STUDIES IN HERD ANALYSIS

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for the Degree of Doctor of Philosophy
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by

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Ayr

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To the assistants in the Animal Husbandry Section of the Hannah Institute who helped me so conscientiously with the innumerable calculations, I tender my sincere thanks.

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Part I

Introduction

"We have usually no knowledge that any one factor will exert its effects independently of all others that can be varied, or that its effects are particularly simply related to variations in these other factors..........

"If the investigator, in these circumstances, confines his attention to any single factor, we may infer either that he is the unfortunate victim of a doctrinaire theory as to how experimentation should proceed, or that the time, material or equipment at his disposal is too limited to allow him to give attention to more than one narrow aspect of his problem."

The need to remember these words of R.A. Fisher has been repeatedly emphasised in the realm of animal breeding by the voluminous literature on lactation studies which have often dealt only with particular aspects of the entire problem. It has not always been realised that the reactions of the dairy cow to such environmental factors as month of calving, length of calving intervals and age at calving, may not be as straightforward as it would appear at first sight. The inter-relations among these factors themselves may be so complex that any attempt at studies in herd analysis without adequate allowance for such complexities would be beset with numerous pitfalls, and might lead to faulty conclusions. The present thesis is therefore devoted in part to a study of the environmental factors influencing dairy cattle production, and their inter-relationships.

It is well recognised that the performance of a dairy cow is influenced not only by environmental factors but also by her hereditary potentialities for production. When one wishes to improve the productive level of a herd or breed of dairy cattle, it is important to know how great a change can be brought about from one generation to another by constructive breeding. Only a selection based on genetically caused differences between individuals will be of any lasting value through an improvement in the heritable qualities of the following generation. An accurate evaluation of the genetic and environmental causes of variation is therefore of fundamental importance to any progressive policy of cattle breeding.

Different lines of approach have been recommended by various investigators as being most likely to prove fruitful in relation to this problem. The method of explaining the variation in dairy cattle performance by assigning gene symbols to the animals according to their level of production, has been attempted by several workers - notably Wilson (1911, 1925) and von Patow (1925, 1930). Even as late as 1934, Kronacher emphasised that the task of animal breeding would be very much easier if research were conducted along similar lines with a view to obtaining the Mendelian list of genes involved and their dominance and linkage relations. Fascinating as this suggestion to have a complete scientific knowledge of the genetic make-up of a dairy cow may appear, its impracticability has been discussed by Lush (1936) in his review of Kronacher's work where he says, "How would the author (Prof: Kronacher) and those who hold similar views advise the breeder to proceed even if he had perfect knowledge of the genes and their inter-relations but if there were 10 or 20 or more pairs of genes affecting each important characteristic? In short, the reviewer would like to see this reasoning extended to n genes to see whether such knowledge about the individual genes would after all be very useful, since in their segregations and recombinations the genes would be obeying the laws of Mendelism which automatically result in an offspring population which is distributed nearly like the square of the ratio among the gametes from its parents. That gametic ratio is something like a binomial raised to the n^{th} power. From this it seems to follow that as soon as we embark on a breeding programme dealing with anything except characters inherited in a simple manner, such as colour, the problem becomes too complex to keep track of single genes." It is clear that if Lush's analysis is accepted, little progress may be expected from this method of study.

A second method of approach lies in the region of planned experimentation, involving the experimental control of all environmental factors affecting production. The number of non-genetic causes of variation is however so great, and some which belong to the realm of the internal physiological environment are so much beyond the control of the experimenter, that complete environmental control does not seem feasible. In recent years, identical-twin research, particularly in Sweden and New Zealand, has opened up new possibilities, whereby pairs of cows with an identical genetic complex could be subjected to various environmental factors in order to study their respective responses. Though extremely valuable, a serious limitation is imposed on this method by the very small frequency of identical-twin births as compared with single births. Until such time as a larger percentage of identical-twin births could be induced by experimental techniques involving artificial blastomeric separation, research with identical-twins will not be a universal possibility.

A third method involving the statistical analysis of production figures of cows living under natural conditions of environment, is the one that has been widely used for studies in herd analysis. Enriched by the recent researches of Fisher and other statisticians, its practical application to the science of animal breeding has been developed extensively by Lush and his co-workers. It is this method that has been used throughout the present study. It involves the assessment, under proper statistical control, of the influence of known environmental factors on production, and the subsequent standardisation of the lactation records whenever necessary, with a view to eliminating the effect of these environmental influences. These standardised records are then used for more accurate estimations of heritability than could be obtained from raw data.

It is beyond the scope of the present thesis to review the very extensive literature on dairy cattle production. Such reviews have been made from time to time by different authors (von Patow 1926, Buchanan Smith and Robison 1933, Buchanan Smith 1939, and Shrode and Lush 1947). Reference will however be made in the appropriate sections of this thesis to those papers germane to the subjects under discussion.

Material and Methods

The choice of reliable and representative material is fundamental to all genetical research. Accordingly, the best type of production record that could be employed for studies in herd analysis, is that obtained from accurate and daily records of each cow. But, detailed inquiries into the system of recording in Scotland revealed that the number of farms maintaining daily lactation records is surprisingly small. Owing to the paucity of such data, it was decided to resort to the official records maintained by the Scottish Milk Recording Association. These official records are based on measurements made once in every 14 to 28 days by recorders appointed by the Association. The milk yield of every cow on the farm visited by the recorder is weighed over a period of 24 hours and entered in the milk record book specially kept for the purpose. Each day of visit is regarded as the middle day of the period covered by the test, and the total yield for the period is obtained by multiplying the actual yield on the day of test by the number of days covered by the test. The butterfat percentage of the milk produced by each cow is also determined from a random sample of the milk by the Gerber method. The production of butterfat for the period is then calculated by multiplying the yield of milk by the percentage of butterfat.

