliminated. This opinion is supported by Wilson (252) 1925, who takes the average of the three successive maximum weekly records. Gavin (53) makes a slight modification in that he suggests the maximum daily yield reached three times or exceeded. Pearl corrects lactation to the year of maximum production which he considers to be at eight years of age. Gowen (73) 1924, also applies correction factors and includes animals having only one 365-day record, or if several records, takes that nearest to the time when the cow is eight years old. Animals having a shorter time record are discarded. Hays (102) works on a ten-month-corrected for-age basis - that is the first ten months following calving. Hesse (106) considers five lactations are required.. Sanders (198) introduced a measure of yield/

yield which takes into consideration total lactation yield and maximum yield and is termed the "Shape Figure" (S.F.)

$$S.F. = \frac{\text{Total lactation yield}}{\text{Maximum yield} \times R}$$

R = a value taken from a table drawn up by Sanders which makes adjustment for month of calving.

The Shape Figure is not well adapted for practical use but its value lies in its attempt to measure persistence and ^{therefore} can be used in studies which deal with the main features of the lactation curve - i.e. persistence and maximum yield.

Brumm (15) uses a method somewhat similar to that of Sanders, in that the performance of each lactation month is expressed as a percentage of the total calving interval.

Turner (231) in his studies of Jersey sires, converts 305-day Register of Merit records to a 365-day record basis by means of factors determined from Guernsey data dealing with the rate of decline of fat secretion during the lactation period. By the use of these conversion factors, Turner avoids ignoring the very important persistency factor and thereby not giving due credit to sires having daughters of low persistency but high maximum. He states that the application of the correction factor (1.15) to the 305-day record tests gives remarkably accurate results when/

when compared with the 365 day record averages. If there was more than one 305 day record per cow available, her highest record was taken as being the best indication of her milking or fat producing capacity.

Smith, Scott and Fowler (212) in their analysis of Ayrshire data, used only records which were not less than 245 and not more than 365 days in length, and where the cow calved again within $13\frac{1}{2}$ months. Correction factors were applied for age of cow and the average of all corrected records per animal were taken as the final measure.

Von Patow, in estimating the byre average, discarded all abnormal lactations as well as the first two, as during this time he thinks the animal is still undergoing bodily development and therefore cannot produce to the full extent of her milking capacity. He considers that the calving interval and not the lactation period is the most desirable measure. There is much to be said in favour of the omission of abnormal lactations.

Koláček (120) 1930, wrote an interesting paper on the Black and White cattle of Bohemia in which he fully describes his method of analysis. His object was to obtain an unalterable production capacity and for this purpose he takes the first 305 lactation days/

days. His standard is as follows:-

Milk and fat during^{the} first 305 lactation days, are followed by 60 days dry period therefore calving interval = 1 year. The seventh to eighth year is taken as the age standard.

Formula for normal production of milk or fat =

$$P_n = P_{305} \cdot l + (S \pm O \pm M)$$

= Production in 305 days x l + (sum of coefficients for age \pm S, length of dry period \pm O, and month of calving \pm M).

For this purpose, certain correlations (such as milk or fat yield and age, or dry period or season of year) were worked out and tables determined.

Kolacek maintains that it is possible to obtain from the yield of the first lactation, the P_n value which can be used^{when} making dam and daughter comparisons of the same sire thereby estimating the hereditary value of the bull.

There are various opinions as to the number of daughters which are required to estimate the value of a sire. Turner, Ragsdale and Gifford indicate that ten daughters are sufficient except when dealing with Ayrshire data which must have been more limited as Gifford and Turner here base their investigations on four or more daughters per sire. Pearl considers two or more dam and daughter pairs whilst Graves considers six or more yearly recorded daughters are essential.

Experimental Investigations.

Mention/

Mention will be made of the advantages of experimental as opposed to statistical investigations of this problem and also of the general methods followed. There are some outstanding herds which have been run as a long time breeding experiment. Amongst these may be mentioned the Bowlker herd of Massachusetts now located at Illinois, the Danish herd and the Wisconsin Experiment Station herd. There are several investigators opposed to statistical treatment of data whose papers will be briefly mentioned. One of the oldest of these papers is that by Müller (154) 1910, who demands experimentation in order to trace the mode of inheritance of characters, and causes of variation in milk yield. Von Patow discusses the relative merits of both methods of investigation and emphasizes the mistake which is often made of applying results obtained from mass statistics to the individual.

Johansson, as reported by Funkquist (48) 1921, also objects to the use of statistics on the grounds that investigation of individual pedigree and progeny as individuals is neglected to a great extent. Pearl and Miner stress the importance of preceding biological studies by statistics. Spöttel (214) states that he places no reliance in herd book studies but/

but does not suggest an alternative method of procuring data for preliminary investigations.

Main Trends of Thought resulting from Statistical and Experimental Investigations.

Genetical Relationship between milk yield and butter fat.

Kirchner (119) 1901, appears to be one of the first to conclude that butter fat percentage is inherited. This conclusion he reached is a result of comparing the butter fat percentage of cows of two families which were crossed. Van Norman (238) 1908, studied the 17 year records of grade Guernseys, and concluded that there is great individual variation in the transmitting ability of sires but generally, pure bred sires bring about greater improvement in the butter fat and milk yield of their progeny than grade sires. Muller 1910, indicates that there is unequal transmission from sire and dam. Hansen (97B) 1924, states that not until this year⁽¹⁹⁰⁴⁾ was the knowledge common in German breeding circles that the inheritance of milk yield was affected by the sire as well as by the dam. Where great success in the inheritance of increased milk yield and especially fat percentage has been obtained, the majority of cases have been connected with definite blood lines. Hansen further states that it is possible to have all combinations of/

of fat content and milk yield, and a desire to raise milk yield need not necessarily result in a decreased fat content, thereby indicating that milk yield and fat content are separately inherited. This point is illustrated by results of analyses of figures obtained from the East Friesland Control Association. The effort made by West Friesland to increase butter fat percentage by breeding methods is shown by the fact that 50 percent of all the cows of this district belong to the Association. ~~and~~ The Lowland Cattle Breeding Herd Books demand that the sires' dams have a minimal milk requirement and in Friesland a minimal fat content of 3.25 percent on the part of the paternal dam. Similarly, Frölich (47) emphasizes the need to study the fat content of the sire's dam, and he also states, as a result of Bison and Yak crossing, that different factors are responsible for milk and for fat yield.

Ellinger (36) carried out experiments in Denmark on Red Danish and Jersey purebreds and crosses. His results indicate that from Red Danish data, milk and butter fat percentage are quite independent ($r = + .055 \pm .044$) whilst Jersey data (approached by different methods and the use of partial correlations) give a correlation of $- 0.332 \pm .051$ between milk yield and butter fat percentage. This correlation obtained/

obtained from the various crosses (crossbred, $\frac{5}{4}$ Danish $\frac{3}{4}$ Jersey and $\frac{7}{8}$ Jersey) gradually returns to the parental correlation. Red Danish and Jersey F₁ generations have intermediate yields but slightly nearer the Danish. Second back crosses to Danish have a milk yield practically the same as Danish, whilst second back crosses to Jersey have a yield slightly higher than the Jersey.

Graves (91) analysed data gathered from the dairy cattle breeding experiment initiated by the Bureau of Dairying, Washington (1918) and concludes that percentage butter fat and milk yield seem to be inherited independently. Reagin (188) states that higher milk yield is negatively correlated with fat percentage but a high positive correlation appears with total fat yield.

Copeland (25) working on American Jersey Cattle Club figures, considers that a parent may be prepotent in increasing fat percentage separately from affecting milk yield or may increase or decrease both. In agreement with other investigations, he obtains a negative correlation for fat yield and milk yield. He finally states that an increase in total fat can be accomplished by selection for high^{fat} percentage as well as ^{high} milk yield.

X % fat.

Lowe/

Löwe (137) discusses in some detail the problem of breeding for increased fat content and he draws his conclusions from various herds, and individuals. He points out the necessity for establishing good female lines to ensure the maintenance of high fat content. AS Milk yield and fat ~~being~~ inherited independently, increase in fat need not produce a decreased milk record as both can be raised simultaneously.

Peters (177) examined the twenty-eight years records of East Prussian Dutch Cattle and, amongst his observations, states that within a single herd, cows giving the most milk have the lowest fat percentage, also on the whole, good mothers have good daughters but yields of daughters of inferior dams are usually higher than that of the dams. There is need to select cows coming from good families as well as good parents. Woodward (256) carried out work similar to Peters, and found that high producing daughters come from dams with relatively high records although the difference between the daughters is not so great as between the dams. Davenport, as reported by Hansen (95) 1917, concluded from the results of analyses of sixty-eight good producing Advanced Registry animals that dams of the same yield class gave daughters of different/

different producing capacity and cows of any particular class were descended from widely varying dams. Cows of all yield classes have daughters of varying records, therefore good cows may have only fair daughters but usually good daughters come from good dams.

Studies relating to progeny tests and improvement of production by use of pure-bred sires.

The work of Sederholm (210) 1900, represents one of the earliest Swedish papers on this subject. He analysed the records of offspring of five herd sires. The F_1 generation of three of these sires showed marked improvement in quality of milk, one F_1 generation was slightly improved and the other was inferior to the dams' records. Sederholm wished to demonstrate that ancestral yield influenced that of the offspring, especially the influence of the sire on the fat content of milk of the progeny. All later investigations of this nature give very uniform results. Beam (9) found that of the transmitting powers of seven herd bulls, two failed to increase the average production of their daughters. The statement of O'Callaghan (157), that dairy sires with good production pedigrees almost always produce good daughters and that Guernsey sires are more successful than any other breed in this capacity, seems to need confirmation/

confirmation. Lawritson, Hendrickson, and Nevens (133) emphasize the need for progeny tests and state that a bull's pedigree should contain (1) milk yield and butter fat of his dam and her daughters, and records of her other sons' daughters and (2) records of his sire's daughters and his other sons' daughters. Mackintosh (146) supports Lawritson as to the value of progeny tests and states that sires should be chosen preferably from line bred stock thereby ensuring a concentration of blood of a family of cows. Atkeson, Mathieson and Fourt (8) studied 3,700 Idaho cows and found that as the yield of the dams increased the fewer were the number of sires who increased their offspring's record over that of their dam, thus showing the need for progeny tests. Of other work along these lines might be mentioned that of Schönningh (Black Pied East Friesian cattle data), Faber (Danish methods) Meade (Guernsey data) Davidson, Carroll (Holstein Friesian data) Yapp and M'Candlish. Feige (41) mentions the point before discussed - progeny records do not distinguish between those sires who raise a low herd average from those maintaining or raising a high herd average. He further adds that selection by the male side alone is very slow as only exceptional sires will improve an unequal herd as the effect/

effect of a sire varies in heterogeneous matings.

