

- I. THE INHERITANCE OF BUTTERFAT PERCENTAGE IN DAIRY CATTLE, AND ITS CORRELATION WITH MILK YIELD.
- II. THE AMOUNT OF INBREEDING IN THE SHORTHORN AND THE FRIESIAN BREEDS IN GREAT BRITAIN.
- III. THE MOVEMENT OF TWO BREEDS OF PEDIGREE DAIRY CATTLE IN GREAT BRITAIN.  
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I.

INHERITANCE OF BUTTERFAT PERCENTAGE IN DAIRY  
CATTLE AND ITS CORRELATION WITH MILK YIELD.

INTRODUCTION AND PURPOSES OF THE STUDY.

The problem of milk secretion is two-fold. Firstly, the quantity of the milk; secondly, the quality or the constituents per unit volume of the milk. The latter, to the mind of most people has come to mean for milk production the percentage of butterfat in milk. The butterfat is the most important constituent of milk commercially, and therefore has received the greatest attention in studies of milk production.

Since the fat percentage in the milk is an important index in regard to the feed requirements of its production, and the percentage of fat is a serious legal problem in some countries, the importance of its study has become accentuated. Therefore, dairy scientists have devoted considerable time to the study of the composition of milk, and to the factors causing variation in the amounts of these constituents.

Our interest in the question is essentially from the genetics aspect. More specifically, the aim is not to measure the number of genes controlling butterfat percentage, but to evaluate the relative influences of heredity and environment. Quantitative characters/

characters such as butterfat percentage are governed by a large number of genes, and knowledge of the specific number of genes concerned would be of little use, since they could not be manipulated in farm animals. Selection on the other hand, is one of the most effective tools in the improvement of livestock, and one of the most important factors determining the efficiency of selection is the breeder's ability to select superior animals as parents of the next generation. Therefore, most animal breeding investigations have been planned to investigate the methods for improving the accuracy of selection. For example, the progeny test has been developed as an index of the breeding value of a sire.

Variation between animals may be due to hereditary differences or to environmental differences. It is now well known that only the portion of the variation determined genetically, can be transmitted from parents to offspring.

To increase the effectiveness of selection, the breeder should know the proportion of the total variation in economic characters which is due to heredity. In the absence of such information/

information the breeder tends to assume that all differences between individuals are due to genetic differences. Therefore, he mates the best to the best and is surprised by the regression towards the herd average. This regression is due to only a part of the observed superiority being caused genetically, and the offspring inheriting only that part of the selection differential which is genetic. Due to this fact investigations have been proceeding in many countries and upon different animals in attempts to measure the portion of the observed variance of economic characters which is due to the genetic make-up of the animal, i.e. the heritability. Most of the work done upon the heritability of butterfat percentage is based upon American or Swedish data, no attempts having been made in this country yet.

The aims of the present investigation are :-

1. To investigate the effect of month of calving, of age at first calving upon the butterfat percentage, so that conversion factors can be used if necessary.
2. To measure the repeatability of butterfat percentage from one lactation to another. Such a measurement should be of assistance in selection.

3. To attempt measurement of the heritability of butterfat percentage in some of the dairy breeds in Britain, and to compare our results with those reported by other workers.
4. To study the relationship between milk yield and butterfat percentage by determining the phenotypic and genetic correlations between them. This enables an estimate to be given of how far improvement in one character can proceed without affecting the other.
5. To determine the genetic correlation between the butterfat percentage of different lactations in order to test the assumption that these are conditioned by the same genes.

REVIEW OF LITERATUREa) Environmental factors affecting the butterfat percentage in milk.

There are two fundamental causes of variation in butterfat percentage, inheritance and environment. A host of factors which may be grouped under environment tend to alter the fat content of milk to a greater or less extent. These factors that change the fat percentage temporarily have been discussed by Turner (1936) and by Espe (1946). We are mainly interested in the environmental factors which affect the butterfat content of the cow for a long time during her lactation period, or throughout the whole lactation, such as age of the cow, the dry period and age at first calving, and season of calving.

Most of the reports from yearly and short-time records of the breeds show that the percentage of butterfat in milk tends to decrease as the cow advances in age. On the whole the evidence shows that the highest fat percentage is obtained with young cows, then there is a fall which may not be very marked for a time since the fat content remains fairly constant from year to year during the period of the greatest usefulness of the cow, then/

then in later life there is a decrease which may be significant.

McCandlish (1922) concludes that the fat percentage in the case of the Guernsey cow reaches a maximum when the animal is under 3 years of age. Eckles (1927) has pointed out that there is no appreciable change in the fat percentage with age. Fohrman (1926) analysing the Jersey Register of Merit records reported that the fat percentage shows an almost uniform decline until after 11 years of age.

Gowen (1920-24) emphasises that the low correlation of butterfat percentage with age justifies the use of the raw butterfat percentage records without further corrections.

Holdaway (1916), Hemitt (1932), Ellinger (1923), Turner (1936-37) and Johansson and Hansson (1941) came to the same conclusion.

Johansson and Hansson (1941) have shown that increasing the length of the preceding or current interval between calving results in a slight increase in butterfat content.

It is a well-known established fact that during the summer months, particularly July and August, the fat content of milk tends to be poor. Reports from different countries

Bartlette (1935), Becker (1935), Breaks (1931), Cannon (1935), Dice (1940), Hays (1926), Houston (1942), McDowell (1922), Oxley (1935), Wylie (1925), Ragsdale and Turner (1920-22-30), Turner (1936) and Johansson and Hansson (1941) have shown conclusively that cows usually test up to 1/5th% lower in summer than in winter.

Of course, in case of cows which freshen in the autumn, the test will be maintained in the summer and possibly increased because of the greater influence of advancing lactation, as has been demonstrated by some of the above-mentioned workers. The variation in butterfat percentage from season to season may be attributed to variation in temperature and to the effect of differences in the feed available during different seasons.

The effect of stage of lactation on butterfat content has been thoroughly investigated by Barkeley and White (1924), Eckles and Shaw (1913), Gaines (1941), Ragsdale and Turner (1922), Turner (1928, 1936), Bonnier et al (1946) and by Whetham and Hammond (1935)/

Hammond (1935). They all agree that during the lactation period the percentage of fat in milk varies inversely with the amount of milk secreted although not in direct proportion.

Eckles (1930) has shown that the condition of the cow before calving is an important factor in determining her fat percentage after parturition. Bonnier et al (1948) have demonstrated that butterfat percentage is affected during the whole life of the cow when the heifer was raised under poor feeding conditions.

b) The repeatability of butterfat percentage.

Gowen (1924) studying the Holstein-Friesian records in the United States concluded that the correlation coefficient for the butterfat percentage of one lactation with that of a subsequent lactation is .715, while it is .667 for the milk yield. He has pointed out that the yearly butterfat percentage of one lactation measures the butterfat percentage of another lactation more accurately than a milk yield of one lactation measures the milk yield of another.

Gowen (1920) also found a correlation of .711 between  
the/

the first and the second lactation tests, .687 between the second and the third, .699 between the third and the fourth and .576 between the fourth and the fifth. The material used in this study was the Registry of Merit Jersey records.

Gaines and Dalfrey (1931) have analysed the butterfat percentage records of 186 Red Danish cows, each having at least 9 lactations. They have reported a correlation of .733 between the first and the second lactation butterfat percentage, .774 between the second and the third, .811 between the third and the fourth and .704 between the fourth and the fifth.

Turner (1939) has shown that the correlation between the first butterfat test and the subsequent lactations is .847 for the Guernsey records studied.

c) The heritability of butterfat percentage.

In order to allow comparisons, the estimates of the heritability of milk yield and butterfat yield will be stated together with those obtained for butterfat percentage.

Gowen (1934)/

Gowen (1934) concluded from the Jersey Register of Merit records that inheritance accounts for about half of the variance in milk yield and about  $\frac{4}{5}$ ths of the variance in butterfat percentage. He pointed out that the environmental variations which exist in the Jersey records account for little of the variations in the butterfat percentage and for only 10% of the variation in milk yield, while dominance, assortive matings and environmental variations common only to the cow herself account for the rest of the variation. In Gowen's study no allowance was made for environmental differences between herds and this is responsible for the high estimate obtained for the heritability and for dominance. Lush and Schultz (1935) have shown that the variance due to additive factors in butterfat percentage is about one-half of the total, whereas in total fat production it is about  $\frac{1}{4}$ th. They have also concluded that about  $\frac{1}{6}$ th of the variance in the butterfat percentage, and about  $\frac{1}{3}$ rd of that in the total fat production were caused by management or environment which were alike for all cows in each herd but differed/

differed from herd to herd. They were dealing with cow testing association records which are not selected material.

Rice (1933) reported a heritability of 86% for the butterfat content and 57% for milk yield. Official records for 11 bulls from several dairy breeds, each bull having at least 17 daughter-dam comparisons, were used in his analysis. Rice exaggerated the hereditary part of the variation in butterfat percentage because of the fact that differences between herds were not eliminated.

Johansson and Hansson (1941) have analysed the records of about 3,000 Swedish Red and White cows. Their estimate of the heritability of butterfat percentage was 70-80%, the corresponding figure for milk yield being 30-40%. Bonnier (1939) has studied contemporary records of 2,768 dam-daughter pairs of Swedish Red and White cattle, and obtained the same value as that reported by Johansson and Hansson for the heritability of butterfat percentage.

Tyler/

Tyler and Hyatt (1947) using Ayrshire records estimated the heritability of differences in single unselected records for milk yield, butterfat yield and butterfat percentage. The values found were 31, 28, and 55% respectively.

d) The phenotypic correlation between butterfat percentage and milk yield.

It is a general opinion that the milk of high yielding cows is usually poorer and that of the low yielding cows richer in butterfat percentage. Most of the investigators have reported a correlation between lactation averages for butterfat percentage and milk yield, while <sup>a</sup> few have reported an individual correlation or correlation within lactation.

Wilson (1910) concluded that the quality and quantity of the milk are independent of each other. Pearson (1911) criticised Wilson's work and by means of a correlation table, found a negative correlation of .075 between milk yield and butterfat content. Roberts (1919) has reported a correlation of  $-.345$  for the Jersey R.M.,  $-.296$  for the Guernsey,  $-.133$  for the Holstein-Friesian,  $-.138$  for the Ayrshire and  $-.345$  for the grade Holstein.

Ellinger (1923) using the records obtained from a breeding experiment conducted in Copenhagen concluded that in the case of the Jersey a correlation of  $-.332$  exists between butterfat percentage and milk yield, and the corresponding correlation for the Red Danish cattle is  $.055$ . The cross-bred animals show a correlation of  $-.246$ , while the three-quarter Red Danish have a correlation of  $-.011$  and the three-quarter Jersey show a correlation of  $-.149$ .

Copeland (1927) found a correlation of  $-.311$  between the butterfat percentage and the milk yield of the Jersey cow.

Gowen (1944) has shown that the correlation between the fat content and the milk yield of the Jersey cow is  $-.303$ , while the corresponding figure for the Friesian is  $-.101$ .

Gaines and Davidson (1922) and Gaines (1943) have reported a correlation of  $-.198$  for the Shorthorn breed and  $-.29$  for the Friesian breed respectively. Oxley (1935) reports a correlation of  $-.154$  and  $-.151$  for the afternoon and the morning/

morning milking in a Dairy Shorthorn herd in England. These figures are based on a number of isolated tested tests in each lactation and not on the total figures for the lactation.

Bonsama (1918) with two breeds of Dutch cattle in South Africa has reported a correlation between milk yield and fat content of  $-.27$  and  $-.170$  respectively.

Bonnier (1928) found in an investigation within a herd of Swedish Red and White cattle that the correlation between the milk and butterfat tests of individual cows, throughout their lifetimes, varied between  $+.017$  and  $-.834$ , between the  $r$  of each individual cow and her unweighed average fat percentage, there was, within a group of 79 cows a correlation of  $.469$ .

Gowen (1934) comparing the correlation between fat percentage and milk yield of the daughters and dams of the Jersey R.M. cows, has concluded that the correlation is equal to  $-.290$  for the former and  $-.270$  for the latter. Krizenedy (1934) grouped the published estimates of this correlation for various breeds in America and Europe. He found it to be  $-.199$  for 58 sets of data.

Podhradisky (1940) analysing about 4,000 annual milk records of Bernese cows in Moravia concluded that there is no correlation between milk yield and butterfat percentage.

Solnovgio (1947) has pointed out that there is a correlation of  $-.339$  between milk yield and fat content of the Semmental breed of cattle. The coefficient of correlation mentioned by Solnovgio was calculated between daily milk yield and fat percentage for the complete lactation.

Tyler and Hyatt (1947) have concluded that a correlation of  $-.140$  exists between milk yield and fat content in Ayrshire cattle. Johansson and Hansson (1941) have shown that the intra-herd correlation between butterfat percentage and milk yield is  $-.170$ . They have calculated the correlation between cows and within cows from their records, and the values obtained were  $-.250$  for the former and  $.058$  for the latter.