Most investigators in Scotland have, in the past, employed these official records for their studies, without, however, ascertaining whether such records are sufficiently accurate estimates of true milk yields.

Buchanan Smith (1948) seems to be the only writer who has recognised the importance of this in interpreting the results of a constructive breeding policy. Analytical work in dairy cattle production is fundamentally conditioned by the accuracy with which the available records indicate actual differences in producing ability. A preliminary investigation into the usefulness of the official Scottish Milk records for genetical purposes was therefore made at the commencement of the present work. The results of this investigation are presented in a subsequent section.

The collection and tabulation of data for the main investigation was undertaken as the next step.

Although milk and butterfat recording has been in progress for a number of years in Scotland, it was considered desirable to restrict the present study to a fairly homogeneous period of years during which no drastic changes in feeding and management had taken place. This selection was necessary in the light of present-day knowledge of the disturbing influence of changes in herd management on genetical studies. In consequence, the ten year period from 1930 to 1939 was chosen. This obviated the necessity of attempting to correct for variations in feed-supply and their concomitant effects on milk and butterfat production experienced during the later war years. Personal visits by the author to over twenty herds of Ayrshire cattle in Scotland revealed, however, that even with this restriction in the period of years, the utmost caution was still demanded in the choice of the herds for study. Apart from the drastic effects induced by such a major catastrophe as war, changes in environmental conditions due to other reasons such as the sudden incidence of mastitis or abortion on a large scale, or even radical changes in byre staff, also tend to reduce production considerably. For these reasons, several herds which might otherwise have been used, were excluded from the present investigation. No other kind of selection occurred in collecting the material for this work.

Twelve herds of pedigree Ayrshire cattle located in south-west Scotland were finally used as the basis for the investigations presented in this thesis. For compilation of the data, the original record books of the 12 herds were obtained from the herd owners, and all the records (numbering about 5,000) were abstracted and utilized, except where illness or disease had obviously decreased production. In order to ensure accuracy, all figures of every testing day of every cow and lactation were copied out on specially-prepared sheets, so that the ultimate computations would be self-checking. The data pertaining to the different lactations of the same cow were traced through the different years and detailed accordingly; thereby all available information relating to a particular cow was collected in compact form. This contained in addition to milk, butterfat and butterfat percentage figures, other particulars relating to the date of each calving and age, lengths of the calving intervals and dry periods, and also the names of the sire and dam. Finally, to facilitate statistical computations all the information for each lactation of each cow was transferred from the abstracting sheets to a card index. The abstracting sheets themselves were used for purposes of subsequent checking, and also for calculations not needing the card index.

The methods used in analysing the data were based mainly on Fisher's "Statistical Methods for Research Workers" (1948) and Snedecor's "Statistical Methods applied to Experiments in Agriculture and Biology" (1946). Wherever other techniques of analysis were employed, they are indicated in the appropriate sections of the thesis. The computations themselves were made with the aid of a Marchant Calculating Machine.

Units of Measurement

It will be observed from a study of breeding practices in different countries, that the units of measurement of dairy cattle production vary considerably from one part of the world to another. In Sweden and New Zealand, for example, where the main market for milk is for the manufacture of butter and cheese, the breeders are more interested in the total yield of fat than in any other production characteristics. In Britain, however, the amount of milk produced by the cow, and to a less extent the butterfat percentage in that milk, seem to be the prime criteria for measuring dairy cattle performance. It would appear therefore that a study of the causes of variation in milk yield and butterfat percentage would be of importance from the breeding standpoint of this country.

The usefulness of studies in butterfat percentage has, however, been repeatedly questioned by several authors. von Patow (1930) stated that investigations on the relationship between milk yield and butterfat should deal with the total amount of fat secreted and not with the fat percentage. Buchanan Smith (1939) also supported this contention and adduced evidence for it by an analogy based on a conclusion drawn by Fairfield Smith (1937) in the realm of plant genetics. He maintained that just as the study of the grain:straw ratio in wheat does not supply more information than can be given by a consideration of both grain and straw separately, so also would the argument apply to the question of butterfat percentage. On the other hand, Johansson and Hansson (1940) advanced a counter-argument to this on the same plane. They stated that "it must be just as logical to study the inheritance of fat percentage of the milk as it is to study the genetical basis for the variation of the sugar content in beets or any other similar character with which plant breeders are working." It is clear from this that views regarding the advisability of conducting studies on the fat content of milk are conflicting. In reality, however, the controversy is an idle one, for numerous arguments of this nature can be furnished to support either contention. The point at issue is, what are the advantages in studying butterfat percentage in dairy cattle that are not gained by a study of total milk yield and total fat yield? The answer to this question can be obtained if the subject is considered from a genetical point of view. In the breeding of dairy cattle, it is obvious that the greatest improvement per generation is attained if selection is directed towards those qualities with greatest genetic variation. Investigations by different workers on the heritability of milk and butterfat have shown, however, that the degree of genetic determination is low for both total milk yield and total fat yield. But, for butterfat percentage, it has been found, both in the present study and in past investigations, that the hereditary fraction of the total variance is much larger than for any other production characteristics. If the ultimate aim of breeding dairy cattle is to improve the production level of the cows in regard to milk and fat, this can be achieved by selection on the basis of either total milk yield and total fat yield or total milk yield and fat percentage. The fact that fat percentage has a high degree of genetic determination shows that it is best to concentrate on fat percentage and total milk rather than on total fat and total milk.