Pearl (164) in emphasizing the value of progeny tests, points out that measuring the ability to transmit by Advanced Registry records, is poor when applied to the cow, but is a good indication of the bull's value because he enters as a result of his daughters' yield - the one being phenotypic selection and the other genotypic. Pearl also describes in full the Aroostook Jersey Sires' Futurity Test which appears to be a good form of progeny test. In 1920, Pearl (166) states that sires which are good for transmitting high butter fat percentage do not always transmit high milk yield, as for instance "Hood Farm Torono" and "Spermfield Owl". Much less than half the Jersey sires raised the butter fat yield of their progeny over that of the dams, but about half raised milk and fat percentage. Pearl, Gowen and Miner (167,168) carried out further studies along these same lines. Similar results have been obtained by the Mount Hope investigators in Guernsey cattle.

Terho (219) investigated the inheritance of economic characters in the indigenous Finnish Cattle. He concludes that five progeny per sire should be examined as early as possible and by the time the bull has reached six years, his transmitting ability should be known with a moderate degree of accuracy.

In/

In a preliminary study, Terho (218) made dam and daughter comparisons from which he gathered that sires influence fat content. Gifford and Turner (55) 1928, conclude from an analysis of Ayrshire sires and dams, that the butter fat index of the daughters is a better indication of the sire's transmitting ability to his granddaughters through his sons, than is the dam's index an indication of her transmitting ability to her granddaughters through her sons. Later, (56) in 1929, they estimate that a unit increase in the yearly production of the dams affected their sons' daughters' production to the same extent as ~~a similar~~ increase in the sires' Progeny's average record influenced his sons' daughters' production. Turner (228) 1926, calculates from Guernsey sire data a formula for the sires' potential transmitting ability (P.T.A.)

$$P.T.A. = \frac{\text{Daughter's fat Production} - 0.15 (\text{dam's fat production})}{0.85}$$

He also states that sires are better able to transmit their potential fat capacity through their sons to their granddaughters than are dams able to transmit their own production through their sons to their granddaughters. Turner considers that sires appear to contribute more to their daughters' yields but this is ~~doubtful~~ for the reason that the sire is/

is measured purely by his genotype, whilst the dam can only be measured by her phenotype. Hansen (95) also studied the problem of progeny tests and, for his data, drew evidence from the Lowland Breed in Sweden and also the Ayrshire and Fjall breeds, from which he gathered that the male has great influence in the transmission of butter fat characters. Wriedt (257, 258) was also a strong supporter of progeny testing and recommends that a bull should be mated to twenty of his own daughters.

Many investigations of great economic importance have been conducted with a view to the improvement of scrub herds by the use of pure bred sires. The majority of these investigations have been undertaken in America. M'Candlish has been one of the most active of the investigators and gives some very interesting results. In 1920, he alone (139) and also with Gillette and Kildee (141) measured the effect on the improvement of scrub stock (1) by improved nutrition (2) by improved nutrition and the use of Guernsey, Jersey or Holstein-Friesian sires on scrub cows. They found that the offspring of a scrub sire had an average increase in milk yield of 10 percent and in fat yield of 13 percent over those of their dams. This, presumably, is due to environmental improvement. The average of first generation grades shows an increase of 39 percent in milk yield and 35 percent in fat yield, the highest increase, 90 percent/

percent in milk and 59 percent in fat being found in the Holstein-Friesian grades. Second generation grades show a total increase of 130 percent in milk and 109 percent in fat above that of their scrub grandparents. Persistency in scrub cattle is also low. M'Candlish and Winters (143) 1920, draw attention to the problem of "nicking" which they maintain is not sufficiently recognised, and also to the necessity of rigorous selection even in purebred herds as some purebred sires are not good enough to head a purebred herd, whilst Iowa results show that some are not even good enough for a scrub or grade herd. Later, as a result of further grading-up investigations carried out on scrub cows brought up from Arkansas in 1907, and crossed with purebred dairy sires, M'Candlish concludes that all F_2 grades are at least 50 percent better than their scrub grandparents. Other similar results have been obtained by May, Stevens, Weaver, Matthews and Kildee, White (A.H.), McDowell and also Olson and Biggar.

Studies pertaining to the character "Persistency".

Milk quantity per lactation is determined by persistency and maximum yield. Persistency is therefore a very important character although it has not received the attention of many workers. Sanders has/

has thoroughly investigated this problem in some detail and as a result devised a measure, the "shape figure"^(S.F.), which takes into consideration both maximum yield and persistency.

To quote Sanders (199) 1930, "There are three aspects of the association of maximum and persistencyGenetic, dairy husbandry and physiological respectively. From the comparison of the breeds, no relation was apparent between maximum and persistency"

The S.F. rises markedly and definitely from low to high producers. In good milkers the maximum is lower relative to the total yield than in poor milkers.

Sanders (200) finally considers that persistency seems to be a nutritional factor rather than a genetic one. His explanation is not very clear as he states that the growth of the gland is the main characteristic of the persistent milker. Also the persistent milker is one which has the capacity to utilise great quantities of food for the purpose of milk production. The difference between good and bad milkers is merely their profitable utilisation of food. Brum (15) 1928, from East Finnish cattle data, concluded that the shape of the lactation curve is hereditary and therefore can be used for selective purposes. Gaines (51) 1928, criticises the use of seven day records in/

in statistical studies as such a short time record takes no account of persistency, whilst a yearly one does. Further, he adds that inheritance of persistency is through the female rather than the male, sires showing no difference in their transmitting ability of this character. This conclusion was reached as a result of a study of Guernsey data. On the other hand, Petersen, as reported by Becker and McGilliard (10) holds the opposite view, having found that Jersey sires take an important part in transmitting persistency of lactation to their female offspring. In 1928, Becker and McGilliard (11) state that there are three heritable factors which govern milk production in cattle. They are (1) Maximum daily yield (2) Fat content and (3) Stimulus for persistent milk production. Both sire and dam contribute to the inherited persistency in the offspring and maximum yield is also a genetic characteristic, these statements being based on results gained from analysis of Jersey and Holstein-Friesian material. Later, however, (1930), they are given cause to doubt these statements. Graphs were obtained from a cow who had a non-fecund lactation. A comparison of normal and abnormal lactations showed that in the abnormal lactation, maximum yield was reached at a later date, and rate of decline was much slower owing to/

to the absence of a diminishing influence of an internal stimulus. Maximum daily milk yield, following normal reproduction, was from three and a half to five times as great as that induced by mechanical stimulation alone. They conclude, therefore, that internal stimulus is not necessarily a factor in determining the persistency of milk flow as indicated by the duration of the lactation period.

Turner (225) 1926, states that the normal or hereditary rate of decline in milk secretion during the early lactation period is retarded due to further divisions of cells which become functional through the stimulus of the "follicular" hormone. There is a distinct decline in persistency during the second and third lactations as compared with the first. As an index of persistency Turner uses the ratio between total yearly milk or fat production and the maximum month's production. He considers that persistency and maximum yield are not ^{linked in} inheritance. ~~together.~~ With an increase in dam's persistency there is only a small increase in the daughter's persistency.

Inbreeding in Relation to Milk Yield.

Amongst the earlier papers bearing on inbreeding in relation to milk inheritance, may be mentioned that/

that of Hesse (106) 1913, who investigated several West Prussian herds and came to the conclusion that inbreeding does not influence milk yield unless practised in good "blood lines", thereby favouring the concentration of characters for good yield and butter fat.

Hover (112) 1916, wrote on the subject of finding the prepotent sire, for which purpose he studied Guernsey Advanced Registry records. The value of a sire can be estimated by dam and daughter differences provided there are a sufficient number of pairs available. The lack of numbers is a great drawback as good sires may be in small herds and pass unnoticed owing to the small number of offspring. Although some of the good sires are outcrosses, yet strongly prepotent sires usually belong to certain strains or families, indicating that prepotency is enhanced by inbreeding. Hays (102) concludes from the results of analysis of a limited amount of Guernsey data, that inbreeding to a slight degree seems to be associated with the best production. Increased number of males appear to result from increased inbreeding.

Hansen realises both the value and harm which may result from inbreeding. He believes that inbreeding tends towards the production of a homozygous/

homozygous strain of stock but this homozygosity may not be only uniformity of good, but also of bad characters and therefore inbreeding should only be used with care. Driehaus (32) attempts to establish the genotype of the bull by a comparison of the performance of dam and daughter, but does not regard with very much favour the practice of inbreeding.

Pearl, Gowen and Miner (167) 1919, studied the transmitting qualities of Jersey sires and calculated measures of inbreeding using the following formula:-

$$Z_n = \frac{100 (P_n + 1 - Q_n + 1)}{P_n + 1}$$

$P_n + 1$ = maximum possible number of different individuals involved in $n + 1$ matings

$Q_n + 1$ = actual number of individuals involved in these matings.

Z_n = inbreeding coefficient for the $n + 1$ the ancestral generation.

The progeny of all sires was classified according to the quartile scheme (before described) and it was found that twice as many Jersey bulls in the Jersey breed lowered the butter fat percentage and milk yields of their daughters than increased production. The degree of inbreeding varies from 0 - 41.18 percent of the total possibilities. Superior sires are slightly less inbred than inferior ones/

ones. The percentage for inferior sires being 9.65 percent as opposed to 7.08 percent for superior pure Island bred ones, the ratio of good to bad sires being 1:1.7. The appearance of famous animals in a pedigree is no indication of a guarantee that the stock will be good as it was found that in pedigrees of superior sires, animals appearing more than four times on the male side and three times on the female side also appeared in the pedigrees of inferior sires. Supporting these facts are the statements of Graves (88) 1924, who maintains that inbreeding is not of much value if prepotent sires have the same combination of factors whether they are related or not. Results indicate that a son or daughter may be homozygous for the factors determining high milk and fat producing capacity without its sire or dam being related.