Table 1 shows that most of the investigators have reported a negative correlation between milk yield and fat percentage, although the actual value of the correlation found differs according to the material involved. Most of the investigators/

TABLE 1.

A summary of the investigations on the correlation between butterfat percentage and milk yield.

Investigator	Year	Material	Correlation
Wilson	1910	2866 Records of Ayrshire Cows	0
Pearson	1911	do. do.	-.075
Bonsama	1918	Dutch Cattle in S. Africa	-.270/-.170
Roberts	1918	Jersey R.M. Records	-.345
do.	do.	Holstein-Friesian Records	-.133
do.	do.	Guernsey Records	-.296
do.	do.	Ayrshire Records	-.138
do.	do.	Grade Holstein-Friesian Records	-.345
do.	do.	Grade Jersey Records	-.138
Gowen	1920	Friesian Records	-.101
Gaines et al.	1922	Shorthorn Records	-.198
do.	do.	Friesian Records	-.290
Ellinger	1923	Jersey Records	-.332
do.	do.	Red Danish Records	.055
do.	do.	$\frac{1}{2}$ Jersey - $\frac{1}{2}$ Red Danish Records	-.246
do.	do.	$\frac{3}{4}$ Jersey Records	-.149
do.	do.	$\frac{3}{4}$ Red Danish Records	-.011
do.	do.	$\frac{7}{8}$ Jersey Records	-.282
Gowen	1924	Jersey R.M. Records	-.303
Copeland	1927	Jersey Records	-.311
Kříženecký/			

TABLE 1. (contd)

Investigator	Year	Material	Correlation
Krizenecky	1934	58 sets of data	-.199
Gaines	1943	Shorthorn R.M. Records	-.217
Johansson et al	1941	Swedish Cattle Records	-.170
Tyler et al	1947	Ayrshire Records	-.140
Podhridsky	1940	Bernese Records	o
* Bonnier	1927	Swedish-Ayrshire Records	.016/-.833
* Oxley	1935	Shorthorn Records	-.154/-.151
* Solovgio	1947	Semmental Records	-.339
* Doum	1932	Mountain spotted cattle records	-.07/-.85

\* A correlation within lactation has been reported by those investigators; the rest have reported a correlation between lactation averages.

investigators concluded that there is a breed difference as far as this ~~country~~<sup>character</sup> is concerned.

- e) The genetic correlation between butterfat percentage and milk yield.

The technique for such approach has been recently developed by Hazel (1943), and it is not surprising to find only one report dealing with this subject. Tyler and Hyatt (1947) have reported that the genetic correlation between butterfat percentage and milk yield for the Ayrshire records studied is  $-.20$ .

SOURCE OF DATA.

Four Dairy Shorthorn herds, 2 Guernseys, 2 Jerseys, 2 Friesians, and 1 Kerry herd were involved in our investigations. All of these herds were listed among the top 2% of the high producing cows in England during the year 1947, except the Kerry herd and 1 Shorthorn herd belonging to the Ministry of Agriculture of Northern Ireland on Hillsborough Farm. The records were collected through the Milk Marketing Board.

Under the scheme of the Milk Marketing Board for England and Wales the Recorded visits the farm at approximately six-weekly intervals but the member weighs the milk at least once a week, and the butterfat tests are done in central laboratories. Some members record their milk daily but the Recorded should check their figures.

The information available from these records was extracted onto a standard form, shown below. Only pedigree animals were involved in our study.

				Cow No.	
Breed:	Herd:	Pedigree:	Dam No:	Sire No:	Birth:
Age at 1st calving:	No:	and date of lactation		Sex of calf:	
Services required for calving:	Disease:	Calving interval:			
Length of lactation:	Dry period:	Previous calving interval:			
Previous dry period:	B.F%	Intensity:	Yield:		
305 day yield:					
Persistency:	monthly yield (note if incomplete				
/	/	/	/	/	/

Only lactations of pedigree animals, free from diseases and doubtful information, were utilised in our work.

Lactations less than 6 months were excluded because of the difficulty in predicting the average fat test for a lactation period (Reece, 1942).

The data for milk yield is dealt with on a gallon basis and records for butterfat percentage were taken to one place of decimals. The yield for the first four days of the lactation period was not included. The yield of the herds milked three times a day have been corrected to twice daily milking using the conversion factor .83 suggested by the U.S.D.A. 1940. This correction has been also applied to the periods when three times milking was practised for part of a lactation only. No conversion factors/

factors have been used for butterfat percentage. When age conversion factors for milk yield were essential they were calculated on an intra-herd basis.

SYMBOLS USED IN OUR STUDY

<u>ITEM</u>	<u>SYMBOL</u>
<u>Effect of age at first calving on fat percentage</u>	
The deviations of the age from the mean age	$Sx$
Square deviations of the age from the mean age	$Sx^2$
The deviation of the butterfat percentage from the mean fat percentage	$Sy$
The covariance of age and butterfat percentage	$Sxy$
<u>The relation between the month of calving and the butterfat percentage</u>	
Significant	Sig.
Non-significant	N. Sig.
<u>The heritability</u>	
Deviations of dams fat percentage from the mean	
1st lactation -	$Sx_1$
2nd lactation -	$Sx_2$
1st and 2nd lactations added together.	$Sx_3$
The average of the 1st and the 2nd lactations.	$Sx$
Square deviations of dams fat percentage from the mean. (the same order as above).	$Sx^2_1$
	$Sx^2_2$
	$Sx^2_3$
	$Sx^2$
Deviations of daughters fat percentage from the mean. (the same order as above).	
	$Sy_1$
	$Sy_2$
	$Sy_3$

ITEMSYMBOL

Covariance of dam-daughter deviations:

1st lactation

 $s_{y_1}$ 

2nd lactation

 $s_{y_2}$ 

1st and 2nd lactations added together

 $s_{y_3}$ 

The average of the 1st and the 2nd lactations

 $s_{\bar{y}}$ 

Heritability

 $h^2$ 

Daughter-dam comparisons

D - D

Regression of daughter on dams

 $b_{D-D}$ The phenotypic correlation between milk yield andfat percentage.

Coefficient of correlation

r

FACTORS AFFECTING BUTTERFAT PERCENTAGE.

Many of the factors affecting butterfat percentage have been investigated (see Review of Literature). The present study of such factors is confined to the effect of month of calving and age at first calving on butterfat percentage.

Many workers have shown that the season of calving affects the fat percentage slightly, but significantly, since a definite trend occurs. The aim of the present work is to measure the proportion of the total variance of butterfat percentage, which is caused by differences in the month of calving.

Records of five herds have been used for this purpose, and the significance of differences in the month of calving has been found by application of the analysis of variance method (Snedecor, 1945). The results are summarised in Table 2.

Table 2 shows that the variation due to differences in month of calving is equal to 1%. Therefore, only about 1% of the total variation of butterfat percentage can be assigned to differences in the month of calving.

This/

Table 2.

The relation between the month of calving and  
the butterfat percentage (level of sig. 5%).

Herd No. and breed.	Total Mn. Sq.	Mn. Sq. within months.	Mn. Sq. between months.	Nature of the variance ratio.
1 Shorthorn	.1189	.1139	.1790	N. Sig.
5 Friesian	.1594	.1525	.3018	Sig.
7 Guernsey	.2206	.2098	.3045	N. Sig.
8 Guernsey	.2120	.2313	.1472	N. Sig.
9 Jersey	.2127	.2675	.2900	N. Sig.
Average of 5	.1967	.1950		

Percentage variation due to month of calving =  $\frac{0.1967 - 0.1950}{0.1967} \times 100 = 1\%$

This analysis although based upon the first lactation, shows that the season of calving has only a very slight affect upon the butterfat percentage.

In the past, no attempts have been made to study the effect of age at first calving on butterfat percentage, although several studies have been made of the effect of this factor upon milk yield. The records of four herds have been analysed to determine the effect of age at first calving upon the butterfat percentage.

Table 3 gives the results obtained. It shows that the regression of butterfat percentage upon age at first calving is .028, i.e. for every month delayed in the age of a heifer at calving beyond the average (27 months in our data) we should expect that the fat percentage will be increased by .028% during her first lactation.

Eckles (1913, 1930) has shown experimentally that the fat content and the total milk yield during the first weeks after parturition are materially increased when the cows calve in a high/

Table 3. \*

The effect of age at first calving  
on butterfat percentage.

Herd No. and breed.	No of records.	$Sx^2$	$Sxy$
9 Jersey	48	1093	10.2
7 Guernsey	50	2234	1.2
8 Guernsey	98	1458	66.4
5 Friesian	238	5120	197.3
Total		9905	275.1

The regression of butterfat percentage on age at first calving =

$$\frac{275.1}{9905} = .028$$

\* Units used : Months for the age at first calving and butterfat in percentage.

high condition of flesh, compared to the yield and butterfat percentage in poor condition. Therefore, we may account for the higher fat test of heifers which calved at a greater age than the average age, by the fact that such heifers are probably in better condition of flesh than their contemporaries which calved below or at the average age.

Tables 2 and 3 show that the effect of month of calving and age at first calving on the butterfat percentage is so slight that they can be left out of consideration in comparing the butterfat percentage of different cows, and therefore all the records for fat percentage can be used without any correction factors.

Table 2 shows that the variation in fat percentage is higher within the Jersey and the Guernsey breeds than that for the Friesian and the Shorthorn breeds. Turner (1936) studying the variation in the fat percentage of the milk of the Holstein, Ayrshire, Guernsey and the Jersey breeds, has reported that the variation in butterfat percentage is higher for the Channel Island breeds than that for the other two breeds. He pointed out/

out that the fat content of the milk will not alone characterise the breed, as some cows of the four breeds have the same average yearly fat percentage. It seems that the higher the butterfat test the higher is the variation within the breed.

REPEATABILITY OF BUTTERFAT PERCENTAGE.

Many of an animal's important characteristics vary in their expression from time to time. It is a common observation among dairy men, that the variation in the milk yield of a cow from one lactation to another is much more than the variation in her fat content. This is due to the fact that milk yield is more sensitive to environmental changes than fat percentage.

Repeatability can be defined as the fraction of the variance in the single record which was caused by permanent individual differences between cows. Repeatability indicates the degree to which records of the same cow repeat themselves. It measures the sum of the variance due to additive genes, dominance effects, epistasis, and permanent effects of the environment on the cow herself which were not the same for her herd mates.

Since dominance deviations are not inherited from parents to offspring, and since very little of the epistasis effect is transmitted the variance due to these factors plus the variance which is due to permanent individual peculiarities are treated/

treated together as one source of variance and called by Lush "permanent but not transmissible differences between individuals".

A knowledge of the repeatability of an economic character is important in breeding operations and cattle improvement. The success of selecting breeding females on the basis of production record depends upon the accuracy with which the future production of a cow can be predicted from her present record, i.e. it depends upon the repeatability of the production records.

Given the repeatability, and some production records a prediction can be made of the total producing ability of an animal. Lush (1945) presents the following formula for calculating the best estimate of a cow's producing ability based on more than two records for each cow.

$$\text{Herd average} + \frac{n r}{1 + (n-1)r} (\text{cow's average} - \text{herd's average})$$

where  $r$  is the correlation between successive records and  $n$  is the number of records on which prediction is made.

RESULTS AND DISCUSSION.

The repeatability of butterfat percentage has been calculated from the correlation between successive butterfat percentages. These have been calculated for all the possible combinations of the first, second, third and fourth lactation's butterfat percentage. Lush's (1931) technique for averaging correlations has been applied. This method is also represented by Snedecor (1946).

Table 4 shows the results obtained for each herd separately and for all the possible combinations. Table 5 presents the overall repeatability for the 11 herds studied. Figure 1 illustrates the overall repeatability obtained for all breeds for each possible combination, the number of lactations involved in each estimate are given in parenthesis.

The records show that there is a tendency for the correlation to be greater for closely successive records than that of the records separated by longer time. Although this observations does not hold true for all herds, nevertheless it is very noticeable in most of the herds studied. This may be attributed/

Table 4.

The repeatability of butterfat percentage for all herds.

Herd No. and Breed.	Bivariates Correlated.											
	No.	1st and 2nd	No.	2nd and 3rd	No.	3rd and 4th	No.	1st and 3rd	No.	1st and 4th	No.	2nd and 4th
1 Shorthorn	94	.495	54	.435	34	.665	44	.504	19	.340	25	.215
2 "	27	.440	13	.476	13	.663	-	-	-	-	-	-
3 "	152	.497	86	.484	47	.511	89	.580	50	.520	48	.470
4 "	108	.585	61	.468	57	.558	59	.449	38	.575	38	.664
Total	381	.509	214	.463	151	.563	192	.541	107	.512	111	.484
5 Friesian	137	.666	111	.714	56	.663	105	.725	49	.454	56	.603
6 "	13	.802	12	.818	10	.783	-	-	-	-	-	-
Total	150	.682	123	.723	66	.702	105	.725	49	.454	56	.603
7 Guernsey	47	.585	35	.428	25	.645	35	.324	24	.335	23	.503
8 "	60	.830	36	.594	22	.753	39	.777	17	.733	18	.485
9 Jersey	26	.783	16	.788	13	.696	14	.832	9	.731	9	.631
10 "	13	.409	12	.428	10	.448	6	.778	-	-	-	-
Total	146	.675	99	.362	70	.653	94	.697	50	.311	50	.448
11 Kerry	149	.849	104	.819	56	.750	86	.655	40	.724	55	.710

Table 5.