The next important problem was to determine what particular measure of milk yield and butterfat percentage should be employed in the present investigation. The yield during the total lactation period was at one time the most popular measure of milk production, but in recent years the 365 day yield and more particularly the 305 day yield have come into common usage. During a study of the existing literature on the subject, attention was drawn to certain Norwegian, German and Swedish work where production records from calving up to the 180th day of lactation had been used for measuring the milk secreting activity of the cow. The use of the 180 day yield has several distinct advantages. In the first place, it excludes the effect of one of the major sources of variation in milk yields, namely variations in length of current calving interval. With yields taken over a longer period of time than 180 days, pregnancy begins to exert an influence on production, and unless due allowance is made for this effect, real differences between cows cannot be measured accurately. Secondly, the correlation between the 180 day yield and the total yield has been found to be remarkably high. Tuff (1931), working with Norwegian herds found that the correlation between milk yield in 180 days and yield during the whole lactation period, with the calving interval held constant, was 0.895. This high correlation has been confirmed subsequently by Zorn and Funke (1935) working with German herds, and also by Johansson and Hansson (1940) working in Sweden with herds at a higher level of production. Finally, there is the added advantage mentioned by these previous workers, of the greater possibility of making early and more accurate progeny tests when using 180 day records. The importance of this point will be increasingly realised when it is also noted that a number of poor milkers in most herds are generally culled after about six months of their lactation period, with the result that if a longer record than the 180 day yield is used as the measure of milk production, then the material available for progeny tests is bound to be selected to some extent at least.

The objection may, however, be raised that the 180 day period is too short for measuring a cow's milk producing ability. But then it should be remembered that the number of uncontrolled physiological and environmental influences that enter into the latter part of the lactation curve is so great, that even

<u>Table 1</u>

Analysis of variance of the 180 day yields of 326 cows, each of which had completed the first four lactations

Source	d.f.	Mean square	Composition of mean square	Variance component
Between lactations	3	180,184,881	$\sigma_W^2+326\sigma_L^2+n_o\sigma_{HL}^2$	549,856
Between herds	11	39,059,275	$\sigma_W^2+4\sigma_C^2+n_o\sigma_{HL}^2+n_1\sigma_H^2$	344,647
Herd lactation interaction	33	931,756	$\sigma_W^2+n_o\sigma_{HL}^2$	16,420
Between cows within herds	314	2,691,459	$\sigma_W^2+4\sigma_C^2$	546,942
Remainder	942	503,693	σ_W^2	503,693

Intra-cow correlation within herds after elimination of variance due to age $= \dfrac{\sigma_C^2}{\sigma_W^2+\sigma_C^2} = 0.521$

<u>Table 2</u>

Analysis of variance of the total lactation yields of 326 cows each of which had completed the first four lactations

(Same cows as in Table 1)

Source	d.f.	Mean square	Composition of mean square	Variance component
Between lactations	3	22,561,189	$\sigma_W^2+326\sigma_L^2+n_o\sigma_{HL}^2$	59,397
Between herds	11	112,940,663	$\sigma_W^2+4\sigma_C^2+n_o\sigma_{HL}^2+n_1\sigma_H^2$	988,397
Herd lactation interaction	33	3,197,737	$\sigma_W^2+n_o\sigma_{HL}^2$	57,081
Between cows within herds	314	8,382,508	$\sigma_W^2+4\sigma_C^2$	1,668,218
Remainder	942	1,709,638	σ_W^2	1,709,638

Intra-cow correlation within herds after elimination of variance due to age $= \dfrac{\sigma_C^2}{\sigma_W^2+\sigma_C^2} = 0.494$

[**Footnote:** The terms σ_W^2, σ_C^2, σ_{HL}^2, σ_H^2 and σ_L^2 denote the variances corresponding to the appropriate sources e.g. σ_L^2 is the variance between lactations, σ_H^2 is the variance between herds, etc. The terms n_o and n_1 represent respectively the average number of cows and lactations in each herd, and are obtained from the general formula (see Snedecor 1946), which gives in the present instance:-

$$n_o = \frac{\Sigma k - \frac{\Sigma k^2}{\Sigma k}}{11} \quad \text{and } n_1 = 4n_o$$

For further details of this method of analysis which is used also in subsequent sections of the present thesis, reference should be made to Winsor and Clarke (1940) and Hetzer, Dickerson and Zeller (1943)] after correction for known environmental factors, the accuracy of the results obtained often leaves much to be desired. It is therefore concluded that a more accurate evaluation of the cow's inherent potentiality for milk production can be made on the basis of 180 day yields than on yields based on longer periods imperfectly corrected.

The relative usefulness of the 180 day record for genetical purposes was studied with the present material by two analyses of variance of the 180 day yields and the total lactation yields of 326 cows, each of which had completed the first four lactations. The measure of usefulness employed was the within-herd correlation between records of the same cow after elimination of the variance due to age. This has been termed "repeatability" by previous investigators (Lush and Shultz 1936, Lush and Arnold 1937, and Dickerson 1940), since it indicates the degree to which records of the same cow tend to repeat themselves from one lactation to another. Tables 1 and 2 show the results obtained with the present material. It is apparent that the repeatability was in fact slightly greater for the 180 day record than for the total lactation record, proving thereby that the 180 day yield is quite an adequate measure of milking capacity in dairy cattle. It should, however, be noted that the variance due to age is very high for the 180 day yield, so that the need for an age-correction is greatly increased with this type of record. In fact, in the present data, about 28 per cent. of the total variance in 180 day yields was due to age. The corresponding figure for total lactation records had a surprisingly low value of 1 per cent. - which is probably peculiar to this material only.

When it had been decided that the 180 day yield would be used as a measure of total milk production, the next question was whether any such restriction is also required for butterfat percentage. The results of studies presented in Part IV of this thesis show quite clearly that the butterfat percentage of a cow is practically independent of variations in length of the current calving interval. It was therefore decided that for butterfat percentage, the total lactation period would be used.

Investigations on the persistency of lactation have also been carried out with the present material. The unit of measurement employed for these studies was based on the "shape-figure" idea used notably by Johansson and Hansson (1940) and also by other investigators. A discussion of the present method of study in relation to previous work is given in Part III of this thesis. It may, however, be mentioned here that persistency as described in this work, was measured by the formula :-

$$\text{Persistency} = \frac{A-B}{B},$$

where A is the milk yield during the first 180 days and B is the milk yield during the first ten weeks of lactation - subsequently termed the "initial yield".