The opinion of Peters on this point varies as formerly he used to support inbreeding but at present regards it with suspicion as being likely to have harmful results. Robertson (195) examined milk records which date back to 1904. The results of her analyses indicated that inbreeding to a male relationship tends to increase both quantity and quality of milk produced, whilst inbreeding to a female relationship/

relationship has the opposite effect especially upon the quality of the milk.

Larson (131) reports on the result of an inbreeding experiment which has been carried out by the United States Department of Agriculture since 1913. No degeneration of vigour has been noted. Kronacher (124) 1929, describes an interesting inbreeding experiment which has been conducted since 1908 on Grey Brown Mountain Cattle. These cattle have been inbred for eighteen years with the result that all the animals are fertile, free from disease and giving milk above the average quantity for the district. Kronacher concludes that inbreeding used with care is a good breeding practice. Löwe states that good female lines must first be selected if high butter fat content is to be maintained and having selected these good lines, the best method is then to inbreed. Smith (211) analysed Jersey data and results show higher yielding cows to be less inbred than those of breed average milk records.

Investigations involving the theory of sex linkage.

Miles' and Sedgewick's studies provide one of the earliest evidences of sex linkage. As reported by Cole (19) 1913, they mention that "Milk bulls" were said to have a greater influence upon the inheritance/

inheritance of milk and fat than the cows, the sires receiving these characters from their grand^dam. In 1899, Hittcher (108) concluded from his investigation of the milk records of sixty-three purebred Dutch cows that the male has a greater influence than the female in transmitting characters for milking capacity to his offspring. Hills and Boland (107) indicate that characters for production are based on two factors, one of which is dominant and the other probably sex linked. Lawritson, Kendrickson and Nevens (133), in giving the essential points which should be considered in the pedigree of a bull, state that investigations tend to show that characters for good records are transmitted by the sire to his daughters and by the dam through her sons. The papers of Hays (102) and Spöttel (214) seem also to support this statement although less definitely. Cole (21) reports on the result of the Wisconsin Experiment in cross-breeding, and states that the F_1 generation show a distinct tendency to resemble the sire rather than the dam. Finlay (42) is also in agreement with the sex linkage theory, and Zorn states that characters for milk yield are mainly transmitted by the sire. Of the work of more recent origin may be quoted that of Smith (211) and Smith, Scott and Fowler (212) and Corner (26) all of whom bring forward positive/

positive results regarding the sex-linkage theory.

There are other opinions as to the relative importance of sire and dam in the transmission of dairy qualities but these are tabulated on Page 63

There are a few theories which are of interest although of no great economic importance. Arenander (7) collected evidence, both statistical and observational, to show the superiority of polled breeds as milk producers. In spite of the apparent agreement in the invalidity of the escutcheon theory, Brun (14) analyses the data from 305 Brown and Pied cattle and obtained a positive correlation of $r = 0.6 \pm 0.06$ between escutcheon and milk yield. This correlation is however of no great value as it is based only on one breed and data of which leaves much to be desired. Other studies carried out at the Kentucky Station failed to support these results.

The work of Ivanova (116) and Juler (117) is worthy of mention in that it presents another point of view of the inheritance of milk. Their investigations are directed towards the significance of the presence of supernumerary teats but their results are contradictory. Ivanova distinguishes between the three types (1) those situated between the normal teats (2) those more or less connected with the normal ones and (3)/

(3) those situated behind the normal ones. She concludes from data obtained from 1385 cattle that type 3 is dominant and based on the same autosomal factor which raises milk production by 15 percent.

Duerst (33) 1927, studied goniometer measurements in cattle. He classified cattle into two **distinct** types - respiratory (work and milk) and digestive (beef). The respiratory type evolves into two other groups - meat as well as milk in which case a dual purpose animal would result. The digestive type never alters. Duerst found that in several uniformly bred strains, ~~that~~ the angle of the rib is transmitted by the sire to his daughter and by the dam to her son - the angle of the rib being actually the axis of the last rib with the horizontal. Dechambre (29) also investigated the relation between dairy aptitude and rib angle, and based his work on the different shapes of the chest. His results are in agreement with the earlier work of Duerst.

Castle (18) 1919, from studies based on data from the Bowlker herd, concludes that the reason for the milk yield of the first generation crossbreds being 3.8 times as close to the Friesian parents as to the Guernsey parents is due to the presence of heterosis. Ellinger(36) from his Red Danish and Jersey breed crosses/

crosses experiment, drew evidence to support these statements. He concludes that the tendency for the F_1 F_2 and F_3 generations to produce a quantity of milk more nearly approaching that of their high yielding parent whilst the butter fat percentage is slightly less than the average of that of the parental strains may be accounted for, either by a slight tendency for the factors for high milk yield and low butter fat percentage being dominant, or for heterosis to act in raising the milk yield and lowering the fat percentage. Castle and Ellinger are both supported by Cole.

The problem of the relation between conformation and milk yield has received much attention, and many correlations have been calculated. Gowen (67,73) especially, has studied this question in some detail and has come to the conclusion (generally accepted) that the reliability of body signs as indicators of probable milk yield is not great, even a short time milk record has far greater reliability. Matorin, however, has obtained some fairly high significant correlations between certain body measurements and milk yield.

Graves (92, 93) constructed a herediscope which is designed to show the results of various matings. It demonstrates/

demonstrates the method by which the use of a homozygous sire can completely smooth out variations at the end of six generations.

Amschler (4) investigated the daily yield and fat content of the half wild Yak in Siberia. He had data from 116 Yak cows and 6 Yak hybrids (Yak x Altai). He believes that he will be able to prove that the various performances of the cultivated breeds are, from a genetic standpoint, fundamentally related in their primitive form and from this hopes to be able to justify the method of "Line Breeding".

Lauprecht (132) introduces another aspect of the mode of inheritance of milking capacity. He attempted to correlate degree of colour in the Black and White Dutch cattle with milk yield. From the results of his investigations carried out on 542 animals he concludes that fat content has no unequivocal relation to the degree of marking, generally the animals with more white gave milk with a higher fat content. This is supported by Esskuchen and opposed by Gaude (both of whom worked with Black and White Lowland Cattle). Higher milk yield, however, appears to be associated with darker coloured animals (this bearing out the results of Kronacher on Hohenfleckvieh cattle).

Theories relating to the number of Factors involved in the transmission of the character of milking capacity.

There is much controversy as to the number of factors involved in the transmission of the character of milking capacity. Theories and views relating to this problem can be briefly enumerated as follows -

Wilson has considered this problem for many years and has altered his opinion latterly. In 1910 (248) he analysed data from some 8132 Ayrshires and attempted to prove that milk and fat were separately inherited characters owing to the fact that high yielding cows gave poorer milk than low yielding cows. For this purpose, he grouped records according to class intervals of 100. This paper was severely criticised by Karl Pearson (169) 1910. In 1911, Wilson (249) confirmed his opinion as a result of a study of the records of Red Danish cattle. He classifies the records into three groups and found that high yielding cows had good daughters, low yielding cows had low yielding daughters, and medium yielding cows had daughters of various records. Wilson concludes that milk yield is inherited in the same manner as the three Shorthorn colours. Later, in 1925 (252) he revised his theory and states that four pairs of factors are involved in the transmission/

transmission of this character. These four pairs produce sixteen grades of milk. The four dominant factors produce individually, 20, 15, 10, and 5 lbs. of milk respectively and 50 lbs. collectively. The four corresponding recessive characters produce 4, 3, 2, and 1 lbs. respectively and 10 lbs. collectively. A sure test of a sire's or a dam's transmitting ability is the yield of the poorest daughter. Dunne (34) supports the two pair factor theory after having studied Red Danish Records.

From results of crossing and back crossing with Jersey and Red Danish cattle, Wriedt (258) states that fat transmission is based on one factor and perhaps another modifying factor. Some Jersey bulls may have a modifying factor which causes an increase in butter fat percentage but the existence of the factor is not known. The difference in the butter fat percentage of Jersey and Red Danish cattle is due to a single Mendelian factor. Hills and Boland (107) studied advanced registry records of Holstein-Friesians and put forward a suggestion that there is segregation of factors in a 7:1 ratio. Of these factors, one is dominant and the other probably sex linked, acting/



acting in a simple 3:1 ratio, the dam having greater influence than the sire.

Funkquist (48) 1921, stresses the need for more accurate analyses of the entire genotype in order to obtain complete knowledge of factors of economic importance. He worked on family pedigrees and concludes from the degree of variation which he obtained that fat content is conditioned by at least three harmonic factors. Cases of "extreme" segregation occur, and these extreme variations make analyses more difficult.

Hansen (95) 1917, accepts the theory that milk yield and butter fat content are each dependent upon triple homomeric factors. He demonstrates his theory as follows:- each female must have the characters responsible for the minimum amount of milk which he represents thus - m. All possible genetic constitutions are expressed in the following combinations $M_3 M_3 \text{----} m_3 m_3$. As milk yield and fat content are not in any fixed relationship to each other, butter fat must, therefore, be considered independent, and Hansen expresses the possible combinations of the factors for fat content in the same way as those for milk yield. $F_3 F_3 \text{----} f_3 f_3$.
A bull homozygous for both high fat content and high milk/

milk yield would, therefore, have a genetic constitution which could be expressed by this formula

$$M_1 M_1, M_2 M_2, M_3 M_3 + F_1 F_1, F_2 F_2, F_3 F_3.$$

The occurrence of such a bull is, of course, extremely rare. Furthermore, Hansen adds that the sire has a marked influence on raising the fat content of the produce of his progeny, and lastly, every bull transmits a definite factor for fat content to his offspring.