Summary of repeatabilities obtained for different herds.

Herd No. and breed.	No. of lactations.	Intra-herd correlation.
1 Shorthorn	270	.461 ± .061
2 "	53	.400 ± .137
3 "	472	.512 ± .046
4 "	361	.550 ± .053
Total	1156	.511 ±
5 Friesians	35	.804 ± .169
6 "	512	.662 ± .044
Total	547	.673 ±
7 Guernsey	189	.452 ± .073
8 "	192	.733 ± .072
9 Jersey	87	.744 ± .107
10 "	41	.476 ± .156
Total	509	.621 ±
11 Kerry	490	.771 ± .045

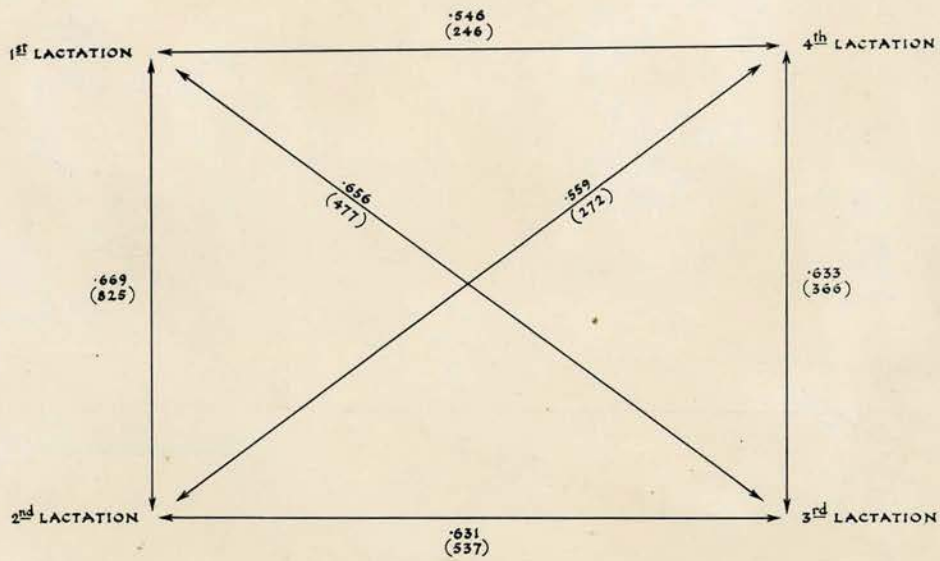


FIGURE 1

The repeatability of fat percentage for all the herds and for all the possible combinations for the first, 2nd, third and fourth lactation butterfat records.

attributed to differences in feeding and management during the period between non-consecutive lactations. In other words differences in the environment being greater for greater intervals of time.

The averaging of the estimates of the repeatability for each breed show that there are breed differences in the repeatability of butterfat percentage. Due to the fact that the repeatability varies from herd to herd/<sup>it</sup> is difficult to attach a standard error to the breed figure. The Kerry breed have the greatest repeatability, the Shorthorn breed the lowest.

Our estimate of .547 for repeatability in the Friesian breed is lower than the value of .715 obtained by Gowen (1924) for the Holstein-Friesian breed in the United States. However, since the repeatability is expected to increase with reduction in the variation of environmental conditions, this difference can be explained by the fact that Gowen's estimate was based upon animals kept under uniform conditions as far as feeding and management are concerned. For the same reason Gowen (1920) reported a higher value than our estimate of .621 for the repeatability/

repeatability of butterfat percentage for the Jersey breed.

However, it should be mentioned that Gowen's estimates are higher than ours because of the fact that the former's include differences between herds which are eliminated in our estimations.

There are few reports in the literature concerning the repeatability of butterfat percentage for other breeds. The results reported by Gaines and Palfrey (1931) on the Red Danish data come very close to our results on the Kerry breed.

Our estimate for the repeatability of butterfat percentage for all breeds grouped together comes to  $.633 \pm .020$

This was based upon 11 herds containing 2700 lactations.

All the possible correlations between the first four butterfat percentages were calculated whenever possible.

Therefore, we may say that about 63% of the total variance of butterfat percentage can be attributed to the additive effects of genes, dominance effects, epistasis effects and to permanent environmental differences between cows.

THE HERITABILITY OF BUTTERFAT PERCENTAGE.

During the last decade the study of the inheritance of quantitative characters has been shifted from attempts to measure the number of genes involved, to attempts to measure the fraction of the variance of the character which is heritable. This change in approach has been due mainly to the theoretical analysis of the implications of Mendelian inheritance developed by Fisher (1918) and Wright (1921, 1935). Lush and his co-workers at Iowa State College have used this new approach extensively.

The main concept of this approach is that of heritability. This may be defined as the fraction of the observed variance which is caused by differences in heredity. In other words, it is the degree to which quantitative characters are transmitted from parents to offspring.

Wright has demonstrated methods of dividing the total variance of the character into the following fractions:

1.  $\sigma_g^2$  or the variance due to genes which act in an additive manner,
2.  $\sigma_D^2$  or the variance due to dominant deviations from the additive scheme,

3.  $\sigma_I^2$  or the variance due to epistasis deviations from the additive scheme,
4.  $\sigma_{Eg}^2$  or the variance due to non linear interaction of heredity and environment,
5.  $\sigma_E^2$  which is the variance due to environmental variations.

Lush (1940) points out that the heritability in its narrow definition measures only  $\sigma_g^2$ , where in its broad sense it measures the sum of  $\sigma_g^2 + \sigma_D^2 + \sigma_I^2 + \sigma_{Eg}^2$ .

Since the part played by dominance, epistasis and non linear interaction of heredity and environment is not yet well understood, heritability in this report is used in its narrow sense.

Some knowledge of the heritability is useful to the breeder in estimating how rapidly progress can be made in selecting for a trait. The heritability of the trait is one of the most important factors to consider in deciding upon the breeding plan which is most likely to be successful in bringing about improvement. Moreover, a dependable estimate of heritability helps in deciding how much emphasis should be given different characters in selection and in constructing selection indexes.

The following three methods can be used in estimating the heritability.

1. Isogenic lines (identical twins in farm animals);  
Variation within isogenic lines is wholly environmental. Comparing this with the variation in an otherwise similar random breeding population may give an estimate of heritability. Maternal effects and contemporaneity bias the estimates based on that method.
2. Experiments with selection in opposite directions over several generations. The difference produced in this way between the means of the population, when divided by the amount of selection practised gives an estimate of the amount of the initial variance which was additively genetic but includes a little of the epistasis variation.
3. Correlation between relatives. The most widely applicable methods of estimating heritability are based upon comparisons of the degree of resemblance between closely related animals, e.g., daughter-dam, half-sibs, etc. The correlations between parent offspring are in general the most useful approach, because the sampling error is reduced, and the environmental correlation is adequately discounted. All of the variance due to dominance deviations, and most of the variance due to epistasis, are excluded in estimates of heritability derived from parent offspring correlations.

Lush (1940) has developed the intra-sire correlation or regression of offspring on dams, which is used extensively now in estimating the heritability of the

economic characters in livestock. According to Lush, the regression of daughters on dams gives the most dependable estimate of heritability in data where (1) the sire cannot express the character himself, (2) the dams are likely to be more highly selected than the daughters, (3) the environment varies between different herds or sire groups. The intra-sire regression of daughters on dams avoids most of the environmental correlations and overcomes the error which may be introduced by departure from random mating.

The correlation between half-sibs is also widely used. Such correlation in a random breeding population is composed of one-quarter of the additive genetic factors, plus a small part of the variance due to epistasis, plus a part due to environmental correlation between parental half-sibs.

Relations more remote than half-sibs are rarely of much use for estimating heritability, since the genetic correlations expected are small and consequently their sampling errors are high.

METHODS USED AND RESULTS OBTAINED

The methods used for estimating the heritability of butterfat percentage in our data is the intra-sire regression of daughters on dams. This has been calculated separately for the first and the second lactation in each herd. The results are given in Tables 6, 7 and 8. Since the age does not affect the butterfat percentage, table 8 gives the results obtained for the first and the second lactation fat percentage grouped together, and an over-all estimate for the heritability was calculated.

The intra-sire correlation of daughters on dams and the intra-sire regression of daughters on dams were used in estimating the heritability of butterfat percentage for the two biggest herds we have in this study, namely the Kerry herd and the Shorthorn herd No. 3. This has been undertaken in an attempt to compare the estimates obtained from the different techniques. Table 9 summarises the results obtained for the Kerry herd and the Shorthorn herd No. 3.

It is interesting to determine the heritability of the

Table 6.

Showing the heritability of the 1st lactation butterfat percentage.

All breeds measured by the intra-sire-regression.

Herd No. and breed.	No. of bulls	No. of D-D comparisons	$\frac{2}{sx_1}$	$sx_1y_1$	$b_{D-D}$	$h^2$
3 Shorthorn	17	135	11.40	3.19	.280	.560
4 Shorthorn	4	39	3.69	1.57	.425	.850
5 Friesian	6	31	3.58	1.25	.349	.698
7 Guernsey	2	13	1.95	.72	.369	.738
8 Guernsey	4	25	3.96	.82	.207	.414
9 Jersey	2	7	.62	.12	.194	.388
11 Kerry	33	184	33.21	7.68	.231	.463
total	68	434	58.41	15.35	.263	.526
The coefficient of regression of Daughters on Dams = $.263 \pm .055$ Heritability. = $.526 \pm .110$						

Table 7.

Presenting the heritability of butterfat percentage for  
the II lactation.

All breeds measured by the intra-sire-regression.

Herd No. and breed.	No. of bulls.	No. of D-D	$\frac{sx^2}{2}$	$\frac{sx y_2}{2}$	$b_{D-D}$	$h^2$
3 Shorthorn	12	61	5.36	1.06	.198	.396
4 Shorthorn	2	22	2.44	.93	.381	.764
5 Friesian	4	16	1.75	.22	.126	.252
7 Guernsey	2	9	.855	.67	.788	-
8 Guernsey	5	20	3.05	.67	.220	.440
9 Jersey	3	6	.43	.59	1.36	-
11 Kerry	31	113	15.32	8.02	.523	-
Total 7	59	247	32.78	13.41	.409	.818

The coefficient of regression of Daughters on Dams = .409  $\pm$  .063  
Heritability = .818  $\pm$  .126

Table 8. \*

Showing the heritability of butterfat percentage for  
the I and II lactation added together.  
Measured by the intra-sire-regression.

Herd No. and breed.	No. of D-D comparisons.	$sx^2_3$	$sx_y_3$	$b_{D-D}$	$h^2$
3 Shorthorn	196	16.76	4.25	.254	.508
4 Shorthorn	61	6.13	2.50	.407	.814
5 Friesian	47	5.33	1.47	.276	.552
7 Guernsey	22	2.80	1.39	.496	.992
8 Guernsey	45	7.01	1.49	.212	.424
9 Jersey	13	1.05	.71	.676	-
11 Kerry	297	48.53	15.70	.323	.646
Total	681	91.19	28.76	.315	.630
The regression of Daughters on Dams		= .315	± .032		
Heritability		= .630	± .064		

\* Animals for which either the first or the second lactation records are included.

Table 9.

Heritability of butterfat percentage for the  
Kerry herd and herd No. 3 Shorthorn using the intra-sire  
correlation and intra-sire-regression methods.

Herd and breed.	D-D comparisons.	$h^2$ using D-D regression.	$h^2$ using D-D correlation.
11 Kerry	297	.648 $\pm$ .126	.674 $\pm$ .118
3 Shorthorn	196	.508 $\pm$ .140	.536 $\pm$ .142

Table 10.\*

Showing the heritability of the average butterfat  
percentage for the I and II lactation.  
Measured by the intra-sire-regression.

Herd and breed.	No. of bulls.	No. of D-D comparisons.	$sx^2$	$sxy$	$b_{D-D}$	$h^2$
3 Shorthorn	11	57	3.31	.77	.233	.466
4 Shorthorn	3	20	1.66	.59	.355	.710
5 Friesian	2	9	.81	.08	.100	.200
7 Guernsey	2	8	.49	.06	.122	.244
8 Guernsey	4	14	1.84	.22	.119	.238
11 Kerry	25	88	12.66	5.41	.427	.854
Total 6 Herds	47	196	20.77	7.13	.343	.686
Regression of Daughters on Dams		= .343 ± .071				
Heritability		= .686 ± .142				

\* Animals for which the 1st and 2nd lactation records were included.

average butterfat percentage over the first and the second lactations. This is given in Table 10.