PART II

Studies in Milk Yield

Part II

Studies in Milk Yield

1. Accuracy of milk yield determinations made under the official Scottish milk recording system

Numerous researches on the accuracy of different systems of milk recording have been carried out in recent years in many countries - particularly in America and New Zealand. The results of these investigations have all proved to be of fundamental importance in establishing the actual potentialities of dairy cattle in regard to milk or butterfat production. The following study was therefore undertaken along similar lines with a view to testing the accuracy of milk yield determinations made under the official Scottish milk recording system.

Since its inception in 1930 the Kirkhill herd belonging to the Hannah Institute has been recorded on the official Scottish system, while daily records were also kept at the same time. This herd therefore provided the necessary material for making a direct comparison of the official and daily records. A total of 200 lactations covering the periods 1931 to 1935 and 1941 to 1945 was studied, and the correlations and regressions were computed separately for the two periods. The factors correlated were the first 10 weeks yield, the 180-days yield and the 240-days yield as measured by the official system on the one hand, and by the daily records on the other. The results of these studies are presented in Tables 3 and 4.

Table 3

Relationship between determinations of milk yield made under the official Scottish milk recording system and the corresponding yields calculated from dairy recordings (Period 1931 to 1935)

Description of data	Mean yield on official recording (lb.)	Mean yield on daily recording (lb.)	Correlation coefficient	Regression coefficient*	Regression equation **
10 weeks yield	2878.6	2733.1	+0.977	+1.019	$X_2 = 94.2+1.019X_1$
180 days yield	6230.7	5933.6	+0.986	+1.029	$X_2 = 122.7+1.029X_1$
240 days yield	7489.9	7139.4	+0.986	+1.030	$X_2 = 138.7+1.030X_1$

* Regression of official record on dairy record.

** X_1 is the yield in lb. according to the daily record and X_2 is the corresponding yield according to the official record.

Table 4

Relationship between determinations of milk yield made under the official Scottish milk recording system and the corresponding yields calculated from daily recordings (Period 1941 to 1945)

Description of data	Mean yield on official recording (lb.)	Mean yield on daily recording (lb.)	Correlation coefficient	Regression coefficient*	Regression equation **
10 weeks yield	2274.1	2178.8	+0.959	+1.009	$X_2 = 75.4+1.009X_1$
180 days yield	5029.7	4831.8	+0.976	+0.981	$X_2 = 289.6+0.981X_1$
240 days yield	6036.0	5791.4	+0.981	+0.986	$X_2 = 325.6+0.986X_1$

* Regression of official record on dairy record.

** X_1 is the yield in lb. according to the daily record, and X_2 is the corresponding yield according to the official record.

The two sets of corresponding regressions for the periods 1931 to 1935 and 1941 to 1945 were then compared in order to determine whether there was any significant difference between them. The tests of significance showed that the regressions were in fact remarkably similar.

Finally, the percentage differences between the official and daily records were calculated for yields from 2,000 to 7,500 lb. by using the regression equations of Tables 3 and 4 about their respective ranges of mean. It was found that the official record was, on the average, 4.8 per cent. higher than the daily record. This is in close agreement with the 5 per cent. figure reported by Buchanan Smith (1948).

It is evident from the above analyses that although the official records of the Scottish Milk Recording Association are slightly higher than the corresponding daily records, the high correlations of 0.97 - 0.98 indicate that they are sufficiently accurate for genetical studies.

Table 5

The mean and standard deviation (σ) for age at calving, initial yield, 180 day yield and calving interval of the 1st to 10th Lactations

Lactation No.	No. of cows	Age at calving			Initial yield		180 day yield		Calving interval	
		Mean		σ	Mean	σ	Mean	σ	Mean	σ
		Years	Months	Months	(lb.)	(lb.)	(lb.)	(lb.)	(days)	(days)
1	1211	2	8.7	3.72	2420.1	414.7	5571.8	986.2	417.5	58.8
2	915	3	10.4	3.94	3004.3	499.8	6553.9	1143.0	391.2	54.3
3	688	4	11.4	4.30	3181.4	566.6	6994.1	1239.2	382.9	49.2
4	548	6	0.7	4.73	3218.9	566.4	7156.2	1278.9	388.7	57.5
5	386	7	0.8	4.96	3272.8	617.4	7276.1	1394.4	380.8	47.5
6	248	8	1.4	5.03	3276.8	648.3	7283.1	1391.5	384.8	61.5
7	156	9	1.1	5.00	3285.8	624.7	7385.4	1404.4	397.7	66.5
8	105	10	1.2	5.56	3319.5	632.9	7501.7	1344.7	399.6	66.9
9	82	11	2.2	7.73	3165.4	593.0	7254.2	1393.1	390.6	45.8
10	47	12	2.3	6.03	3153.6	572.7	7095.4	1355.2	380.6	58.6

2. Preliminary examination of available data

Some preliminary analyses were made of all the available milk production figures from the 12 herds in order to determine the main statistical constants of these data. The mean and standard deviation for the 180 day yields of each of the 1st to 10th lactations were calculated, and the results are presented in Table 5 together with the corresponding values for the associated calving intervals and age. The table also contains average figures for yield calculated over a shorter period of the lactation curve - from calving up to the 10th week of lactation. This is referred to as the "initial yield". The distribution of the production records shows that the standard deviation for both initial and 180 day yields was lowest for the first lactation, and thereafter it increased up to the sixth or seventh lactation. There was also an increase in the mean initial yield from 2420.1 lb. in the first lactation to 3319.5 lb. in the eighth lactation, and a corresponding increase in 180 day yield from 5571.8 lb. to 7501.7 lb.