Von Patow (161, 163) 1926 and 1930, formulates a distinctly interesting theory the validity of which he tests by applying it to some excellent data which he was able to obtain. His records were those of Black Pied Tiefland Large Spotted cattle and Brown cattle from herds which have been recorded for many years - one even dating back to 1817, but the majority are of about fifty years' duration. As a measure, he used the "Byre Average" but substitutes 8 Kilograms ~~for~~ 10 Kilograms for ease of working.

$$\text{Calculated average} = \frac{(\text{10 absolute performance})}{\text{Byre Average}}$$

As a preliminary, von Patow states that every cow must produce at least a minimum amount of milk and it is ^{as} impossible to have a cow without the ability to produce milk as it is to have milk entirely fat free. Therefore he uses the letter "G" to designate the basic/

basic milk yield in cattle which must always be present in the homozygous state or some animals would be produced which could not produce milk. This factor may be linked with, or based on, the factor for the basic butter fat yield. Increase in milk yield is brought about by the presence of all, or some of three homomeric and equally potent factors - A, B, and C. These factors may be present in varying states of homozygosity and doubt is expressed as to whether they are linked. Von Patow takes the three factors to correspond to the three main characters which determine milk yield viz - (1) Development of the udder to allow for sufficient capacity of glandular tissue to secrete milk (2) the formation of interstices and (3) the innervation of the udder. The effect of these three factors is cumulative, and the presence of any one factor raises the milk yield above the basic quantity (4.6 Kilogram) by one unit (1.3 Kilograms) if in the simplex state and by two units (2.6 Kilograms) if in the duplex state.

Example.

A cow having a genetic formula of $G + Aa + Bb + Cc$, i.e. $G + 3$ would yield in Kilograms

$$4.6 + (1.3 + 0) + (1.3 + 0) + (1.3 + 0)$$
$$4.6 + 3(1.3) = 8.6 \text{ Kilos.}$$

For/

For a statistical analysis, von Patow groups the calculated performances of each herd into 7 classes which represent the 7 possible formulae of performances. ($G + 0$, $G + 1$; $G + 2$;-- $G + 6$). Each animal is given a formula according^{ly} to which class her yield falls. By being able to give dams and daughters a genetic formula of this type, it is possible to estimate the potential transmitting ability of the sire. Regarding butter fat yield, von Patow considers that the characters for milk and butter fat yield are in some way connected and have much the same genetical basis. Butter fat is correlated with a certain amount of milk. Each yield of milk is connected with three butter fat classes, either the two above and next above or the two below and next lower. Von Patow designates butter fat by the letter F. Factor F may be present in three states FF, Ff, ff, which are cumulative in their effect. Further, for butter breeds, still another factor F is postulated - this factor being independent of others which regulate milk and fat). This factor is said to work in the same way (F or FF) but only increases the butter fat yield. There is no racial difference in the mode of inheritance of these characters with the exception of those of the butter breeds.

Von Lochow (136) 1921, works on his own herd which/

which has been recorded since 1876. As a result, he concludes that milk yield inheritance is based upon several factors with the dam having greater influence than the sire in the transmission of such factors. He emphasizes the mistaken idea of not taking sufficient account of the influence of any single ancestors which may appear in the pedigree of an animal.

Yapp (259) working on the Bowlker herd records finds that the variation in the records of the Holstein and Guernsey crosses does not follow the simple 1:2:1 type of inheritance but that undoubtedly more factors are involved. In 1929, Yapp (262) assumes the presence of ten factors in the transmission of milking characters.

Nachtsheim (155) 1926, severely criticises von Patow's paper and states that von Patow's method is weak and his assumptions without proof. Nachtsheim suggests that the size of the mammary gland may be controlled by members of a multiple allelomorphic series. Prepotency may be explained by the possession in the duplex conditions of the most dominant members of a series of multiple allelomorphs.

Spöttel (214) states that he considers many genes are involved in the transmission of this character/

character, whilst Frölich (47) indicates that the number of factors involved is not great.

Turner (231) 1927, and also Turner and Gifford (235) 1927, advance an interesting theory as to the mode of inheritance of butter fat secretion. This is as follows - (1) Milk and fat yield are influenced by many genes (2) Many high production favouring genes are dominants (3) All genes do not have the same effect. Turner illustrates his theory by assuming the presence of 3 genes - A, B and C. Each gene, $a = b = c = 50$ lbs. of fat each or 150 lbs. collectively. In the dominant state $A = B = C = 250$ lbs. each. Each gene is given equal value for convenience. From the yield of a cow it is possible to fit one or other alternative genetic formula by which she can be designated. An analysis is also carried out on the performance of Jersey sires and dams and the following relation calculated:-

1. Son's daughters' yearly fat production =
 $302 + 0.481$ sire's daughters' fat production

2. Son's daughters' yearly fat production =
 $463 + 0.176$ dam's yearly fat production

Gifford and Turner (55) 1928, carried out much the same type of investigation on Ayrshire sires and dams as that of Turner 1927. They conclude that grand-parents/

parents have a small but marked influence on the productivity of the granddaughters and that for every 100 lbs. of butter fat increase per annum in the production of the dam there is a corresponding yearly increase of 15 lbs. in the daughter's fat yield, above the potential transmitting ability of the sire. The use of the partial correlation method is employed for making dam and daughter comparisons whilst the influence of the sire is held constant. Turner (232) 1930, worked on the problem of inheritance of body weight in relation to milk secretion and states that the inheritance of body weight follows much the same course as inheritance of yearly fat production, and for every increase of 100 pounds in body weight, there is approximately an increase of 20 pounds in fat production.

Graves (89) 1925, states that high production is dominant to low production. In 1926 (91) he reports on the cattle breeding experiment initiated by the Bureau of Dairying and suggests reasons for the variations which occur between the daughters' yields by the same sire as being due to (1) High production dominant over low (2) Each sire and dam may have a double genetic nature (that is have factors for low production present in the recessive state which when meeting/

meeting others of a similar type from the sire will result in offspring possessing homozygous recessive characters) (3) The cumulative or multiple factor hypothesis may be based on quantitative characters being produced by cumulative factors. Finlay (42) 1925, drew conclusions from other studies and states that there must be a multiple factor difference in the genetic constitution of high and low yielding cattle. He states that in India, Ayrshires are used for crossing with native breeds, and in Jamaica, Jerseys are used for crossing with the Zebu. The results obtained indicate that the complexity is due to multiple factor differences. Agar (2) 1926, investigating Red Poll data, states that milk production is a complex function influenced by many factors, both hereditary and environmental.

Cole (23) 1925, expressed doubt as to the possibility of milk yield depending upon two pairs of factors owing to the complexity of such a physiological function. He himself considers that the factors for butter fat percentage and milk yield are separate. In crossbreds, the milk yield is higher and the percentage butter fat lower than the average of the two ~~parental~~ parental types although the butter fat yield is slightly higher. From his results, Cole is led/

led to assume multiple factor type of inheritance of milk yield and butter-fat characters. In another paper 1923, Cole (20) describes in detail the organisation of the Wisconsin Cattle Breeding Experiment. Ellinger (37) 1923, also working on much the same type of data as that of Cole, states that the results obtained indicate the relationship between milk and fat percentage to be uncertain. The variation in milk and butter fat producing characters as obtained from cross-breeding experiments (Red Danish x Jersey) displays a typical picture of blending inheritance - the crossbreds being intermediate in every respect and the back crosses again intermediate between the crossbreds and original parental type. There is no significant increase in variability noted in the back cross data.

Garkawy (52) 1928, in the paper which has been referred to earlier, considers that the transmission of the character for milk yield is based on many factors and there is but slight connection between milk yield and butter fat content. Crew (27) 1925, is also of the opinion that the mechanism concerned is of the multiple factor type. Gowen (61) 1918, as a result of a study of records of Jersey, Guernsey, Ayrshire and Friesian data concludes that the factors for/

for high milk production tend to be dominant over those for low milk production, whilst the factors for high butter fat percentage are inclined to be recessive. The factors for these two characteristics are said to act independently. He supports this statement by the results of other investigations (1919, 64, and 1920, 65) and (1920) is doubtful if modifying factors are present. The same author (1924), discusses the relative merits of various methods of selection of dairy cows. He concludes that choice according to type or pedigree is poor while choice governed by performance records is good. The milk yield of the dam predicts the milk yield of her daughter with a considerable degree of accuracy. Also the milk yield of a cow is a good indication of the likely record of her full sister. Lack of information regarding the transmitting ability of a sire may be in part overcome by the records of his full sisters. These statements appear to be open to controversy as there seems to be insufficient distinction made between the genotype and the phenotype. Gowen also adds that a comparison of the genotype of sires may be made by using the record of performance of female cousins, although it is a much less exact method than that of comparison of grandparents. He (78) 1925, analyses the performance of Guernsey/

Guernsey sires' progeny and draws comparisons between sires and daughters by calculating the percentage of offspring which fall into each performance class designated by a letter. This investigator contends that by this method it is possible to compare sires although he has ignored the influence of the dams. Also (76) 1926, he further substantiates his theory of multiple factor inheritance with the sire and dam equally responsible for their daughter's performance. He further adds that his results also show that an animal may be highly heterozygous for milk yield characters and yet have a yield closely similar to a fine strain.

The relation between conformation and milk yield has received much attention from Gowen. He has calculated many correlations which have not yielded any definite evidence in favour of this relationship. He agrees with Turner in finding that the effect of the sire's conformation on his daughters is limited mainly to size. The heavier the sire, the more probable will be his daughters' yields although this indication has only about half the value of records. Gowen (78) and Gowen and Covell (87) both find that great variation may occur between the sire's and the sire's sons transmitting ability as measured by their daughters' /

X

daughters' performance.

The degree of similarity of performance between relatives has been studied in much detail by Gowen but as many of the correlations which he obtained are listed later they will not be mentioned.

Investigations Relating to the Relative Importance of Sire and Dam in Transmission of Dairy Characters to their Offspring.

Amongst the investigators who hold that the sire has greater influence than the dam on the quality of the offspring may be mentioned Fleischmann (44) 1891, and Hittcher (108) 1899. The latter also considers that the factors for milk and fat are independent. Speir (213) states that the male has a definite influence. Reimers (190), Cole (23) and Zorn (263) hold similar opinions whilst Cole states that milk and fat factors are separately inherited. Frölich (47) agrees with Cole and also draws attention to the importance of the sire's dam's fat yield. Hansen states that the sire has greater influence upon the fat yield of his offspring and that there is no connection between fat and milk factors. Köppe (122) is in agreement and Petersen considers that the male has greater effect upon the persistency of yield of his offspring.