#### DISCUSSION

There is considerable variation between the estimates of the heritability of butterfat percentage which have been reported in the literature. This variation is expected since these estimates are derived from particular populations which differ in the environments under which they were maintained. Moreover, different methods have been used in estimating the heritability.

Values of 53%, 82% and 63% were found for the heritability of fat percentage in the 1st, 2nd, and over-all lactations, respectively (Tables 6, 7 and 8). Gowen (1934) found the heritability to be 83% which is higher than that found in the present study (63%). This difference is probably due to his material having been selected, and to environmental differences between herds. Lush (1948) discussing Gowen's results states, "In Gowen's study of milk and test in Jersey cattle no allowance was made for an environmental component in the correlation

between daughters and dams. Environmental differences between herds would have made such a contribution. The excess of full-sib resemblance over parent-offspring resemblance he alternatively interpreted as an environmental component or as a result of dominance. On the hypothesis that there was no dominance he found heritability of test to be .83 and of milk to be .56 or .53 according to whether the departures from random mating were caused by phenotypic assortive mating or by mating relatives together. But if herd to herd differences in environment contributes .10 to daughter-dam correlation for the test and .25 to that of milk then he would have found .64 and about .09 to .08. Or, if the environmental components were only .05 and .20 respectively, he would have found .74 and about .19 or .18."

Rice (1933) found a value of 80%. His material consisted of 10 bulls, each bull having at least 17 daughter-dam comparisons. This restriction to bulls having an unusually large number of daughters results in a higher proportion of cases in which the daughters and the dams were kept under different environmental conditions. This would have added an environmental

portion to the daughter-dam correlation, which may be responsible for the high estimate of heritability obtained.

The estimates of 50% (Lush, et al. 1935), 55% (Tyler, et al. 1947), and 70%-80% (Johansson et al. 1940) agree reasonably with our estimates. However, it should be emphasized that the results from a particular set of data are rigidly applicable only to that data, since estimates of heritability describe a condition prevailing in a population at a given time, and they apply primarily to variance in the performance of individual animals.

Johansson and Hansson (1940) have shown that the heritability of milk yield found from the second lactation record is much lower than that from the first lactation record. Tables 6 and 7 show that this is not the case in our data for the heritability of butterfat percentage. On the contrary, the heritability obtained from the second lactation record is higher than that obtained from the first lactation records. The difference, however, is not statistically significant.

Although our data suggest that there is a breed

difference in the heritability of butterfat percentage, the number of the daughter-dam comparisons is too small to verify such a conclusion.

Table 9 shows that there is a close agreement between the two estimates for the heritability of butterfat percentage for the Kerry and the Shorthorn herd No. 3, calculated on the basis of the intra-sire correlation or regression of daughters and dams. This may be explained by the fact that the dams are not a highly selective group compared to their daughters as far as the butterfat percentage is concerned. For the Kerry herd it has been found that the mean butterfat percentage for the daughters is  $4.50 \pm .151$  while it is  $4.42 \pm .150$  for the dams. Although the butterfat percentage is as important as milk yield in selecting a dairy cow, few breeders take this into consideration when they select their breeding animals. Differences between the two estimates should be expected when the dams are more highly selected compared to their daughters for the character studied, and in such cases the regression of offspring on parents gives more accurate results.

Lush (1945) has shown that the heritable portion of the variance is greater in data which involve more than one record, although such data give a slightly lower spread between the average of those saved as parents and the average of the herd, i.e., the selection differential. He points out that using two records with an average heritability of 20% would give 29% more progress from selection than would result from data involving only single records.

The statement that "using more than one record increases the heritable portion of the variance" is more noticeable when the character in question is low in heritability. The temporary changes which affect the character are reduced by using more than one record, and consequently the fraction of the variance which is genetic is increased. Butterfat percentage is hardly affected by temporary factors, and this may be responsible for the close agreement between the value of .683 and .630 obtained for the over-all heritability for butterfat percentage based on the average of two records and one record respectively in our data.

However, it can be stated that our estimate for the heritability of butterfat percentage is high and does in general agree with the estimates of other investigators. Therefore improvement in butterfat percentage in dairy cattle can be achieved by phenotypic selection. In other words, selection of animals as parents for the next generation, which give a higher test than the average of their herds, will be a satisfactory method of selection.

THE REPEATABILITY AND THE HERITABILITY OF BUTTERFAT PERCENTAGE.

One should expect the repeatability percentage to exceed that for the heritability, for a cow tends to repeat her performance, not only because of her specific inheritance, but also because of certain factors peculiar to herself including those in her environment.

Lush et al. (1937) have found that the heritability of milk yield is approximately two-thirds of the repeatability for that character. We have found that the estimates of the repeatability and heritability for butterfat percentage are very similar, being  $.633 \pm .020$  and  $.630 \pm .064$  respectively. These estimates are based upon 2700 lactations for the former and 681 daughter-dam comparisons for the latter.

This similarity of repeatability and heritability suggests that the part played by dominance, epistasis and permanent environmental changes is very small as a cause of variance between individual records of the butterfat percentage in dairy cattle. The genetic variance must be due largely to additive genes and the environmental to temporary effects.

Lush et al. (1941) using intra-sire regression of offspring in studying the heritability of butterfat and milk yield in dairy cattle, have concluded that dominance and epistasis are of little importance for butterfat production. No work has been reported upon the comparison of the heritability and the repeatability of butterfat percentage. Nevertheless, other investigators have reported the same estimate for the repeatability and the heritability of some economic characters, i.e., Stewart (1945) and Seath (1947), the former studying the litter size in pigs, and the latter studying the individual body temperature in Jersey cattle.

THE PHENOTYPIC AND THE GENETIC CORRELATION BETWEEN BUTTERFAT PERCENTAGE AND MILK YIELD, AND THE GENETIC CORRELATION BETWEEN THE BUTTERFAT PERCENTAGE FOR THE FIRST AND THE SECOND LACTATIONS.

The phenotypic correlation between butterfat percentage and milk yield has been investigated by a large number of workers (Table 1). The genetic correlation on the other hand has never been investigated previously in this country and only one report has been published of work on this subject (Taylor et al. 1947). The genetic correlation between the butterfat percentage for the first and the second lactations has not yet been studied at all prior to the present work. The last part of this study is confined to investigations of these problems.

The phenotypic correlation.

Method used and the results obtained-Discussion.

The phenotypic correlation between milk<sup>yield</sup> and butterfat percentage has been calculated separately for each herd, for the first, second, third, and fourth lactations. The over-all correlation for each breed has also been calculated. The method detailed by Lush of averaging correlations has been used. The results are given in Table 11. Our results confirm most of the reports on this subject, and show that there is a small

TABLE 11.

Phenotypic correlation between milk yield and butterfat percentage (all herds).

Herd No. & Breed	I Lactation		II Lactation		III Lactation		IV Lactation		r within herd		
	No.	r	No.	r	No.	r	No.	r	No.	r	
<u>Shorthorn</u>											
1	130	-.175	91	-.115	52	-.065	36	-.226	309	-.102	
2	35	-.263	28	-.507	21	-.415	18	-.277	102	-.375	
3	244	-.245	152	-.124	90	-.203	47	-.165	533	-.193	
4	140	-.166	101	-.163	87	-.019	65	-.102	393	-.123	
Total	549	-.211	372	-.165	250	-.100	166	-.160	1337	-.185	±.027
<u>Friesian</u>											
5	212	-.412	151	-.181	100	-.414	49	-.461	512	-.363	
6	31	+.009	16	-.556	19	-.058	16	-.390	82	-.171	
Total	242	-.370	167	-.225	119	-.371	65	-.445	594	-.340	±.041
<u>Guernsey</u>											
7	58	-.224	41	-.260	32	-.289	22	-.234	153	-.243	
8	94	-.222	70	+.123	47	-.086	25	-.280	236	-.033	
<u>Jersey</u>											
9	49	-.149	31	-.337	21	-.454	17	+.086	118	-.180	
10	20	+.215	18	+.065	20	+.166	14	-.110	72	+.080	
Total	221	-.175	160	+.050	120	-.168	78	-.163	597	-.114	±.040
<u>Kerry</u>											
11	219	-.263	167	-.204	112	-.192	63	-.255	561	-.227	±.042
									3089	-.211	±.010

negative correlation between butterfat percentage and milk yield.

This differs significantly between breeds.

From the genetic point of view it is important to separate the correlation within cows from the correlation between cows. Table 12 shows the over-all correlation, correlation within cows, correlation between cows, regression within cows and regression between cows. Only cows which had two, three or four consecutive lactations were involved, and age conversion factors were applied to standardise the milk yield. These were determined on intra-herd basis.

The total correlation between milk yield and fat percentage over 970 lactations is  $-0.248$ . This correlation may be split into the correlation between cows ( $-0.362$ ), and that within cows ( $-0.174$ ). Johansson and Hansson (1940), have reported a value of  $+0.008$  for the correlation within cows and they concluded that the fat percentage of the milk produced by one and the same cow during consecutive lactations is practically independent of the milk yield.

Table 12, where milk yield is taken in tens of gallons and butterfat in percentage, shows that the regression of fat

percentage is so small that it is of little practical importance in selecting breeding animals. The table shows that there is a decrease of about  $-.05\%$  of the average fat test when the milk yield is increased by 100 gallons.

It is known<sup>n</sup> that milk fat is synthesised somewhat independently of the other milk ingredients. This is supported by the fact that each fat globule of milk is surrounded by material or membrane, of which phospholipids are characteristic, that are not in the rest of the milk. The amount of fat in the milk is influenced by factors that do not affect the proportion of other milk constituents. High fat content in the diet increases the fat content of the milk, while fish oils in the diet decrease the fat content of the milk without affecting other constituents.

However, the fat percentage of any one sample of milk is the result of a certain rate of fat secretion and a certain rate of milk serum secretion, either of which may be modified independently of the other but not without affecting the final percentage of fat in milk.

A negative correlation between milk yield and butterfat percentage is manifested, as a rule at any time of the lactation

TABLE 12.

Representing the overall correlation, correlation within cows, correlation between cows:  
regression within cows and regression between cows

Herd No. & Breed	No. of animals	No. of consecutive lactations involved	Overall correlation	Correlation within cows	Correlation between cows	Regression within cows	Regression between cows
1. Shorthorn	77	2	+ .025	- .015	+ .024	- .0004	+ .0006
	30	3	- .204	- .084	- .348	- .002	- .006
5. Friesian	84	3	- .273	- .247	- .336	- .007	- .006
	30	4	- .384	- .248	- .369	- .003	- .013
7. Guernsey	56	2	- .249	- .078	- .328	- .001	- .009
	30	3	- .139	- .197	- .104	- .002	- .006
8. Guernsey	37	2	- .352	- .228	- .710	- .008	- .012
	26	3	- .508	- .332	- .617	- .011	- .018
Average			- .248	- .174	- .362	- .00487	- .00943

period, when the rate of milk secretion happens to increase, or decrease, owing to changes in the feeding or other circumstances. It seems that the rate of change in fat secretion is slower than the rate of change in secretion of milk serum throughout the lactation period. Gaines (1940) suggested that as the amount of milk secreted increases, the energy available for fat secretion decreases thereby causing milk of lower fat test to be produced.

Whetham and Hammond (1935), discussing this problem, state, "This suggested that the changes in milk yield during the lactation period are for the most part due to changes in the rate of secretion of the cells, and those due to age are for the most part due to changes in the numbers of the cells secreting. If this is accepted it will follow, that when the yield of the milk is increased by increased rate of secretion of the gland cells, the percentage of fat in the milk decreases (period of lactation), but when the yield of the milk is increased by the number of cells secreting the fat percentage in the milk will remain unchanged (age)."

THE GENETIC CORRELATION BETWEEN MILK YIELD AND BUTTERFAT PERCENTAGE.

An animal's phenotype for a particular character is known to be the sum of the following effects.

- a) The average effects of the genes (strictly additive).
- b) The effect of environment, dominance and epistasis.

If two traits are correlated with each other, the observed correlation may be due (1) wholly to environmental circumstances; (2) to genes which affect both characters, i.e. genes having pleiotropic effect; (3) to a combination of the effect of genes and environment.

The genetic correlation between two characters shows the extent to which these characters are similar because of common genes affecting them. In other words it is the extent to which the genetic variation in one character is affected by the genetic variation in another. Of course the genetic correlation is more accurate than the phenotypic correlation as a basis for selection for two characters, since environment, dominance and epistasis play an important role in the latter. As a matter of fact a phenotypic correlation may exist between two characters either/

either positive or negative without any genetic component at all.

The genetic correlation between butterfat percentage and milk yield has been calculated from our data using the following formula developed by Hazel (1943).