The mean age at first calving in these data was found to be 2 years and 9 months, with a standard deviation of 3.72 months. A frequency diagram depicting the distribution of age at first calving is presented in Fig. 1. It shows a skewness of 0.478, which is probably a reflection of the wide differences in calving programmes in the different herds. The age at subsequent calvings increased by approximately twelve to

FIG. 1.

FREQUENCY DISTRIBUTION OF THE AGE AT FIRST CALVING.

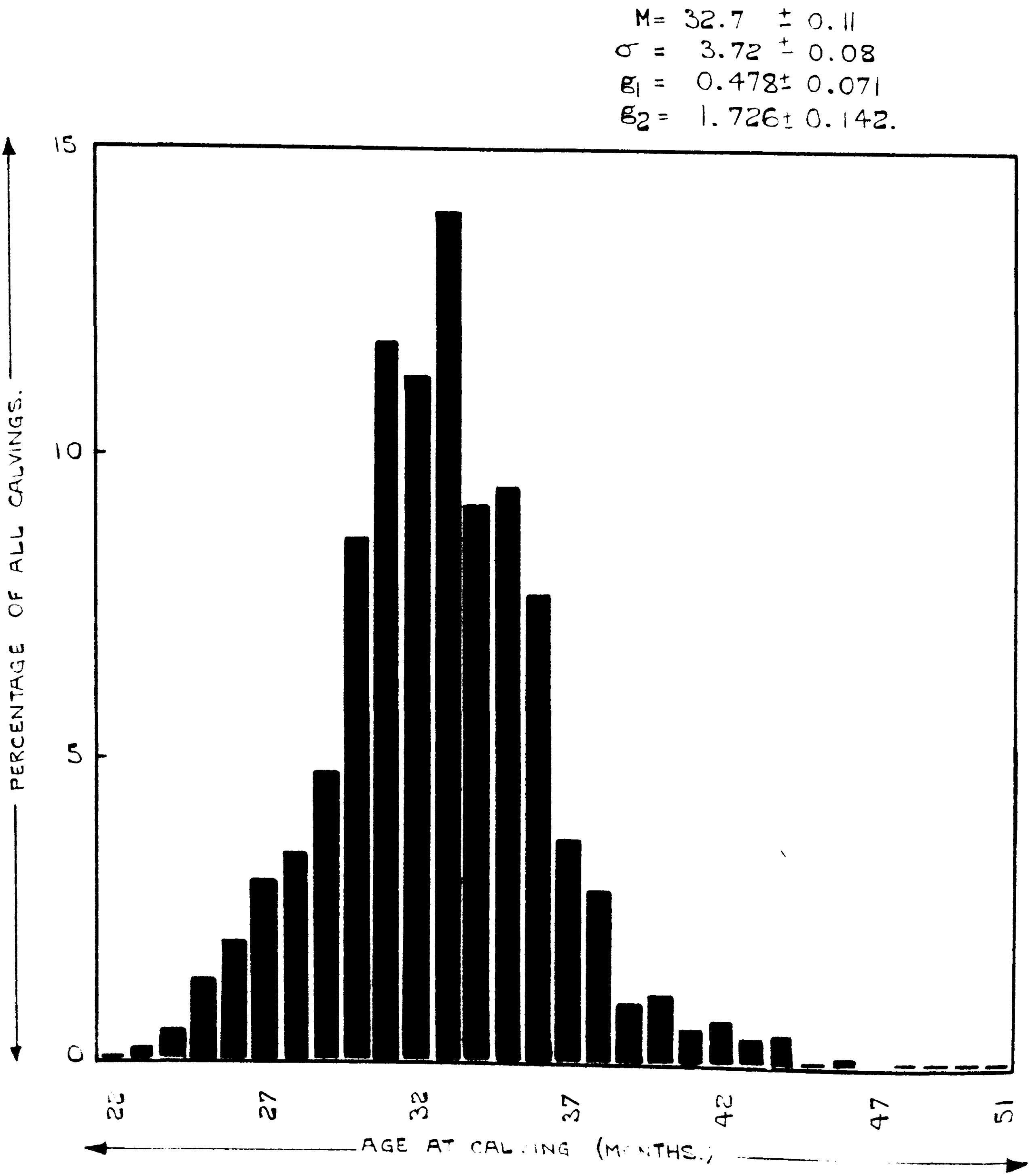


FIG. 2.

FREQUENCY DISTRIBUTION OF THE FIRST CALVING INTERVAL.

$M = 417.5 \pm 1.96$.

$\sigma = 58.8 \pm 1.39$.

$g_1 = 0.928 \pm 0.082$

$g_2 = 1.328 \pm 0.163$.