The number of investigators who consider the female/

female of greater importance are fewer in number. Hills and Boland (107) 1913, and Rohwedder (196) consider that the female is prepotent in fat transmission. Gaines (50) and Terho (218) consider performance is transmitted through the female rather than the male.

Herter (105) 1911, considers that the offspring receives its characters from the sire and dam in equal proportions. Feige, Graves, Ellinger, Copeland and Gowen all indicate that they consider the male and female to be of equal importance in the transmission of the factors for fat and milk characters which are separately inherited, with the exception of Ellinger, who considers milk and fat characters to be only partially independent. Von Patow and Peters are in agreement as to the connection between these characters. They hold them to be to a certain extent physiologically connected and transmitted equally by sire and dam. Faber, Marshall, Olson and Biggar also agree as to the share of transmission by sire and dam. Becker and McGilliard (10) consider the transmission of the factor of persistency to be influenced as much by the sire as by the dam. Among other supporters of the theory of independence of fat and milk characters may be mentioned, Brody, Winningstedt/

Winnigstedt, Wilson, Johansson, von Lochow, Hansson, and Löwe. Kronacher is in agreement with Peters and von Patow whilst Bonnier and Wadsack are both inclined to consider that these characters may be connected.

Conclusions.

An attempt to unravel the problem of milk inheritance by an examination of the work of others shows rather a wild confusion than a well ordered history of critical experimentation. The diversity of results is not surprising considering not only the wide variation in the abilities and prejudice of the investigators but also the dissimilarity of their material and still more their methods. This triple variety is against all the dictates of Science and until the chaos of mind, material and method can be made to approach order, opinion based on the slenderest of facts must reign supreme.

The nature of the problem places it at a great disadvantage as investigations by means of critical experimentation is impossible for the majority. To hope to completely elucidate such a problem by statistics alone is useless. The main difficulty lies in procuring the foundation facts. Much of the data used does not represent a random sample, as the greater number of published records are only those of the/

the higher yielding cows. Many investigators advocate the use of various correction factors but the application of such must eliminate, to a great extent, the effect of individuality in which lies the answer to the problem. Again, the solving of the problem is made more intricate owing to the lack of any form of accepted technique. Therefore the results of different workers can rarely be compared, or, if compatible, on only the very broadest of lines.

Furthermore, much inferior work has been done. There are, however, a few outstanding workers whose hypotheses and assumptions have still to be confirmed by the results of additional research. At present they are still unsupported opinion. In spite of the many investigations which have been spread over a period of thirty to forty years, the amount of actual advance and increase in knowledge of this problem are extremely limited. In fact, the increase in knowledge has been mainly in the form of greater appreciation of the difficulties besetting the path of the investigator of the mode of inheritance of milking capacity.

-oOo-

Thersites. "...A plague of opinion! A man may wear it on both sides, like a leather jerkin".

"Troilus and Cressida"
Act III, Scene 3.

II. AN ORIGINAL STUDY.

II. An Original Study concerning the Mode of Inheritance of Milking Capacity in Cattle.

The present investigation was directed towards a study of the mode of inheritance of milk and fat yield with a desire to demonstrate the presence or absence of sex linkage in the inheritance of these qualities. For this purpose, a statistical study was made of the milk records of Ayrshire cattle. The degree of similarity between the milk and butter fat yields of cows of various relationships was measured and compared with the possible theoretical distribution of autosomes and sex chromosomes. In this way, it was hoped to demonstrate the presence or absence of sex linked factors.

A. The Effect of Non-hereditary influences upon the investigation into the mode of inheritance of milking capacity.

I. Environment.

a. District. The district in which farms are located makes an appreciable difference to the milk records obtained. Altitude has a considerable influence upon yield. High altitude is generally associated with a cold and rougher climate, harder grazing and sparse pasturage. Low altitude suggests more favourable conditions, lower temperature, etc. The effect of temperature upon quality of milk has been/

been studied by Ragsdale and Brody (287) also Weaver and Matthews (292). All come to the conclusion that lower temperatures tend to increase the butter fat percentage.

iv. Type of Farming. To a certain extent type of farming is influenced by district. Apart from altitude etc., the actual farming system practised is of great importance in comparing milk records. With an intensive farming system, heavy feeding and generous application of fertilisers occur. The result is a near approach to maximum production. On the other hand, yields are much lower on an extensive system where cost is cut to the minimum, and feeding at its lowest. Sanders and Hammond (291) state that they have found an increase of from 8 to 9% in milk yield when, with 1 ac. of grass, the arable land is increased from $\frac{1}{2}$ ac. to 3 ac. Farm management practices again influence milk records by the method of disposal of milk. The market decides whether the milk output is to be regular all the year round, or purely seasonal as on some cheese making farms. Records from a cheese making farm could not fairly be compared with those of other types of farms. It is not economically possible for all herds to have a high average.

1c. Individuality of Farmer. Breeders vary considerably in their ability to produce high records from their herds even under similar conditions. In such countries as America, the variation is much greater as there the effect of national as well as individual characteristics is marked. Therefore choice of data for inheritance studies is not only limited to areas but also to individual farms.

2. Nutrition.

a. Effect of systemized rationing. It is obvious that improved feeding methods will have a great effect upon milk records. Various figures have been quoted for the increase obtained from cows kept under test conditions where feeding methods should be at their optimum. Woodward (295) maintains that it is possible to procure 50% more milk and butter fat whilst Eckles (277) states that advance Registry Records are usually $1 \frac{2}{3}$ rd times higher than records produced under quite normal conditions. Less sharply defined is the result of agricultural education upon the farmer. Records obtained twenty years ago can not be accurately compared with those of the present day.

b. Effect of Seasons. In choosing data for analyses, care must be taken to avoid records produced during/

during abnormal seasons. A very dry period and therefore reduced pasture, results in lower milk yields of high butter fat percentage. This problem has received the attention of Ragsdale and Turner (288).

1c. Effect of War Periods. The war did not affect British records to such a great extent as those of other countries. Where food is insufficient, production will suffer and exceptional records result. Ragsdale and Turner (289) state that when the ration is reduced by 50%, fat content increased up to a peak on the 3rd day but milk yield decreased.

3. Individual.

The non-genetic individual variation in records is very great, but in a statistical analysis of data, individual variation can be counter-balanced or corrected whereas herd variations carry more weight.

The main causes of individual variation are age of cow, time and season of calving, length of lactation, dry period, and service period. These and other similar factors have received the attention of many workers amongst whom may be mentioned Sanders (198, 290, 199, 291) Kay (284), M'Candlish (284, 278), Glen (278) Hammond (291) Gowen (279, 280). Various tables for correction factors have been suggested/

suggested and used.

B. Difficulties and Methods of investigating the Mode of Inheritance of Milking Capacity.

1. Estimation of the genotype of dairy cattle.

The previous section briefly enumerated some of the most important of the environmental factors affecting milk and butter yield. The elimination or counteraction of their effect upon statistical studies presents a great problem ~~and~~ thereby necessitating the most careful selection of data in order to avoid undue inaccuracy. It is clear that to obtain sufficient data of such selection will not be easy.

Assuming that the source of data is as free from environmental influences as possible, the next problem which arises is the measurement of the genotype of the individuals. This measurement is almost as difficult in the female as in the male. Certainly the performance of the cow can be estimated but this is only the phenotypic side of her performing ability and in many cases her yield as noted may not be the full expression of her milking capacity in which case her phenotypic characters will be misleading and a poor indication of her genotype. In any case, a high milk record is not a sure indication of the cow's transmitting ability. It is probably because some of/

of the factors for high milk yield appear to be dominant over those for low milk yield, that the phenotype and genotype of a cow often show great dissimilarity. Again the number of progeny produced by a cow is very small. M'Candlish and Kay (142) give interesting figures on this point. Their estimate of the number of daughters added to a herd by a cow is at the most 3, whilst a bull may have from 6 to 10 and even up to 27 daughters. The range of variation of milk production between dams and daughters was found to be from -27% to +14% in milk yield and -26% to +18% in fat yield.

An estimation of a bull's transmitting ability is limited by the fact that the character for which selection is being carried out, is not a directly measurable one in the male. This means that expense and risk are great until the sire's genotype has been proved. The process of testing is long and costly but essential if improvement is to be attempted. A sire cannot be proved until he has at least 6 daughters in the herd by which time he will be about five years old. At present there is no bull index which is entirely satisfactory (although suggestions have been made by Gowen (85), Yapp (260) Goodale (59) etc. and this renders improvement still more difficult.

The/

The actual difference between dam and daughter's yield is not sufficient as this measure does not take into account the sire who raises and maintains his daughters' yields above those of a high yielding dam.

It is this ignorance of so many essentials regarding both male and female which makes this study of the problem as elusive and hard to grasp as it is.

2. Statistical Methods. a. There are many objections to the application of statistics in the solving of this problem yet they must be employed. Their value is great when they are carefully used. As a preliminary study and as a forerunner of genetical analyses their application is essential. They must act as an indicator to further detailed and individual work. Provided numbers are sufficiently great and selection of data very stringent, valuable results should be obtained. Their weakness lies in the use of averages, which cannot be applied to the individual. The application of statistics must be limited and results serve only as an incentive to further detailed study and experimentation.

b. Origin of data. The value of the results rests to a large extent upon the origin of the data. From previous sections of this paper, it is obvious that quantity alone is not all that is required. A heterogeneous/

heterogeneous mass of unselected data is useless. As far as possible the source of material should be limited to uniform districts, herds and breeds.

C. Measurements used. Many measures have been used to express the degree of variation between animals of different relationships, such as difference between averages, correlations (partial and multiple) coefficient of variation, standard deviation and almost purely graphical methods. A new method, formulated by Dr. R.A. Fisher, has been used in the investigation and is detailed on Page 78. The difficulty always arises in the expression of the sire's share in transmission. Sometimes the plus or minus differences between the yields of dam and daughter are used or letters are designated to various performance classes into which the yields of dams and progeny fall, and the whole worked to a percentage. Gowen uses an indirect form of correlation.