The genetic correlation between fat percentage and milk

$$\text{yield} = \sqrt{\frac{b_1 \times b_2}{b_3 \times b_4}}$$

where

- $b_1$  = the regression of daughter's fat percentage on dam's milk yield.
- $b_2$  = the regression of daughter's milk yield on dam's fat percentage.
- $b_3$  = the regression of daughter's fat percentage on dam's fat percentage.
- $b_4$  = the regression of daughter's milk yield on dam's milk yield.

Table 13 represents the values obtained based on 492

daughter-dam comparisons. Applying the above mentioned formula

to Table 13 gives a value of  $-.20$  as the genetic correlation

between milk yield and butterfat percentage. This estimate agrees

with that found by Tyler and Hyatt (1947) in Ayrshire cattle.

The phenotypic and genetic correlation between different

traits are of great importance in constructing and using

selection indexes.

TABLE 13.

The genetic correlation between milk yield and butterfat percentage

$b_1$	$b_2$	$b_3$	$b_4$
-.001	-2.1164	.3231	.1474

The genetic correlation between milk yield and fat percentage =

$$\sqrt{\frac{-.001 \times -2.1164}{.3231 \times .1474}} = -.201$$

TABLE 14.

The genetic correlation between the butterfat percentage for the first and the second lactations.

$b_1$	$b_2$	$b_3$	$b_4$
.1904	.3862	.2131	.3573

The genetic correlation between the butterfat percentage for the 1st and the 2nd lactations =

$$\sqrt{\frac{.2131 \times .3573}{.1904 \times .3862}} = 1.018$$

The genetic correlation between two characters is also an important item in selecting simultaneously for the two characters. If the breeder knows such a correlation, he will be in a better position to predict how fat percentage is affected when he selects for milk yield alone.

However, the genetic correlation of  $-.20$  obtained indicates that about 20% of the genes responsible for fat percentage are also responsible for milk yield, assuming that all the genes have the same effect.

If we know the heritability of milk yield and the heritability of fat percentage, the phenotypic standard deviation for milk yield and butterfat percentage and the genetic correlation between the two characters, we can estimate the change in butterfat percentage when milk yield is improved. The calculations mentioned below are an attempt to estimate the genetic regression of butterfat percentage on milk yield when milk yield is improved by a hundred gallons. We also, can calculate the amount of improvement expected in butterfat percentage when selection is practised for that character in closed herds.

Preliminary work

in this Institute has shown that butterfat percentage is not taken into consideration in selecting dairy cattle.

It has been found by many workers that the phenotypic standard deviation of milk yield is about 20% of the herd average. Therefore, in a herd with an average of 1,000 gallons of milk yield for 305 days, the phenotypic standard deviation will come to 200 gallons. This estimate will be used in our calculations. Our data shows that the phenotypic standard deviation within breeds of butterfat percentage is .44%.

Knowing the following values we are able to estimate the change in butterfat percentage when milk yield is improved for a 100 gallons, or the genetic regression of butterfat percentage on milk yield.

.25 = the heritability of milk yield

200 gallons = the phenotypic standard deviation of 305 days milk yield.

.63 = the heritability of butterfat percentage.

.44% = the phenotypic standard deviation of butterfat percentage.

since  $h^2 = \frac{\sigma_g^2}{\sigma_p^2}$  then  $h = \frac{\sigma_g}{\sigma_p}$

Therefore :-

The genotypic standard deviation of 305 day milk yield  
= 100 gallons,  
and  
The genotypic standard deviation of butterfat  
percentage = .35%

Since 
$$b_g = r_g \times \frac{\sigma_g}{\sigma_g} \text{ Fat percentage} / \text{Milk yield}$$

Then,

The regression of butterfat percentage on milk  
yield =  $-.20 \times \frac{.35}{100}$

The change in butterfat percentage when milk  
yield is increased by 100 gallons =  $-.20 \times 100 \times 100$   
= .07%.

The above mentioned calculations indicate that  
selection for milk yield affects butterfat percentage very  
slightly. In other words when the milk yield is increased by  
100 gallons butterfat test is decreased by .07%.

IMPROVEMENT TO BE EXPECTED PER YEAR FROM DIRECT SELECTION FOR BUTTERFAT PERCENTAGE IN CLOSED HERDS.

Robertson and Rendel (1949) have calculated the genetic gain in milk yield by selection in closed herds of dairy cattle.

This is an attempt to estimate the theoretical improvement from direct selection for butterfat percentage using the same techniques applied by the above mentioned authors.

Let us consider a closed herd of dairy cattle, in which:

- 1) Selection is practised for butterfat percentage, and it is based on the first lactation record.
- 2) The bulls are bred from the top 5%.
- 3) The culling percentage is 35%.
- 4) No progeny testing is practised, and bulls are chosen solely on the fat percentage records of their dams.

The following information is known :-

- a)  $L$  or the total of the mean age of the parents when their offspring are born = 18 years
- b)  $h^2$  or the heritability of butterfat percentage = .63

c:/

c)  $\sigma_P$  or the phenotypic standard deviation of butterfat

percentage = .44%

d)  $I$  or the genetic superiority of the mean

of the cows kept for breeding purposes = .64

e)  $I_1$  or the genetic superiority of the mean

of the bulls' dams = 2.03

Therefore,  $\sigma_g$  = .44 x .8 = .35

$I_g$  for c-c = .35 x .8 x .64 = .180

$I_g$  for c-B = .352 x .8 x 2.03 = .572

Since there is no selection amongst bulls,

$I_g$  for B-B = 0

$I_g$  for B-c = 0

Since the total genetic improvement per year =  $\frac{\sum I}{\sum L}$

The genetic improvement expected per year =  $\frac{.752}{18} = .042\%$ .

Therefore, under optimum conditions for mass selection the expected theoretical rate of genetic improvement is about 1% of the average butterfat content per year. About one-third of the improvement comes from the early culling of heifers, and the rest from selection of the dams of bulls.

Robertson/

Robertson and Rendel (1949) reported the same value for the expected genetic improvement in milk yield. The same authors have calculated the actual genetic improvement in milk yield for a dairy herd in England, which was found to be 3.3 gallons per year. This corresponds to about .7% per year of the average milk yield for that particular herd.

Of course the rate of the genetic improvement depends on many factors. These factors are briefly listed below :=

- 1) The mean of the generation length. The larger the generation length the smaller the improvement expected. Artificial Insemination in dairy cattle should increase the improvement per year.
- 2) The heritability of the character studied, the higher the heritability the greater is the genetic gain.
- 3) The information available on the breeding stock, especially for animals brought into the herds.
- 4) The genetic correlation between different characters.
- 5) The variance of the characters under investigation.
- 6) The amount and the kind of selection practised.

THE GENETIC CORRELATION BETWEEN THE BUTTERFAT PERCENTAGE OF THE FIRST AND THE SECOND LACTATIONS.

It has been always assumed that the genes responsible for butterfat percentage during the first lactation are also responsible for the butterfat percentage during the second lactation. No published work has been reported yet to confirm such belief. This assumption has been tested by calculation of the genetic correlation for butterfat percentage for the first and the second lactations from our data.

The following formula developed by Hazel (1943) has been used in our study.

The genetic correlation for fat percentage for the first and the second lactations

$$= \sqrt{\frac{b_3 \quad x \quad b_4}{b_1 \quad x \quad b_2}}$$

where

- $b_1$  = the regression of daughter's fat percentage during the first lactation on the dam's fat percentage during the first lactation.
- $b_2$  = the regression of daughter's fat percentage during the second lactation on the dam's fat percentage during the second lactation.
- $b_3$  = the regression of the daughter's fat percentage during the first lactation on the dam's fat percentage during the second lactation
- $b_4$  = the regression of daughter's fat percentage during the second lactation on the dam's fat percentage during the first lactation.

Table 14 shows the values of the regressions obtained based on 200 daughter-dam comparisons. The genetic correlation between butterfat percentage for the first and the second lactations is therefore 1.018, which can be taken as unity, confirming the belief that the genes which control fat percentage do not change from one lactation to another, more precisely from the first to the second lactation in our analysis.

DISCUSSION - GENERAL

Our investigations dealing with butterfat percentage cover some important items which have a bearing on methods of selecting for butterfat percentage in dairy cattle.

The first part of the work deals with the effect of age at first calving and season of calving on butterfat percentage. Our analysis shows that age at first calving affects butterfat percentage slightly. Cows which calve at older ages give a higher test. The regression of age at first calving on butterfat percentage is so small to be negligible.

Season of calving is responsible for only about 1% of the total variance in butterfat percentage. Therefore, it can be stated that age at first calving and season of calving are of little practical importance in determining the butterfat percentage of different cows, and records of individual animals can be used without any correction for those environmental factors.

Other investigations have shown that the age of the cow does affect butterfat percentage very slightly. The dry period/

period and calving interval have been shown to have a negligible effect on butterfat test. Therefore, it may be concluded that butterfat percentage is hardly affected by environmental factors, and raw butterfat percentage records can be used for investigations without further corrections.

The repeatability of 63% obtained for butterfat percentage based on 2700 lactations indicates that 37% of the total variance is due to variation from lactation to lactation. Our analysis suggests that repeatability of butterfat percentage is a breed characteristic, although the number of lactations for some breeds are too small to verify such a conclusion.

The heritability of butterfat percentage calculated separately for the first and the second lactations were 53% and 82% respectively. Since many workers have shown that butterfat percentage is slightly affected by age, it is reasonable to average these estimates. The value of 63% was found for the heritability of butterfat percentage based upon 630 daughter-dam comparisons using both first and second butterfat percentage records.

Studies of milk yield show that the heritability based on the first lactation records is higher than that based on the second lactation records. This is probably due to the intensive selection of milk yield after the first lactation. However, our results show that the heritability for butterfat percentage based on the second lactation records is higher than that based on the first lactation records. Probably this is due to breeders in this country not taking butterfat percentage into consideration during selection.

The heritability of butterfat percentage is high enough to make selection on the phenotype alone effective in improving this character in dairy cattle. Jersey and Guernsey breeders are strongly advised to select for butterfat percentage, because of the fact that this character is as important as milk yield in such breeds. On the other hand some Friesian herds produce milk which tests below 3%, and selling such milk for human consumption is illegal in many countries. In such herds, using high testing cows and bulls that have been known to transmit high butterfat percentage to their daughters, will raise the butterfat content.

Since/

Since the heritability of a character is high, mating of individuals possessing the greatest development of that character will be the quickest tool for bringing about improvement in such characters; little use being made of information on pedigrees and relatives in planning a breeding programme for improving high heritable characters such as butterfat percentage. On the other hand if the heritability is low, the best breeding plan is to make full use of all information available on the pedigree, collateral relatives and the information can be obtained from progeny testing, in deciding which animals to use for breeding purposes.

Our work has shown that dominance, epistasis and permanent environmental conditions do not play a great role in butterfat percentage inheritance. Because of the close agreement between the values obtained for the repeatability and the heritability of this character it can be concluded that butterfat percentage is controlled mainly by additive genes since the additive genetic variance and variance from one lactation to the next account for all the observed variance. If this result is accepted/

accepted and further workers come to the same conclusion, it would be much easier to estimate the heritability of butterfat percentage from its repeatability. In other words, the correlation between successive lactations will give us a reasonable estimate for the heritable part of variation in butterfat percentage. This will overcome the handicap that in some herds, especially in nonpedigree ones, the number of daughter-dam comparisons available is too small to be of a great value in the estimating of the heritability of butterfat percentage.

If butterfat percentage is controlled mainly by additive genes, breeding for this character will not be difficult, since the part of the variance due to additive genes is transmitted from parents to offspring, while the part of the variance due to dominance and epistasis is not all transmitted. Also, dominance and epistasis hinder the progress that can be achieved by the breeder if he used phenotypic selection only in improving this character in his cattle, because of the fact that such factors mask the genotype of the animal and the breeder is liable to be/

be deceived during the course of selection.

Both the intra-sire regression of daughters and dams and the intra-sire correlation between daughters and dams were tried in estimating the heritability of butterfat percentage, and the two methods gave more or less the same result. This may be explained by the fact that selection for butterfat percentage is not practised in the herds analysed and therefore the dams are not actually a highly selected group compared to their daughters as far as butterfat percentage is concerned.

The heritability of the average of the first and the second butterfat percentage records comes very near to the heritability based on both records added together.

The phenotypic and the genetic correlation between butterfat percentage and milk yield are of great importance in dairy cattle breeding. Our investigations show that there is a small negative genetic and phenotypic correlation between the two characters, ( $-.20$  for the former and  $-.21$  for the latter).

The

The individual or the physiological correlation is displayed very clearly during the course of the lactation period, where the fat content of the milk varies inversely to the rate of milk yield. The fat percentage is lowest at a point of the lactation period where the rate of milk secretion attains its maximum, and thereafter it is gradually increasing with diminishing yield towards the end of lactation.

We are interested in the correlation between cows in regard to lactation yield and butterfat percentage, because these two characters form the basis of selection of breeding animals. Our data has shown that the correlation between cows is higher than the correlation within cows and both of them are negative being  $-.362$  for the former and  $-.174$  for the latter.