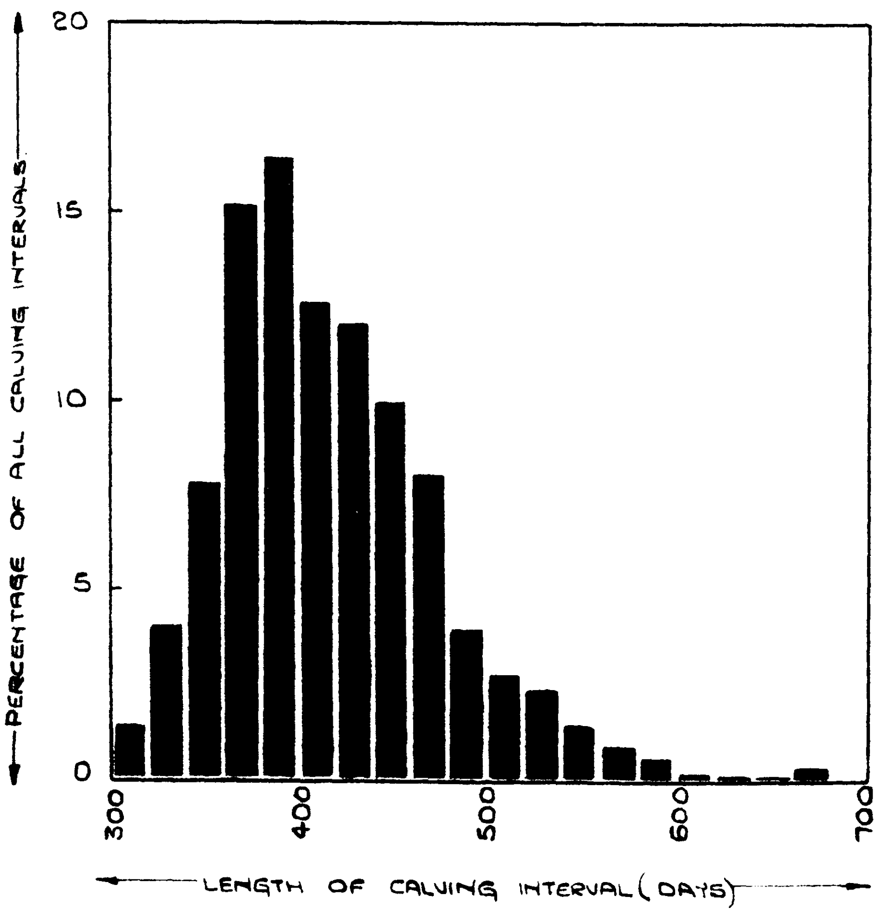


FIG. 3.

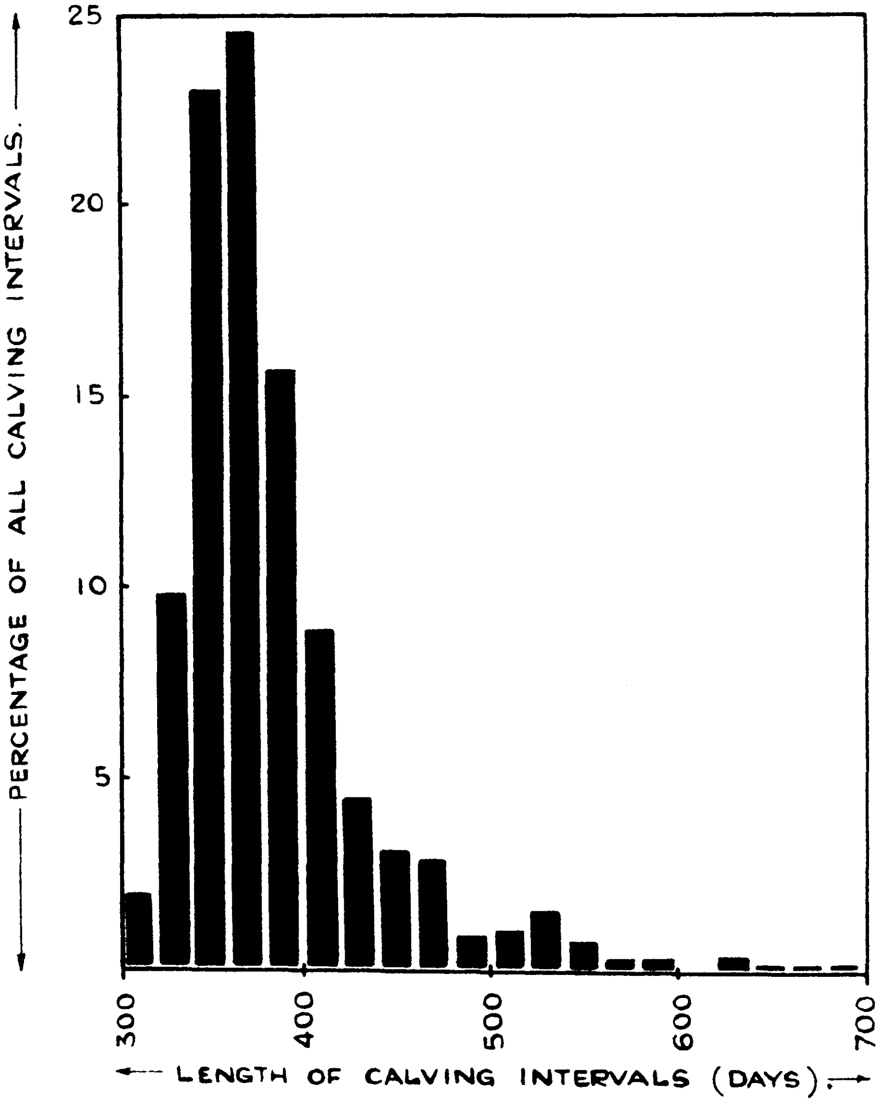
FREQUENCY DISTRIBUTION OF THE 3RD TO 5TH CALVING INTERVALS.

$M = 384{\cdot}4 \pm 1{\cdot}52$

$\sigma = 51{\cdot}8 \pm 1{\cdot}08$

$g_1 = 2{\cdot}043 \pm 0{\cdot}072$

$g_2 = 6{\cdot}146 \pm 0{\cdot}144$



thirteen months for each lactation.

It will be observed from Table 5 that the first calving interval was on the average about 30 days longer than that of subsequent lactations. The frequency diagrams, Figs. 2 and 3, showing the distribution of the first calving interval as distinct from that of the third to fifth lactations, provide measures of the skewness of the distribution. The curve for the first calving interval had a skewness of 0.928, while the corresponding figure for the third to fifth lactations was 2.043. The means were 417.5 $\pm$ 1.96 days and 384.4 $\pm$ 1.52 days respectively for the two groups. The modal class for the former distribution was between 380 and 400 days, and for the latter it was between 360 and 380 days.