3. Experimental Methods.

Obviously critical experimentation is the only method which can be expected to give really conclusive results, as milk production is such a complex physiological function influenced by many factors both genetical and environmental. Unfortunately, owing to the length of time required, expense of animals and so on, breeding experiments are very costly.

There/

There is, however, a limited number of breeding experiments in progress at the present time though not in the British Empire. Such experiments are generally run along one of two lines, either inbreeding or crossing of two extremes.

a. Inbreeding and Line breeding.

Inbreeding and line breeding experiments have been conducted for many years, especially in Germany and America. Soviet Russia, as reported by Garkawy (52) is endeavouring to embark upon a very large scale breeding experiment. If successfully organised the results should be invaluable. Environment and nutrition are to be standardized as far as possible in order to facilitate the measurement of genetic constitution. Inbreeding and line breeding are to be practised. Experiments of this type aim at the production of a class of stock homozygous for high production and also of known genetic constitution thereby allowing for the study of the mode of transmission of factors for milking capacity. The occurrence of "prepotency" of sires has received much attention.

Formerly, the crossing of breeds showing considerable variation in performance was popular as a method of gaining a broad outline of the dominance or recessivity of the characters involved in high milking capacity. Such work as this is very slow but in all probability, after many years, the/

the **findings** should be of value in the elucidation of this problem. Such results as there are need individual interpretation, as the application of biometrical methods would cloud the underlying principles of transmission of any particular factors.

Briefly, the difficulties of studying the inheritance of milk and butter fat yield can be summarized as follows:-

1. The confusion which arises owing to the interaction of genetic constitution and environment.
2. Limited ability to measure the inheritance of these factors as (a) Direct measure can only be made through the cow, (b) Frequent lack of knowledge regarding the genetic constitution of sires used (c) Absence of inbreeding occurring amongst dairy stock.
3. Insufficient supply of reliable material.

G. Material used for this investigation.

1. The data used in this survey were collected from the Annual Scottish Milk Records Association and the Ayrshire Cattle Herd Books. The cows were selected in alphabetical order and all herds had been continuously recorded from 1922-1928. In all, about 5,000 records were obtained, these having been drawn from some 300 herds which contained 1518 cows.

2. The greatest care was taken in the selection of material/

material, in order to avoid as far as possible the distortion of results by environmental factors. The elimination of the effect of environmental factors was achieved to a great extent by confining the location of herds to the South West of Scotland. Here climatic conditions, types of farming and systems of farm management and nutrition are uniform to an unusual degree. This, of course, limited the amount of data available but increased the accuracy to a high degree.

Pedigree cards for each animal included such details as age of animal, length of each lactation, dates of service and calving, gallons of milk and average percentage of butter-fat for each lactation together with ancestors to the grandparental generation. (See specimen card).

D. Procedure.

1. Application of Correction factors.

Having obtained as many lactations per animal as possible, certain correction factors were applied. The necessity for adjustment for length of individual lactations was avoided by the elimination of all records of less than 245 or more than 365 days in length. Corrections for age of animal were essential. Kay and M'Gandlish calculated the following table for Ayrshire cattle from the **S**outh **W**est of Scotland and these were the correction factors employed.

SPECIMEN RECORD CARD.

HEAD BOOK NUMBER 78490.

AVERAGE BUTTER FAT YIELD OF ALL CORRECTED LACTATIONS.

NAME *Beecher Margie II.*

(A) 464.39 lbs.

(B) 1281 gals.

AVERAGE MILK YIELD OF ALL CORRECTED LACTATIONS.

YEAR OF BIRTH 1921.

AGE AT LAST CALVING 5 yrs. WEEKS IN MILK 48

YIELD IN GALLONS 1136

MILK YIELD CORRECTED FOR AGE 1205

DATE OF LAST CALVING 3rd Feb. '26. DUE TO CALVE 9th Feb. '27

PERCENT BUTTER FAT 3.50

POUNDS BUTTER FAT CORRECTED " 417.48

Auchenbravi Major. 17542.

SIZE (HEAD BOOK NUMBER)

Auchenbravi Sunlight 15832.

PATERNAL GRAND SIRE (HEAD BOOK NUMBER)

York Madge II 31669.

PATERNAL GRAND DAM (HEAD BOOK NUMBER)

Kellogg Sunrise 11044.

MATERNAL GRAND SIRE (HEAD BOOK NUMBER)

Beecher Wallflower III. 56805.

DAM (HEAD BOOK NUMBER)

Beecher Wallflower II 49848.

MATERNAL GRAND DAM (HEAD BOOK NUMBER)

BREEDER *A. Cochran* *Arthur* *Ray*.
OWNER *P. Allen*, *Beecher*.

This card is duplicated for every lactation. Figures A.B. are obtained by taking the average of the corrected yields of every lactation available. The percentage is not repeated on each card.

TABLE IV

Correction Factors for Age.

Age in years	Milk Yield	Fat Yield
3	1.16	1.13
4	1.12	1.12
5	1.06	1.05
6	1.03	1.03
7	1.00	1.00

Both the pounds of butter fat and gallons of milk of each lactation for every animal were converted to the maximum yield of seven years. Their corrected yields were then averaged ~~and~~ thereby obtained ~~ed~~ the average maximum lactation yield of fat and milk for each animal.

Corrections for length of dry period were not required as, with but few exceptions, the length of dry periods was exceptionally uniform.

2. Statistical Method. In a study such as this the problem arises as to the best statistical method to use and it is here that Dr. R.A. Fisher, F.R.S., of Rothamsted, so kindly gave assistance by evolving a completely new formula. The statistical method employed was one involving much calculation but avoiding several difficulties encountered by the use of other methods. For instance, there is the question of holding the influence of the sire constant when calculating dam and daughter correlations. Some of the earlier work along these lines ignored the effect of different sires upon dam and daughter relationships/

relationships. Another difficulty is that of choosing the measure of the sire's influence as milk yield and butter fat, unlike such qualities as beef etc., can only be measured directly through the female. Methods have been evolved, as for instance by Gowen, whereby the sire's potential ability is given due weight. Gowen's method is as follows:- (73)
p. 299. "The basis of this method is, as already noted, the fact that the grandsire must of necessity fall in only one array of the correlation table since if we had an actual milk record on this sire, this record could fall in only one column of the table. With this fact and the known relations of the standard deviation of the arrays to the standard deviation of the whole table it is possible to calculate the correlation coefficient".

The method used in this study avoided these approximations.

The data were first classified according to the paternal grandsire which classification resulted in groups of animals with at least one common ancestor. The granddaughters of each paternal grandsire were compared one with every other and classified under one of the following 25 relationship groups.

TABLE V/

Relationship of Dams

TABLE V.

Degrees of Kinship.

Relationship of Sires.

	Same	Full Brother	Paternal Brother $\frac{1}{2}$	Maternal Brother $\frac{1}{2}$	Not Brother
Same					
Whole Sister					
Pat $\frac{1}{2}$ Sister					
Mat. $\frac{1}{2}$ Sister					
Not Sister					

If a grandsire had less than 5 granddaughters such a group was not included. It is clear that the number of pairs possible in each group increased rapidly with a small increase in actual numbers, as every animal was compared with every other one. For example, 10 cows with the same common grandparent would give 45 possible pairs but 20 animals would increase the number of pairs to 190 - the formula for the possible number of combinations being $\frac{n}{2} (n - 1)$. During the investigation it was found that certain relationships would occur between animals which were not provided for in the table and such being the case these pairs were neglected. Again, as the results will indicate, some of these degrees of kinship are most remote, as for example two heifers whose sires are full brothers and dams full sisters, or whose sires are maternal half brothers and dams maternal half sisters.

The milk yields of each pair were taken and the difference between their two yields was squared. From this, it was possible to obtain the mean of the summation of the differences squared ($\frac{\sum D^2}{N}$ where D = differences between individual milk yields and N = number of pairs) for each relationship group, thus completing the calculation as regards the paternal grandsire classification.

Obviously/

Obviously this process is extremely slow and laborious involving much work, and to avoid this Dr. Fisher suggested two short cut methods the formulae of which are given below. The first method applies when members of one group of animals have each to be compared with members of a second group. The second method applies when each animal in a group has to be compared with every other animal of that group.

Formula of First Method

$$\text{The sum of pq values of } (x_p - y_q)^2 = pq (\bar{x} - \bar{y})^2 + ps^q (y - \bar{y})^2 + qs^p (x - \bar{x})^2$$

When p = number of animals in 1st group

q = " " " " 2nd group

\bar{x} or \bar{y} = Difference between the mean of x and y data

$s^q (y - \bar{y})^2$ = the sum of the squares of the deviation from the mean in y data

$s^p (x - \bar{x})^2$ = the sum of the squares of the deviations from the mean in x data

Formula for Second Method

The sum of $\frac{1}{2}p(p-1)$ squares of differences within a single group of p values is $ps^p (x - \bar{x})^2$

When p = number of animals in the group.

$s^p (x - \bar{x})^2$ = the sum of the squared of the deviations from the mean.

The same procedure was followed for the three remaining grandparents, these being maternal grand-sire and maternal and paternal grandams. It is obvious that in the case of both female grandparents certain/

certain relationship groups would overlap with those on the male side, especially in classes of a high degree of kinship. Such being so, these were not taken into consideration.

When this procedure was completed the yield of each animal had been compared with every other eligible one of its group.

The last step in the milk yield study involved taking random samples to make up the non-related group (dams not sister, sires not brother) and for this purpose the samples selected contained groups of from 30 to 40 animals in whose pedigrees there did not exist one common ancestor (as far back as the cards indicated). When selected, the same procedure was followed as above, thus finding the mean of the summation of the differences squared. The number of pairs in this class was 6,660 and the total number of pairs in the investigation was 26,091.

For the second part of the work - the mode of inheritance of butter fat, exactly similar operations were carried out but this time the corrected figures for pounds of butter fat per lactation were used.

The total number of pairs here was the same as with the milk yield data. The two branches of this investigation included over 52,000 pairs of animals.