The genetic correlation between the two characters is a very important item in selecting simultaneously for the two characters. If the breeder knows the value of this correlation he will be in a better position to predict how butterfat percentage will be affected when he selects for milk yield, or vice versa.

The negative genetic correlation which has been found between milk yield and butterfat percentage, indicates that some of the genes responsible for milk yield are not responsible for butterfat percentage, and consequently selecting for one character will result in selection against the other character. However, the negative genetic correlation that exists between the two characters is too small to affect butterfat percentage greatly when we select for milk yield alone.

The genetic correlation for the first lactation fat percentage and the second lactation fat percentage has been found to be unity, showing that the genotypic value of the character does not change from lactation to lactation. Therefore, selection for butterfat percentage based on the first lactation is as effective as selection based on the second lactation records. Furthermore, fat percentage is very slightly affected by age, and therefore, selection for this character should be based on the cow's first record.

SUMMARY AND CONCLUSIONS.

A statistical analysis has been undertaken on the records of 10 herds from 5 different breeds of dairy cattle, namely, Kerry, Dairy Shorthorn, Friesian, Jersey and Guernsey. About 85 cows were involved in our investigations.

The main purposes of this study were to determine the relative importance of heredity and environment on the variation of butterfat percentage, to study the relationship between milk yield and butterfat percentage and to know how genes responsible for butterfat percentage operate from one lactation to another.

Our investigations have led to the following

conclusions :-

1. The month of calving and the age at first calving have a small effect on butterfat percentage. Month of calving is responsible for about 1% of the variance in butterfat percentage. Heifers which calve at an older age give a higher fat percentage than those which calve at the average or below the average age.

2./

2. Since age of the cow, the dry period and the calving interval have a negligible effect on butterfat percentage, and our work has shown that age at first calving and month of calving does affect butterfat percentage slightly, raw butterfat percentage records can be used without any conversion factors for those environmental causes.

3. The repeatability of butterfat percentage accounts for 63% of the total variance, while the change in environment from lactation to lactation is responsible for the rest. Our estimate for the repeatability of  $.633 \pm .020$  for fat percentage was based upon 2700 lactations.

4. The heritability of the butterfat percentage in our data proved to be  $.526 \pm .110$ ,  $.818 \pm .126$  and  $.630 \pm .046$  for the first butterfat percentage records, the second butterfat percentage records and for the first and the second records added together respectively. These estimates were based upon 434, 247, and 681 daughter-dam comparisons respectively.

5. The heritability estimate based on the second butterfat percentage record is higher than that based on the first records, which/

which does not agree with the reports on the inheritance of milk yield.

6. The heritability of the average for the first and the second percentage record comes to  $.686 \pm .142$  based upon 196 daughter-dam comparisons. This estimate comes very close to  $.630$  which was obtained when the first two records were grouped together.

7. Our analyses have shown that there is a close agreement between the two estimates obtained for the heritability and the repeatability of butterfat percentage, which indicates that this character is controlled mainly by additive genes.

8. Since the heritability of butterfat percentage is high and the character is controlled mainly by additive genes, phenotypic selection is a satisfactory method for selection, little use being made of progeny testing.

9. The phenotypic correlation between milk yield and butterfat percentage based upon about 3,000 lactations was found to be  $-.21 \pm .010$ . The correlation between cows and the correlation within cows were found to be  $-.362$  and  $-.174$  respectively./

respectively.

10. The genetic correlation between milk yield and butterfat percentage was found to be  $-.200$ . Our estimate was based upon 492 daughter-dam comparisons. This means that about 20% of the genes responsible for fat percentage are also responsible for milk yield.

11. We have found that the genetic correlation for the first lactation butterfat percentage and the second lactation butterfat percentage is unity. Such conclusion indicates that butterfat percentage is controlled by the same set of genes from one lactation to another. It also shows that selection for butterfat percentage based on the first lactation record is as effective as selection based on the second lactation record.

12. Our calculations have shown that selection for milk yield alone does affect butterfat percentage slightly. This is due to the fact that the genetic correlation between butterfat percentage and milk yield, although negative, is small. The maximum possible gain is approximately 1% of the average fat percentage per year, when selection for butterfat content is practised in closed herds.

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THE AMOUNT OF INBREEDING IN THE SHORTHORN AND THE FRIESIAN  
BREEDS IN GREAT BRITAIN.

INTRODUCTION AND PURPOSE OF THE STUDY

The centre of early Shorthorn breeding and improvement was in the fertile valley of the River Tees. Credit for the first improvements is held by the Collings brothers who followed the system of inbreeding and selection used early in the 17th century by Bakewell for improvement of Longhorn cattle. The Collings brothers were followed by Thomas Bates of Kirklemington and Thomas Booth of Killerby. The last outstanding step in the Shorthorn history was made by Amos Cruickshank of Sattytons in Aberdeenshire who also used inbreeding and selection to develop and improve the Scottish Shorthorn.

The Friesian breed was originally developed in two provinces of Holland, namely - North Holland and Friesland. During the latter half of the last century large numbers of black and white Dutch cattle, both Friesians and closely related types, reached Britain. The British breed society was started in 1909 and the first herd book issued in 1912. Importations took place from Holland in 1914 and 1936, from South Africa in 1922 and more recently/

recently from Canada.

This study was undertaken to find how much inbreeding per generation occurred in the Dairy Shorthorn and the Friesian breeds of Great Britain in present breeding practice.

As the names of the highest producing animals are available from the Milk Marketing Board reports, it is interesting to compare their degree of inbreeding to the average for the breeds. The lengths of generation for the two breeds have been calculated and also the relationship of important individual animals to the breed as a whole and to high producing cows.

REVIEW OF LITERATURE

Wright (1922-23) was the first investigator to develop a general method for measurement of the amount of inbreeding and the relationship, which could be applied to livestock pedigrees. Wright and McPhee(1925) (a) gave a short method for calculating the coefficient of inbreeding and relationship by which it was possible to analyse genetically the importance of inbreeding and of particular animals in our pure breeds of livestock. Wright (1923) studied the Duchess family of Shorthorns and concluded that Bates kept his herd highly related to "Favourite" one of the most important bulls of the breed. This family was highly inbred, the coefficient of inbreeding being around 40%. McPhee and Wright (1925) (b) found that the average coefficient of inbreeding for the Shorthorn breed in Britain was 26% in 1920. They showed that the average relationship of the breed to "Favourite" and to "Champion of England" in 1920 was 55.2% and 45.5% respectively.

McPhee and Wright (1925) (b) have concluded the American prize winning sires do not form a specialised group within the Shorthorn breed. McPhee and Wright (1926) found that the inbreeding of/

inbreeding of 100 of the high producing British Dairy Shorthorn cows was 26.9% compared with 23% for the random sample. They pointed out that the British Dairy Shorthorn do not appear to be a genetically distinct sub-group within the Shorthorn breed.

Lush et al (1936) studied the genetic history of the Holstein-Friesian cattle in the United States and concluded that .47% of the heterozygosity existing in the foundation stock has been lost per generation in the ten generations from 1881 to 1928. Only the cow "Dekale II" influenced the breed to any extent.

Willhem (1927) found that the inbreeding coefficient for the Hereford breed in the United States rose to 8.1% in 12.9 generations. The average relationship of the breed to "Anxiety IV" in 1930 was 18.5%. He has reported that the prize-winning animals were more related to "Anxiety IV" than the average of the breed. Yader and Lush (1937) have shown that no one animal dominated the Brown Swiss breed in the United States. The amount of inbreeding per generation in this breed was .5%.

Stonaker (1943) reported that inbreeding in the

Aberdeen- /

Aberdeen-Angus breed in the United States rose .30% per generation during the period 1900 to 1939, and the average relationship of the breed to the bull "Black Prince of Tillyfour" was 24% in 1939.

Fowler (1932) found the amount of inbreeding in the Ayrshire breed in Scotland for the period 1877-1927 to be 8.3% in 1927. Comparing bulls with cows, he found no difference between them in the degree of inbreeding. He pointed out that high milk yielding cows showed markedly lower inbreeding than the breed average, while cows producing 1000 gallons of milk per lactation showed no difference from the breed average.

Smith (1928) reported that the average inbreeding for Jersey cattle in Britain was 3.9% in 1925. Comparing the high producing cows with the average of the breed, he found that the inbreeding was only 1.8% in the former group.

Brokelbank and Winters (1931) found that the average coefficient of inbreeding for the Shorthorn show-winners was 2.06%, while that of random selected individual was 1.03%. Asdell (1945) in the Guernsey and the Friesian found no difference between the highest producing cows and a random sample as far as the amount of inbreeding is concerned.

Shrode and Lush (1947) reviewing the whole subject have mentioned that the Telemark registered bulls born in Norway from 1898 to 1921 were studied by Brege. During that time the average inbreeding rose from less than 1% to over 7%.

The average interval between generations for cattle was reported by most of the investigators above. It was usually between 4 - 5 years.

SOURCES OF DATA

Two groups of cows (1000 Shorthorns and 1050 Friesians) have been chosen at random from 1943 and 1945 herd books respectively. This data has been used previously to estimate the amount of movement of these breeds in Britain. Similarly a hundred bulls of each breed have been selected at random from the same herd books. The high producing pedigree Friesian and Shorthorn cows are taken from the Milk Marketing Board Report for 1946. The first 50 Friesian cows and the first 40 Shorthorn cows have been included in this study. The pedigree of the 1000 Shorthorn and 1050 Friesian cows have been tabulated for two generations. Out of these two samples a hundred animals were chosen at random and their pedigrees were traced for four generations. The bulls and the high producing cows were treated in the same manner, i.e. their pedigrees for four generations were tabulated.

Wright's formula (1922) has been used to calculate the coefficient of inbreeding and the coefficient of relationship.

The/

The interval between generations was calculated using

200 bulls and 200 cows of each breed.

Tables 3 and 4 represent the average interval between generations for the Shorthorn and the Friesian breeds respectively.

TABLE 3.

Interval between generations for the Shorthorn breed.

Average age of dams at the birth of registered males	5.88 years
" " " " " "	
registered females	5.86 "
Average age of sires at the birth of registered males	3.26 "
" " " " " "	
registered females	3.96 "
Average interval between generations	4.74 "

TABLE 4.

Interval between generations for the Friesian breed.

Average age of dams at the birth of registered males	5.76 years
" " " " " "	
registered females	5.38 "
Average age of sires at the birth of registered males	3.78 "
" " " " " "	
registered females	3.41 "
Average interval between generations	4.58 "

Tables 1 and 2 show that about .3% to .4% of the heterozygosity existing in the foundation animals for the Shorthorn and the Friesian breeds is lost per generation. This result was obtained when the pedigrees of the animals were traced back for only two generations. The difference between the two breeds in the amount of inbreeding is not significant.

Out of 26 inbred Friesian cows in the first group, 25 were produced by half-sibs mating, while one animal was produced by sire-daughter mating. Similarly of the 30 inbred Shorthorns in the first group 29 were by half-sib matings and one by sire-daughter.

When the sub-sample of 100 cows for each breed were traced back for 4 generations, the average coefficient of inbreeding per generation was found to be .2% for both the Shorthorns and the Friesians. Tables 1 and 2 show that the Shorthorn bulls are less inbred than the cows while the reverse holds for the Friesian breed. However, such comparison should be based within herds/

herds. The high producing cows in the two breeds show higher coefficients of inbreeding per generation than the random samples of females. The difference being significant in the Friesian breed.

No animal appeared sufficiently frequently in the four generations studied for it to have an outstanding influence on the Shorthorn breed. The bull "Terling Marthus" (21533) who had been imported from South Africa in 1922 appears more frequently than any other animal in the pedigrees studied. The relationships of this bull to the groups of cows, bulls and high producing animals studied are given in Table 2.

DISCUSSION

Wright's coefficient of inbreeding expresses the amount of heterozygosity being lost as compared with the amount existing in the foundation stock. The coefficient of relationship measures likeness to be expected between the genotypes of animals concerned. The Shorthorn breed has been thoroughly analysed by Wright and McPhee. The amount of inbreeding per generation they found for the period ending in 1920 was .27% per generation. Our analysis covered the last four generations and the amount of inbreeding per generation was found to be .2 to .4% which is very near to their estimate. It seems that the mating system, or the method of breeding of the Shorthorn breed in this country has not changed very much during the last twenty years.

Wright (1931) devised a formula by which it is possible to estimate the effective number of males in a limited population in which there are far fewer breeding males than females, and in which all of the sires have equal chances to leave offspring. In such a population the inbreeding will rise, and/

and about  $1/8M$  of the remaining heterozygosis is lost per generation, where  $M$  is the number of males being used for breeding.

Applying this formula to our results shown in Tables 1 and 2 gives the number of males used for breeding as 41 in the Shorthorn breed and 31 in the Friesian breed. Such numbers are small compared with the numbers which have actually been used in the two breeds. The smaller effective number may be attributed to the fact that there is a tendency in every breed to separate into distinct families, and there is always an amount of selection for or against certain animals or their progeny.