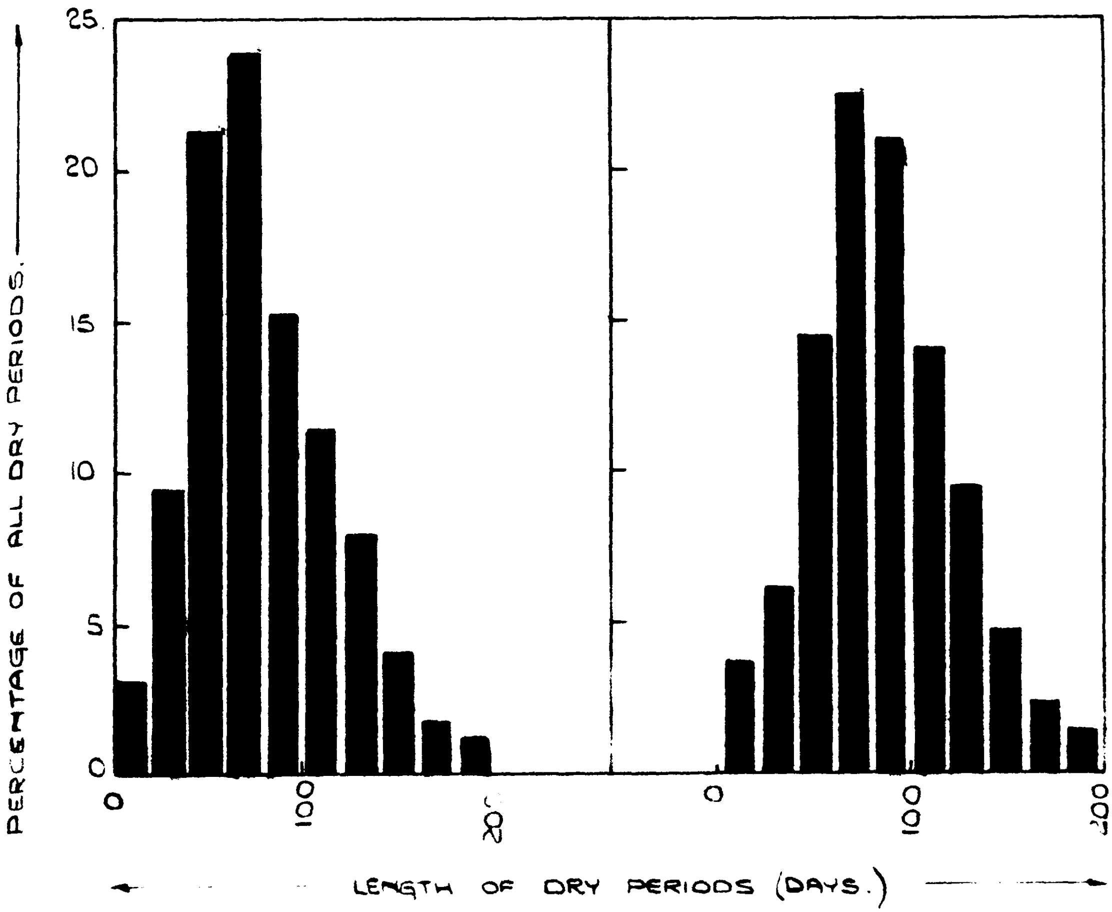
The frequency distributions of the first dry period and the dry periods of the third to fifth lactations were also studied, but this was handicapped to some extent by the system of recording prevailing in Scotland, in that it was not possible to determine from the available data the exact date when a cow went dry. It might have occurred on any one of the 14 to 28 days intervening between the two tests made at that time by the recorder. The figures for dry period obtained from the data used here are therefore bound to be rather in the nature of estimates. However, they may be considered fairly satisfactory for obtaining frequency diagrams for the population as a whole. Such diagrams for the first dry period and for the third to fifth

FIG. 4.

FREQUENCY DISTRIBUTION OF THE FIRST DRY PERIOD.

FIG. 5.

FREQUENCY DISTRIBUTION OF THE 3RD TO 5TH DRY PERIODS.



dry periods are presented in Figs. 4 and 5. The modal class of distribution was between 60 and 80 days in both cases, with mean values of 79 days for the first lactation and 86 days for the third to fifth lactations.

Averages of the production figures independent of lactation number were also calculated for the entire population, and these gave an initial yield of 2964.4 lb. and a 180 day yield of 6616.9 lb. per cow per lactation. These figures may be considered high when compared with those of the country as a whole. Appendix Tables 1 and 2 give details of the average values for initial and 180 day yields during the period 1930 to 1938 for each of the herds studied. The figures for the year 1939 have not been included in these tables, because the records of a large number of cows calving in the latter half of that year were not available during the compilation of the data. It will be observed that on the average, the figures show little or no permanent change through the years 1930 to 1938 - a fact which was verified by a preliminary analysis of variance of the 180 day yield between years and herds (Table 6).

The analysis of variance shows that the mean square "between herds" was very highly significant, while the mean square "between years" was not significant. This means that the herds differed very considerably among themselves in regard to their levels of production, while there was no evidence of improvement or deterioration in mean yield between the years 1930 and 1938.

Table 6

Analysis of variance

(Based on the mean 180 day yields of each herd in each year from 1930 to 1938)

Source	d.f.	Sum of squares	Mean square	F	Signif-icance
Between herds	11	30,269,211	2,751,746	15.71	***
Between years	8	2,342,074	292,759	1.67	N.S.
Error	88	15,410,278	175,117		
Total	107	48,021,563			

Coefficient of variation = 6.2 per cent.

It should perhaps be pointed out that the above analysis is based only on the average yields of each herd in each year, and consequently the results might not agree completely with those obtained from more detailed analyses using the individual yields of cows (as shown later). However, the conclusion remains valid that there was no significant change in the mean yield of the 12 herds from 1930 to 1938.