E. Results.

Owing to the remoteness of some of the relationships and to lack of inbreeding amongst dairy herds, several squares in the relationship table remain unfilled and still others have an insignificant number of pairs. From experience, specially gained during the study of unrelated animals, it is thought that the number of pairs necessary to give reliable results should be from 1,000 to 2,000. The variation occurring in individual milk yields is great and a few extreme yields influence results considerably, therefore great numbers are essential.

Butter Fat.

TABLE VI/

TABLE VI.
Summary of Butter-Fat Yield of Ayrshire Cows in Different Relationship Groups.

Sires Dams	SAME			WHOLE BROTHER			PATERNAL $\frac{1}{2}$ BROTHER			MATERNAL $\frac{1}{2}$ BROTHER			NOT BROTHER		
	Number of Pairs ΣN	Summation of Differences Squared ΣD^2	Mean of Sum of Differences Squared $\frac{\Sigma D^2}{N}$	ΣN	ΣD^2	$\frac{\Sigma D^2}{N}$	ΣN	ΣD^2	$\frac{\Sigma D^2}{N}$	ΣN	ΣD^2	$\frac{\Sigma D^2}{N}$	ΣN	ΣD^2	$\frac{\Sigma D^2}{N}$
Same	200	829778	4150				7	41916	5988				158	688631	4358
Whole Sister	41	134702	3285										29	94821	3270
Pat. $\frac{1}{2}$ Sister	2027	9212597	4545	3	12878	4292	29	139562	4812	2	3400	3400	2303	15144791	6576
Mat. $\frac{1}{2}$ Sister	69	277907	4028				1	361	361				185	996889	5389
Not Sister	6361	31630549	4973	415	1968344	4742	6435	41418225	6435	1166	7038079	6036	6660	52949834	7950

The results indicate that the mode of inheritance of butter fat yield is autosomal. In this type of inheritance, the smallest differences would occur in the nearest relatives whilst as the degree of kinship increases, so the variation widens.

The smaller the figures for the summation of the differences squared ($\frac{\sum D^2}{N}$ that is the measure of variation), the greater the similarity between the records of the animals in that particular class, and therefore it may be assumed the more nearly alike are their genetic constitutions (regarding factors for milk or butter fat yield). The measure of variation should be smallest in the same dam by same sire group (as here the animals compared are full sisters) and increase towards the right hand and bottom of the table with the largest variation in the non-related groups. On looking at Table VI, and taking the groups with significant numbers, this is seen to be the case.

TABLE VII/

TABLE VII.

Comparison of actual with theoretical figures for variation in different Kinship Groups.

			<u>Actual</u>	<u>Theoretical</u>	
			$\frac{\sum D^2}{N}$	r^2	
1.	Same dam and same sire	sire - same	4150	.48	50%
2.	Dam - paternal $\frac{1}{2}$ sister;	sire - same	4545	.42	31%
3.	Dam - no relation;	sire - same	4973	.37	25%
4.	Dam - no relation;	sire - paternal $\frac{1}{2}$ brother	6435	.19	6.25%
5.	Dam - no relation;	sire - maternal $\frac{1}{2}$ brother	6036	.24	6.25%
6.	Dam - maternal $\frac{1}{2}$ sister;	sire - no relation	6576	.32	6.25%
7.	Dam - no relation	sire - no relation	7950	.00	0

Cows with:-

* r is obtained from the formula -

$$r = 1 - \frac{\frac{\sum D^2}{N}}{\frac{\sum D^2}{N}} \text{ for Group considered}$$

$$\frac{\sum D^2}{N} \text{ for unrelated group}$$

In Table VII a brief comparison between the actual and theoretical differences has been drawn up. The figures for the theoretical are those representing the chances of similarity which each group of animals of given relationship will have to inherit the same the same factors and so be alike.

Turning back to Table VI it can be seen that in the same sire and same dam group, $\frac{\sum D^2}{N} = 4150$, this measure increases to 4545 in group of paternal half sister by same sire, and finally rises to 4973 in not sister by same sire. Taking the relationship groups where the dams are unrelated, (not sister) it can be observed that $\frac{\sum D^2}{N}$ commences at 4973 (same sires), to 6435 (sires - paternal $\frac{1}{2}$ brothers) to 6036 (sires - maternal $\frac{1}{2}$ brothers) and eventually to 7950 in the totally unrelated group. Unfortunately, the group containing sires as unrelated (not brothers) are small the one significant class being that of dams as paternal $\frac{1}{2}$ sisters where $\frac{\sum D^2}{N} = 6576$. This agrees well with the reciprocal cross of dams not sister and sires paternal $\frac{1}{2}$ brothers where $\frac{\sum D^2}{N} = 6435$.

2. Milk Yield

TABLE VIII/

TABLE VIII.

Summary of Milk Yield of Ayrshire Cows in Different Relationship Groups.

Sires Dams	SAME			WHOLE BROTHER			PATERNAL $\frac{1}{2}$ BROTHER			MATERNAL $\frac{1}{2}$ BROTHER			NOT BROTHER		
	ΣN	ΣD^2	$\frac{\Sigma D^2}{N}$	ΣN	ΣD^2	$\frac{\Sigma D^2}{N}$	ΣN	ΣD^2	$\frac{\Sigma D^2}{N}$	ΣN	ΣD^2	$\frac{\Sigma D^2}{N}$	ΣN	ΣD^2	$\frac{\Sigma D^2}{N}$
Same	200	4964468	24822				7	238699	34099				158	5188262	32837
Whole Sister	41	502663	12260										29	281275	9699
Paternal $\frac{1}{2}$ Sister	2027	56402718	27821	3	3877	1292	29	497683	12264	2	18850	9425	2303	55773684	24218
Maternal $\frac{1}{2}$ Sister	69	1875174	27176				1	15129	15129				185	6140381	33191
Not Sister	6361	227073155	35698	415	23206895	55920	6435	321305317	49931	1166	51453601	44128	6660	158109201	45579

In this table, $\frac{\sum D^2}{N}$ is in much larger figures as it is an expression of gallons of milk as opposed to pounds of butter fat as in Table VI.

Again results show a gradual widening of variation as the degree of relationship falls. In Column I where the sires are the same, $\frac{\sum D^2}{N}$ rises from 24,822 (same dams) to 27,821 (dams - paternal half sisters) and finally to 35,698 (dams - unrelated). Following the same line of comparison as in the Table VI the next considerations are these groups including dams unrelated. Here $\frac{\sum D^2}{N}$ commences at 35,698 (sires - same) to 49,931 (sires - paternal half brothers) to 44,128 (sires - maternal half brothers) and finally to 45,579 in the non-related groups. Lastly, of the significant number of pairs, there is the reciprocal cross to not sister x paternal $\frac{1}{2}$ brother - that of not brother x paternal $\frac{1}{2}$ sister, where $\frac{\sum D^2}{N} = 24,218$.

On comparing the results in Tables VI and VIII one outstanding difference can be seen, that is the difference between $\frac{\sum D^2}{N}$ for the groups dam not related by sires paternal $\frac{1}{2}$ brothers - (that is the common ancestor is the paternal grandsire), and its reciprocal cross of unrelated sires by dams paternal half sisters (that is the common ancestor is the maternal grandsire).

TABLE IX/

TABLE IX

Comparison of Milk and Fat Yields of Animals with common paternal and maternal grandsires.

	$\frac{\sum D^2}{N}$	
	M. Y.	B. F.
Cows with common paternal grand-sire and dams unrelated	49,931	6435
Cows with common maternal grand-sire and sires not related	24,218	6576

The differences occurring here can be said to be significant. $\frac{\sum D^2}{N}$ for the butter-fat yield is similar in both groups. However, the measure of the difference of the milk yield of cows with common paternal grandsires is almost twice that of the same measure of animals with common maternal grandsire. The extent of variation between the reciprocal crosses either supports or condemns the theory of sex linkage in the inheritance of milk and butter-fat yield. Assuming that some of the factors influencing milking capacity are sex-linked, $\frac{\sum D^2}{N}$ of animals with only common paternal grandsire will be larger than that for animals with common maternal grandsires. The difference found in the investigation in the milk yield data is 25,713 or an increase of more than 100 per cent over the measure for animals with common maternal/

maternal grandsires.

A second degree of kinship which is of interest to the sex linkage theory, is that of the class in which dams are unrelated and sire maternal $\frac{1}{2}$ brothers, that is, the only common ancestor being the paternal grandam. In a purely autosomal inheritance, the variation between the yields of animals with common paternal grandams and with common paternal grandsires would be about the same. If, however, any of the factors are sex linked, then the extent of variation will be greater in the group with the common ancestor as paternal grandsire than in the paternal grandam group. Factors on the x-chromosome can be inherited from the paternal grandam to her granddaughters but not through the paternal grandsire.

TABLE X.

Comparison of Milk and Fat Yield of Animals with different paternal grandparents.

<u>Common Ancestors</u>	$\frac{\sum D^2}{N}$	
	B.F.	M.Y.
1. Paternal grandsire	6435	49,931
2. Paternal grandam	6036	44,128

The $\frac{\sum D^2}{N}$ for butter fat yields are approximately the same, as a difference of 400 is negligible. The difference between these two values in the milk yield data is proportionately twice as great as that for the butter/

butter-fat yield. Although the difference is not very great, yet it is in support of the theory.

TABLE XI.

Measure of Variation in different Kinship Groups.

	(212)						
	Gowen(73)			Smith etc.		Found	
	M.Y.	B.F.	Milk Yield	M.Y.	B.F.Y.		
	r	r	r	r	r	r	r
Pat. grandsire	.005	.119	.259 ₊	.0163	-.100	+.19	
Pat. grandam	.171	.214	.049 ₊	.061	+.03	.24	
Mat. grandsire	.206	.216	.478 ₊	.0134	+.47	.17	
Mat. grandam	.234	.244	.131 ₊	.053	*+.27	* .32	

* = number of pairs insignificant

It is of interest to note the similarity between those results. Gowen, however, does not emphasize the possibility of sex linkage occurring in the inheritance of milking capacity.