It has been observed in analysing the pedigrees of the Shorthorn animals, that there are no animals which dominate the breed during the period studied. This may be due to the fact, that such imported animals always appear in the formative period of each breed, when it is very possible for an individual with the high reputation to dominate the breed. The Shorthorn breed is now well established, and it is not surprising to find that there are no predominant animals in the period of our analysis.

It has been found that the amount of inbreeding per generation/

generation for the high producing cows both in the Shorthorn or in the Friesian is higher than the rest of the breed. In the Friesian breed about 20% of the high producers came from the Manningford Herd and 10% came from the Elmwood Herd, both essentially of the same breeding, while in the Shorthorn breed 45% of the high producing cows came from three herds namely, the Iford Herd, the Winton Herd and the Kentish Herd. Since special herds contributed a higher percentage of high producing animals than other herds, a test of significance of difference in the amount of inbreeding between the high producing animals and the rest of the breed is not justifiable.

It may be concluded that inbreeding does not have any detrimental effect on the milking ability of the animals. Of course, this holds true only to a certain level of inbreeding, after which inbreeding will cause a decrease in milk production. The amount of inbreeding recorded by different workers who have studied high producing animals or show-winners, is too small to affect the productive ability. Such problems should be studied by conducting long-time experiments.

Although the figures obtained for the Shorthorn females do not differ significantly from those obtained for the Friesian females, yet the Friesian breed in Great Britain is in a quite different position to the Shorthorn. The Shorthorn breed has been well-established and is at present probably declining while the Friesian breed is still expanding. Moreover, the importation of Friesian animals from Holland and South Africa has affected the breed genetically and of course this type of breeding affects the amount of inbreeding in the breed.

The bull "Terling Marthus" (21533) is one of the most important bulls in the Friesian breed in Great Britain. This bull born in 1921 and imported from South Africa in 1922, was used for 15 years in the Terling and Manningford herds. It has been estimated that this bull has 166 registered daughters and 59 registered sons in the Terling herd alone. Odium (1947) has mentioned that "Terling Marthus" has 55 R.M. daughters and 11 R.M. sons in the Manningford herd.

Table 2 shows the relationship of the breed to "Terling Marthus". The total relationship of the breed to an animal depends/

depends upon the animal's coefficient of inbreeding, the number of sons and daughters the animal leaves and its collateral relationship to the breed through other descendants. The higher relationship of the high producing cows to "Terling Marthus" may be due to the fact that this bull has been used very extensively in the Manningford and Terling herds, which are the leading Friesian herds in England, and which play a great role as a source of replacement in the Friesian breed. It can be stated that the blood of this bull through himself and his offspring has undoubtedly become more widely distributed in the expanding breed and that it influences the breed to a greater extent than that of any other individual.

It is intended to use Wright's short method in studying the genetic history of the Friesian breed in Great Britain. This should yield valuable information upon the amount of inbreeding in the breed during different periods, upon the amount of interse relationship and the influence of important animals and herds on the breed.

The/

The average length of time from one generation to the next is a matter of considerable interest since (1) it will enter into the breeder's plan of what he can accomplish if he undertakes deliberately to perpetuate the influence of some noted animals by some system of line breeding; (2) it is useful in estimating what has been accomplished in the past by the breeding systems actually followed; (3) the replacement rate depends upon the length of generation. The average length between generations was found to be 4.74 years for the Shorthorn breed and 4.58 years for the Friesian breed.

The average length between generations depends upon the age at first calving, the interval between calving and the age of animals used for breeding purposes. Lush (1945) has reported that the mean generation interval in dairy cattle runs between  $4-4\frac{1}{2}$  years. Rendel and Robertson (1949) have obtained a value of 4.6 and 4.7 years for the generation length for the Friesian and the Shorthorn breeds respectively, which agrees with our finding. The same authors have reported the estimate of 3.4 years for one of the biggest Kerry herds in Great Britain which is exceptionally/

exceptionally short.

Tables 3 and 4 show that the average age of sires at the birth of registered males is 3.26 years for the Shorthorn, while it is 3.78 for the Friesian breed. This is probably due to the fact that progeny testing is practised more in the Friesian breed. This also might be due to the extensive use of imported males and keeping pure imported bulls as long as they are serviceable. The Milk Marketing Board Report 1947 shows that the average age at first calving is higher for the Shorthorn breed than that for the Friesian breed. This may be responsible for the higher estimate obtained for the Shorthorn breed.

SUMMARY AND CONCLUSIONS

The amount of inbreeding per generation in the Shorthorn and the Friesian breeds in Great Britain was studied for the last four generations starting in 1945 for the Shorthorn and 1943 for the Friesian breed. Cows, bulls and high producing cows were included.

The amount of inbreeding per generation was estimated to be .20, .14 and .29% for cows, bulls and high-producing animals in the Shorthorn breed respectively. For the Friesian breed the following values were obtained given in the same order as the Shorthorn, .20, .35 and .38%. These results were obtained when the pedigrees of the animals were traced back for four generations. When the pedigrees of 1,000 Shorthorn cows and 1,050 Friesian cows were traced back for two generations, the amount of inbreeding per generation was found to be .40 and .32% for the Shorthorn and the Friesian breed respectively.

No individual animals were found to predominate in the Shorthorn breed during the period studied. The bull "Terling Marthus"/

Marthus" (21533) influenced the Friesian breed in Great Britain more than any other individual. This bull was imported from South Africa in 1922. The relationship of bulls, cows and high producing cows to this bull is 3.50, 3.75 and 9.25% respectively.

The average length between generations was found to be 4.74 years for the Shorthorn breed and 4.58 years for the Friesian breed.

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University of Edinburgh

31<sup>st</sup> October 1949

TRANSMISSION OF THESIS

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for examination, a thesis by A. A. Saks

submitted for the Degree of Ph.D.

Please sign this form and return it (postage 1d.)  
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**III. THE MOVEMENT OF TWO BREEDS OF PEDIGREE DAIRY  
CATTLE IN GREAT BRITAIN.**

Published as a joint paper

with

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INTRODUCTION AND PURPOSE OF STUDY

There is a considerable regional variation in the annual milk yield per cow in the various parts of Great Britain. Very roughly, the centre of high yield and low butterfat percentage is in the south-east, with a decrease in yield and an increase in fat percentage westwards and to a smaller extent northwards. This point was raised by Edwards (1946) when he pointed out that the milk yield in Lancashire for Friesians and Shorthorns was only 75 per cent of the yield of the same breed in Essex. The general picture for the whole of England and Wales is given in Fig.1 which shows the average 305-day yield and fat percentage for Friesians and Shorthorns in the different Milk Marketing Board Regions. These figures, of course, refer to all animals of the breed type in the region. In addition, there is given the percentage of all milk-selling cows which are recorded in that region.

Edwards also suggested that the difference in yields might be related to the general level of the dairy industry in/  
in/

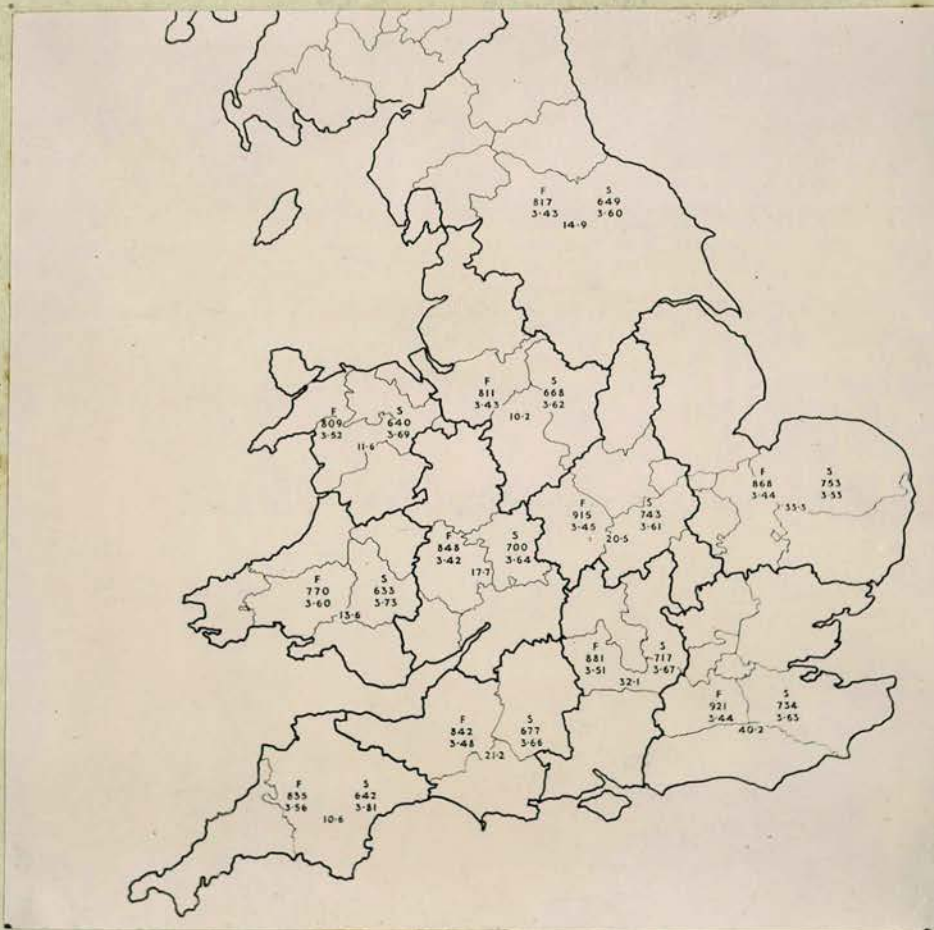
in the two counties concerned. The density of cattle is very much higher in Lancashire and there is also a smaller supply of home-grown foodstuffs, such as beans and sugar-beet tops, than in Essex. In addition, it is probable that Lancashire farmers deliberately rely more on grass and hay, whereas on the east coast pasture conditions are not so good and more expensive foodstuffs must be fed. This paper is an attempt to discover to what extent any regional adaptation could be possible within the breeds. If the amount of movement of breeding stock is small, then there is a high probability that selection under the different climatic and feeding conditions could set up local genetic isolation. However, the results show that the flux of genes is so great as to even out, with few exceptions, any regional genetic differences there may be and to render very unlikely the formation of any new adapted sub-breeds.

It has been suggested that some of the regional variation may be due to differences in the level of recording. As willingness to record is presumably connected with good management/

management, it would be expected that within any given region the higher percentage of herds recorded the lower the average yield. If the percentage recorded is low, only the cream of the herds will be measured, and as more herds are recorded, the general level of those recorded will drop. However, reference to Fig.1 shows that the low yielding regions are also those with a low percentage recorded. This can only mean that the true average yield will show a greater variation than is apparent from the above figures.

#### Measurement of migration -

For each breed, about ten districts of the country were chosen, generally of the size of one or two counties. They were chosen as far as possible to have roughly the same total pedigree population of the breed under consideration. Owing to the different geographical distribution of the two breeds, slightly different counties had to be chosen in the two cases. Then the last available herd-books were taken (1943 for Friesian and



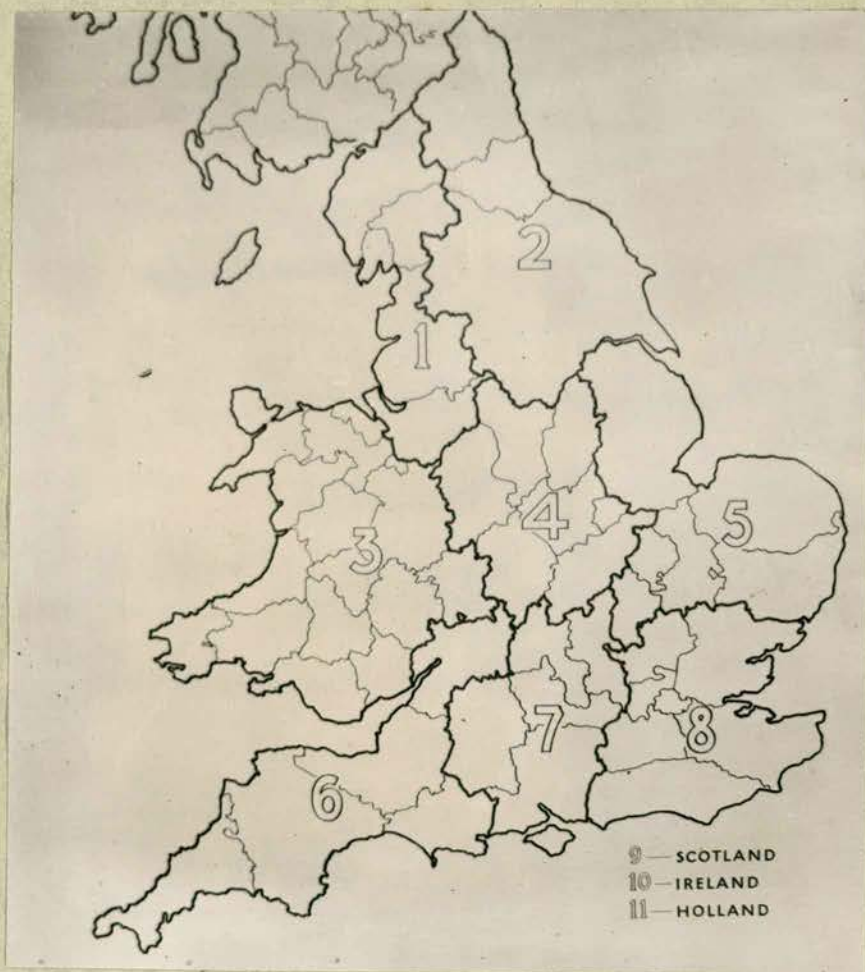
**Fig.1.** 305-day yield and fat percentage for Friesians and Shorthorns and the percentage of all milk-selling cows recorded, for the Milk Marketing Board regions.

1945 for Shorthorn) and a list made of the female entries in each 'county'. Then 100 females were taken at random from each 'county' and their pedigrees traced back for two generations. The county of birth of the various ancestors was then noted. (The male entries were excluded since the breeder's decision to enter would, in that case, be more likely to depend on the pedigree of the animal.)

For the purpose of classifying the origin of the ancestors, England and Wales were divided into eight areas, as shown in Fig.2. In addition, ancestors were found coming from Holland, Ireland and Scotland. The only main difference in the method used in the two breeds was that sample counties were taken from Scotland for Friesians and not for Shorthorns, as it was considered that the majority of Scottish Shorthorns would be of the beef type.

### Results

If 22 of the animals born in Cumberland had sires born outside the county, then we will say that the 'replacement index' for/



**Fig.E.** Classification areas for place of birth of ancestors.

for sires is 22 per cent. If we average the indices for sire and dam we get the genetic replacement, that is, the fraction of genes brought in from outside during one generation. The results for the two breeds are given in Tables I and 2.

In addition, the number of animals whose sires were born in the same herd as themselves was determined. It was 17 per cent. for the Shorthorns and 21 per cent for the Friesians.

In considering the detailed origin of the ancestors, we can proceed slightly differently. We can find the total contribution of sires by an area to the total number of sires in the sample, but that would bias in the case of those areas containing two sample counties. This can be avoided by considering only half the animals from those areas with two counties. We can thus find the relative contributions of the different areas to the total sample. The results are given in Tables 3 and 4.

Figures above 100 for areas from which samples were taken (1-8 in Shorthorns, 1-9 in Friesians) show that these areas are contributing more than would be expected. In fact, there is a regular flow of genes from the sample areas whose contributions

**TABLE 1. - 'County' Replacement in the Shorthorn Breed**

County	Sire	Den	P.g.S.	P.g.D.	M.g.S.	M.g.D.
Cumberland	22	4	30	18	13	9
Northumberland and Durham	63	20	84	73	64	33
Lancashire	9	13	24	24	23	14
Shropshire and Hereford- shire	78	30	95	84	81	51
Norfolk and Suffolk	50	18	82	57	77	32
Warwick	70	26	79	78	67	39
Garnarthen	50	9	66	59	53	18
Somerset	49	21	60	47	54	34
Wiltshire and Hampshire	64	18	79	65	56	32
Kent	43	21	54	62	57	29
<b>Average</b>	<b>50.3</b>	<b>18.0</b>	<b>65.3</b>	<b>56.7</b>	<b>54.5</b>	<b>29.1</b>

**TABLE 2. - 'County Replacement in the Friesian Breed**

County	Sire	Dam	P.g.S.	P.g.D.	M.g.S.	M.g.D.
Aberdeen, Fife and Kincardine	64	24	82	63	63	37
Ayr and Renfrew	54	19	69	60	64	26
All Scotland	20	0	50	21	21	3
Cumberland	62	54	94	72	80	60
Northumberland and Durham	54	25	87	65	49	42
Lancashire	59	19	83	59	59	38
Shropshire and Herefordshire	73	33	88	88	80	46
Norfolk and Suffolk	71	21	89	75	66	39
Warwickshire and Leicestershire	54	31	81	72	65	55
Garnarthen	71	43	93	90	81	54
Somerset	54	21	82	64	51	39
Wiltshire and Hampshire	57	32	71	66	48	35
Essex	34	10	52	42	34	21
Average	55.3	28.9	79.0	64.9	57.6	38.3

Note to Tables : P.g.S. = Paternal Grand Sire, &c.

TABLE 3. - Shorthorns

Contribution of the Areas to the Total Sample (800)

Area	1	2	3	4	5	6	7	8	9	10
Ancestor:										
Sire	202	53	57	74	69	87	109	113	33	1
Dam	154	89	93	87	88	94	106	100	7	0
Total parental	168	71	77	80	78	91	107	106	20	1
P.g.S.	229	31	30	92	54	93	107	125	30	6
P.g.D.	217	44	48	67	64	84	126	95	27	4
M.g.S.	216	61	45	82	51	95	125	91	24	10
M.g.D.	165	81	80	79	79	85	115	101	12	4
Total grandparental	207	54	51	80	62	89	118	103	23	6

TABLE 4. - Friesians

Contribution of the Areas to the Total Sample (900)

Area	1	2	3	4	5	6	7	8	9	11
Ancestor:										
Sire	97	110	48	96	50	69	59	183	173	15
Dam	105	84	68	87	93	107	84	119	149	7
Total parental	101	97	58	91	71	88	71	150	161	11
P.g.S.	49	63	24	53	30	28	36	246	108	263
P.g.D.	79	79	45	89	52	83	90	146	178	58
M.g.S.	85	95	37	75	54	67	63	185	193	54
M.g.D.	89	68	69	71	89	96	102	126	179	12
Total grandparental	79	76	44	72	56	68	73	176	160	97

are more than 100 to those whose contributions are below 100.

Tables 5 and 6 show the county contributions of males to different areas for the Shorthorn and the Friesian breeds respectively.

### Discussion

The figures reveal a very considerable amount of migration from area to area. As might be expected, the migration is larger among bulls than cows, between two-thirds and three-quarters of the total migration being due to the former. The overall figures for the breeds would seem to show more movement of breeding stock in Friesians than in Shorthorns, more particularly amongst the cows. The general level of migration is very high with the exception of areas like Cumberland and Lancashire for Shorthorns, and Essex and Scotland for the Friesians. In Shorthorns, for instance, the lowest genetic replacement per generation (with the exception of the above two counties) is 35 per cent. This would mean that in 4 generations (16-20 years) at least 87 per cent of the genes in an area will/

TABLE 5. - County 'contributions' to different Areas (Shorthorn - sires)

Area County	1	2	3	4	5	6	7	8	9	10
Cumberland (1)	78	6	2	2	0	1	2	5	5	1
Lancashire (1)	91	2	0	2	1	0	1	2	0	1
Northumberland and Durham (2)	46	37	0	3	0	0	1	1	12	0
Shropshire and Hereford (3)	18	6	22	11	2	12	20	6	3	0
Warwick (4)	22	0	6	30	8	7	14	13	0	0
Norfolk and Suffolk (5)	10	0	1	16	50	6	6	6	3	0
Somerset (6)	7	2	6	9	0	51	23	2	0	0
Wiltshire and Hampshire (7)	7	2	4	3	10	10	36	28	0	0
Kent (8)	11	4	3	3	0	2	12	52	13	0
Carmarthen (3)	10	3	50	6	3	5	12	8	3	0
Average %	16.3	2.7	2.8	6.1	2.6	5	10	7.7	4.3	0.2

TABLE 6. - County 'contributions' to different Areas (Friesian - Sires)

Area	1	2	3	4	5	6	7	8	9	11
County										
Cumberland and Westmorland (1)	19	7	0	1	0	0	0	3	20	0
Northumberland and Durham (2)	3	46	0	4	0	0	0	11	32	4
Garmarthen (3)	6	6	29	7	5	3	5	22	16	1
Lancashire (1)	51	14	3	8	0	0	0	6	17	1
Norfolk and Suffolk (5)	3	11	2	8	29	1	1	35	8	2
Warwick (4)	10	16	4	46	3	7	2	3	6	3
Somerset (6)	3	2	3	8	0	46	8	26	4	0
Wiltshire and Hampshire (7)	4	1	3	4	8	12	43	17	7	1
Essex (8)	7	5	5	3	5	1	0	66	8	0
Scotland (9)	1	5	0	6	1	0	2	5	80	0
Shropshire and Hereford (3)	24	15	27	11	2	0	1	6	7	8
Average %	6.7	8.2	2.2	6.0	2.4	2.4	1.9	13.4	12.5	2.0

will be of outside origin. It is difficult to believe that any local differentiation could persist against this migration pressure, or that any selection pressure could be sufficiently large as to set up new differentiation. This is not to deny any herd differences within the districts but to show that, in the main, the districts themselves are not likely to form genetically distinct units. As far as concerns the sources of genes and breeding stock, as might be expected, those areas with low replacement indices themselves are the ones which contribute most to the rest of the country. Thus, in the Shorthorns, the north-west contributes 16 per cent. of the bulls used elsewhere and 25 per cent. of the bulls used in the whole country. The only two other areas which are sources of genes are the central southern and south-eastern areas. Most of the bulls from the north-west actually come from Cumberland and Westmorland which, oddly enough, have one of the lowest average yields of any part of England and Wales. The breeders there are, of course, well known for their dual-purpose type of animal.

In the Friesians the two main sources in the parental generation are Essex and Scotland, with the northern areas of England just holding their own. Scotland has a greater influence than Essex, the influence of the former being mainly due to the Douneside and Dennistoun herds, and of the latter mainly to the Rayleigh herds. In the grandparental contribution there is a very large part played by sires imported from Holland. These would have for the most part been from the 1936 importation, which consisted of 47 bulls and 48 cows. In fact, in 1943, these animals had contributed over 10 per cent of the total genes in the breed. The use of the sons of these bulls has caused an under-representation of home-bred bulls amongst the paternal grandsires. This seems in particular to have affected the bulls drawn from Scotland, since the grandsire contribution is less than would be expected from that of the sires.

In general the results suggest that there is very little genetic isolation within these pedigree breeds, with the possible exception of the north-west of England for Shorthorns.

Here, however, the isolation is only in the sense that there are few replacements. However, in fact, the influence of the area on the breed is fairly high so that, to some extent, the other parts of the country must be becoming genetically similar to the north-west, because they are continually using bulls from that area. The case of the Friesian breed is somewhat different from that of the Shorthorn, since this is a breed which is still expanding. Here, instead of genetic differences existing and being slowly evened out, any local differentiation would have to build itself up against the great levelling effect of migration.

It may be argued that the figures of the Milk Marketing Board (1947) refer to pedigree and non-pedigree cattle and that the above approach applies to the former only. The latter will actually be sired mostly by local bulls themselves drawn from the pedigree herds, so that the levelling process is somewhat slower. However, the fact that the same pattern of regional variation in yield is also shown by the Channel Island breeds, in which pedigree/

pedigree cattle are the rule, is additional evidence to suggest that the regional differences are mainly environmental. If, in fact, the gradient in yield and butterfat is assumed to be due to environment and not breeding, any systems of genetic evaluation on absolute yield would tend to penalise unduly those breeders on the west coast. However, the fact that the north-west of England, with a very low yield, contributes so many sires, suggests that this cannot play a very large role in Shorthorns.

From the long-term view of breed improvement, the tendency of the breeds as a whole to operate as breeding units is probably not advantageous. Wright (1939) has suggested that probably the best type of breed structure is one in which the breed is split into several semi-isolated sub-groups, which cuts down the chance of the loss of rare genes, possibly advantageous in the future, by chance fixation. In addition, it allows of much greater adaptation to local conditions.

The results here presented have suggested strongly that there is at the present moment little local differentiation in these

two breeds. It is proposed shortly to attack the problem in a more direct manner by considering the actual milk yields of daughters of, say, Cumberland bulls used in different counties, and so on. This will enable a direct check on the relative genetic levels in the different areas to be made.

#### Summary

An investigation has been made by a sampling method of the magnitude of the migration of breeding animals in Friesians and Shorthorns. The movement is of such a magnitude as to preclude the possibility of the existence of much local genetic differentiation, except for the north-west of England in Shorthorns, and Scotland and the region around Essex for Friesians. Apart from these areas, approximately 35-40 per cent. of the genes in any area of county size are replaced in each generation.

Approximately 20 per cent. of the females in these breeds are sired by animals born in the same herd as themselves.

The north-west of England is the main centre of movement of Shorthorns, with the southern counties also contributing a

fair/

fair proportion. Essex and Scotland are the main contributing centres for Friesians, although Holland contributes a high proportion of the grandparents. Approximately 10 per cent of the genes carried by animals born in the Friesian breed in 1943 come from the 1936 importation.

This finding suggests that the greater part of the geographical variation of milk yield and butter-fat in England and Wales is due to differences in climate, soil, feeding and management.

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