3. Occurrence of Certain Relationships.

Apart from conclusions which can be drawn as to the mode of inheritance of milk and butter fat yield, Tables VI and VIII bring out another interesting fact. The number of pairs which are in each kinship group give an indication of the popularity of various matings. The data at hand show that it is the history/

* Footnote: r obtained here by formula given on P. 87.

history of the bull which receives the attention of the breeder. Out of twenty-six thousand pairs of cows, 6361 pairs fall in the group of same sires whilst another 6435 fall into the sires in paternal $\frac{1}{2}$ brother class. This indicates that the selection of the herd bull is based more upon the bull's sire than upon his dam. The next two most frequent matings are those involving paternal half sisters - paternal half sisters with same sires or with unrelated sires. Again it is the male side which seems to be the controlling factor. The effect of famous bulls is felt by the selection of their daughters for breeding.

If breeders selected their stock according to the value of the dam, then the number of pairs in the maternal lines would be greater. As it is, the number in the maternal lines (that is those classes in which the cow has been the influencing factor in selection) is 1493 as against that of 11,253 in the paternal lines. The group of cows with same sire and same dam has not been included.

These figures give a good example of prevalent breeding practices. The sire carries much more influence than the dam. The herd bull is more commonly selected because he is the son or brother of a famous bull than because he is the son of a famous cow/

cow. In this data, the figure for selection of the son because of his sire is 6645 as opposed to 1166 where the bull must have been selected as coming from a famous cow.

F. Conclusions.

From the analyses of these data, the mode of inheritance of butter-fat yield appears to be purely autosomal, whilst that of milking capacity appears to be affected by sex-linked factors. But consideration must be taken of the fact that unfortunately these data do not constitute a purely random sample of all cows in a herd and the elimination of low yielding cows may cloud the results to some extent more especially as the Ayrshire breed has been selected to a greater extent for milk production than for butter fat. Making allowances, however, for this fact and also the effect of environment etc., the great difference in the measures of variation between the milk yields of the two sets of granddaughters (paternal and maternal grandsires) is significant. This significance is supported by similarity of this same measure in the case of butter-fat yields.

These results point towards the possibility of the inheritance of milking capacity being sex-linked. From the analyses of these data, it is impossible to say what part of the milking capacity of an animal is affected in this way as it may be the maximum yield or persistency/

persistence of the lactation or again it may only affect cows above or below a certain yield.

Should this theory of sex-linkage be proved, it will be of great value to the breeder and improver of livestock, as it will give at least one definite course to follow in breeding practices. Great value would lie in the facilitation of the choice of stock for the purposes of introduction of new blood lines into a herd. Especially in a dairy herd, the purchase of a new sire is a serious question as an unfortunate choice can do great harm which takes years to obliterate. At present, the choice of selection of the bull is influenced largely by the quality of his sire or brothers and of secondary importance, his dam. A great number of untested bulls depend for their value upon their sires. Should any of the factors for milking capacity be sex-linked, then the value of the bull's sire, in so far as his transmitting powers of characters for milking capacity are concerned, will be greatly decreased. Attention regarding milking qualities will then have to be directed more towards the bull's dam and her parents, rather than to his sire.

Until further investigations have been made more definite proof cannot be found to support the theory of sex linkage. Such proof would be abundantly found/

found in systematic development of progeny tests. Less emphasis should be laid upon the sire of the bull and his pedigree but of utmost value is the quality of his offspring as an indication of his powers of transmission. In judging the quality of offspring, the quality of the dam must be taken into consideration. A sire used in a herd of low milk record average can easily raise the herd average to quite a large extent without himself being of much value. The valuable sire is one who, either maintains, or raises, his daughters' average above those of high yielding dams. Pedigree alone is no indication of transmitting ability as some purebred sires are not even good enough for use in scrub herds. Great advancement has been made in Denmark along these lines and all herd sires used must have previously passed the progeny test. Faber (38,39) states that the Danish Government will not allow a bull to be eligible for a Government prize unless his daughters' records, as well as his pedigree, can be shown. Also some cattle breeding societies note the yield of the dam, sire's dam and dam's dam of bulls bought by them. Wriedt advises the publication of a list of bulls suitable for use as herd sires. The sons of these bulls should be selected by genotype regarding the performance of sire and dam and finally sire's dam/

dam. Lastly selection should be influenced by the exterior when the most important economic characters should be considered. In this country, apart from an occasional progeny class at an agricultural show, very little attempt at improvement has been made in this direction. Milk recorded cows which reach a certain standard can become qualified bull breeders but no emphasis is laid upon the necessity of using bulls from such dams as herd sires. Granted, their market value may be higher but the vital importance of using such sires is not sufficiently recognised. Bulls considered unfit for breeding purposes in Ireland are imported into this country, where, presumably they finally become herd sires. A glance through the literature dealing with the improvement of dairy stock in America through the use of purebred tested sires shows what can be accomplished by practising rigorous systematic selection and breeding.

G. Summary of Results of Original Investigation.

1. Material consisting of the milk and butter fat yields of over 50,000 pairs of Ayrshire cows is used in the study of the mode of inheritance of milking capacity.
2. Correction factors are applied to age of animals and selection of data eliminated effect of environment length of lactation, etc.

3. Butter-fat yield analyses results indicate that as the degree of relationship increases, the measure of variation between these yields also increases.

4. Milk yield analyses suggest the occurrence of sex-linkage in the inheritance of milking capacity.

The measures of difference in groups where the common inheritance of sex linked factors is possible, is smaller than in groups where such is not possible.

5. Examination of number of pairs in each class indicates that breeders select their stock according to the male ancestry rather than the female.

Summary Correlation Table.

<u>Breed</u>	<u>Investigator</u>	<u>Correlations</u>
Holstein-Friesian	Gowen (73)	dam and daughter (Milk Yield) = + 0.497 ± .021
"	Hills and Boland (107)	dam and daughter (Fat Prod.) + 0.29
"	Rietz (193)	dam and daughter (Fat Prod.) + 0.63
"	"	dam and immature daughter (Fat Prod.) 0.25
Guernsey	Gowen (x)	dam and daughter (Milk Yield) + 0.36 ± .02
"	Turner (223)	" " " (Fat Prod.) + 0.30
Red Poll	Agar (2)	" " " (Fat Prod.) + 0.235 ± .06
Jersey	Turner (231)	" " " (Fat Prod.) + 0.346 ± .011
Ayrshire	Gifford (55) and Turner	" " " (Fat Prod.) + 0.25 ± .02
"	Smith, Scott and Fowler (212)	" " " (Milk Yield) + 0.418 ± .038

* As reported by Turner, C.W. The Mode of Inheritance of Yearly Butter Fat Production. Missouri Agril. Expt. Sta. Bull. 112. 1927.

Summary Correlation Table (Contd.)

<u>Breed</u>	<u>Investigator</u>	<u>Correlations</u>
Jersey	Ellinger (37)	Milk yield and fat% - .332 ± .051
Red Danish	"	" " " " + .055 ± .044
Red Danish x Jersey	"	" " " " - .246 ± .073
Brown Cattle and Pied Cattle	Brun (14)	Escutcheon and Milk Yield + 0.6 ± .06
	Aldrich and Dana (276)	Size of Milk Wells and Milk .15 ± .03
	"	fat yield or .26 ± .027
	"	Diameter of milk veins and milk yield .19 ± .04
	"	and .28 ± .027
	"	Body length and milk vein length .376 ± .023

Summary Correlation Table (Contd.)

<u>Breed</u>	<u>Investigator</u>	<u>Correlations</u>
Holstein	Gowen (73)	Full Sisters (Butter-Fat Percentage) .464 ± .032
Friesian	"	" " (Milk Yield) .548 ± .027
"	"	Paternal ½ Sisters (Milk Yield) .362 ± .015
"	"	" " (Butter Fat %) .374 ± .015
"	"	Maternal ½ Sisters (Milk Yield) .381 ± .033
"	"	" " (Butter Fat %) .173 ± .037
E. Friesian	Köppe (122)	Fat yield and milk yield + .95 ± .008
"	"	Fat % and milk yield + .045 ± .08
"	"	Fat % and fat yield + .0396 ± .068
Swedish	Bonnier (12)	Milk yield and fat % + .0169 - .8337
Ayrshire	Copeland (25)	Fat yield and fat % + .233 ± .032
Jersey	"	Milk yield and fat % - .311

Summary Correlation Table (Contd.)

<u>Breed</u>	<u>Investigator</u>	<u>Correlations</u>
Ayrshire	Smith, Scott and Fowler (212)	Granddaughters and paternal grandsire = + 0.259 ± .016 (based on indirect correlations)
		Granddaughters and maternal grandsire = + 0.478 ± .013 (based on indirect correlations)
		Granddaughters and paternal granddam = + 0.049 ± .061 (based on direct correlations)
Holstein Friesian	Gowen (73)	Granddaughters and maternal granddam = + 0.131 ± .053 (based on direct correlations)
		Granddaughters and paternal grandsire = + 0.07 ± .014 (based on correlation factor method)
		Granddaughters and maternal grandsire = + 0.244 ± .016 (based on correlation factor method)
"	"	Granddaughters and paternal granddam = + 0.258 ± .04 (direct correlation)
		Granddaughters and maternal granddam = + 0.307 ± .047 (direct correlation)

Summary Correlation Table (Contd.)

<u>Breed</u>	<u>Investigator</u> Gifford and Turner (55)	<u>Correlations</u>
Ayrshire	"	Sire's daughters and Sires' sons' daughters (Fat Prod.) = + 0.430 ± .064
"	"	dam and dams' sons' daughters (Fat Prod.) = + 0.380 ± .066
Friesian	Carroll (17)	sire's daughters and sire's sons' daughters (Milk Yield) = 0.633 ± .072
Ayrshire	Smith, Scott and Fowler (212)	sires' daughters and sires' sons' daughters (Milk Yield) = 0.253 ± .07
"	"	sires' daughters and sires' daughters' daughters (Milk Yield) = 0.322 ± .041
Holstein	Rietz (193)	granddaughters and maternal grandam = +0.138 ± .024
Friesian	"	" paternal grandam = +0.086 ± .017

Summary Correlation Table (Contd.)

<u>Breed</u>	<u>Investigator</u>	<u>Correlations</u>
Jersey	Gowen (279)	Milk yield of one lactation and a succeeding lactation + .7306 - + .2144
"	"	Milk yield of one lactation and the first five + .86 - + .74

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A. Inheritance

B. Miscellaneous

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