3. Non-genetic causes of variation in milk yield and their inter-relationships

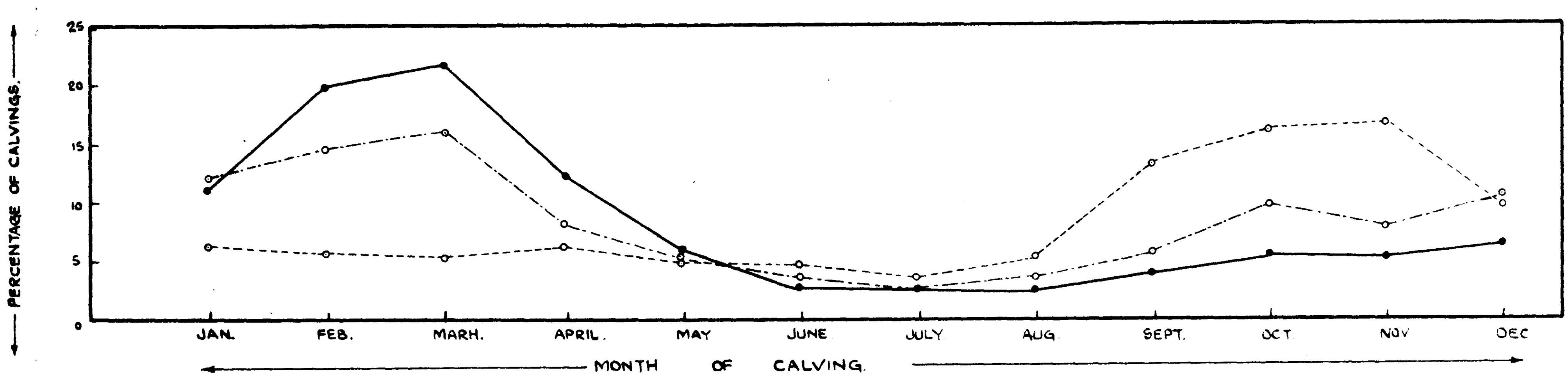
It is well known among dairy farmers that the milk yield of a cow is affected by numerous environmental factors such as the month in which she calves, the age at calving, and the length of the calving intervals. As early as 1927, Sanders drew attention to the influence of four major factors on milk production - age, calving interval, dry period and season of calving. Subsequent investigators, notably Johansson and Hansson (1940), have probed further into the problems relating to the non-genetic causes of variation, while others like Turner (1927), Matson (1929), Frederiksen and Ostergaard (1931), Tuff (1932), Copeland (1934), Plum (1935) and Sikka (1940) have also contributed valuable information on different aspects of the subject. The methods, statistical and otherwise, used by most of these workers, are however open to criticism, and therefore a re-investigation of the whole problem seemed desirable. Moreover, the study of Ayrshire cattle in this country has not kept pace with the progress of the science of animal breeding, and although certain facets of production performance have been investigated by Kay and McCandlish (1929), Glen and McCandlish (1930) and Sikka (1940), insufficient attention has been paid to all the relevant causes of variation.

In the present data all cows were milked twice daily, so that no differences existed between cows in this respect. Moreover, the use of the 180 day record as the measure of milk production, excluded the influence of pregnancy on lactation, because, as mentioned earlier, the effects of pregnancy do not manifest themselves until after the sixth month of the current lactation. Therefore, no correction was required for variations in length of the current calving interval. With regard to dry period, Johansson and Hansson (1940) showed quite clearly that "there is a significant intra-cow correlation in length of dry period, and in the case of an individual cow it is practically impossible to decide if the dry period is short or long owing to the heredity of the cow or owing to environmental causes. Through a correction for length of dry period, genetic differences between the individuals may be eliminated." On the other hand, variations in the length of the preceding calving interval (of which the dry period is a part) appear to be wholly environmental. In consequence, a correction for length of preceding calving interval would be appropriate, and this would also eliminate the major part of the non-genetic variation in length of dry period.

Therefore, the factors that required investigation were age, season or month of calving, and preceding calving interval. At first sight it may appear possible to eliminate the influence of these environmental factors on milk yield by standardising the records on the basis of the averages for each factor.

FIG 6.

DISTRIBUTION OF THE FIRST, SECOND, AND LATER CALVINGS ACCORDING TO MONTHS.



But the non-genetic causes of variation in production do not necessarily act independently of one another; the inter-relations among the factors themselves may be so complex that they should be studied in order to arrive at adequate techniques to meet these complexities. In the past, only the Swedish workers, Johansson and Hansson (1940), seem to have paid sufficient attention to this aspect of the problem. The following sub-sections are devoted to a study of these relationships in the present data.

(i) Relationship between month of calving and age in lactations

The distribution of the first, second, and subsequent calvings according to the months in which the calvings occurred, is presented in Fig. 6. It will be observed that there was a larger proportion of first calvers in autumn and winter than in spring and summer, while with increasing age of the cows spring calvings tended to predominate. In other words, there was a pronounced correlation between the age of the cow in lactations and the month in which she calved. Hence, any attempt to standardise the lactation records for month of calving and age must allow for this correlation. The method of multiple regressions might suggest itself, but the regressions were distinctly non-linear, and therefore this method was not applicable.

(ii) Relationship between month of calving and age within lactations

The association between month of calving and age in months within lactations was also studied, and the results for the first lactation are presented in Table 7. No significant trend was discernible in this distribution; it was therefore not necessary to make any correction for it in a study of the influence of these variables on milk yield.

Table 7

Relation between month of calving and age in the first lactation

Month of calving	Number of cows	Age at first calving (months)
January	83	33.4
February	70	31.8
March	68	32.8
April	77	32.8
May	56	33.8
June	55	32.6
July	40	30.7
August	63	32.3
September	159	32.7
October	196	32.8
November	197	32.7
December	144	33.0
Total and average	1208	32.7

(iii) Relationship between month of calving and the length of the calving interval

Table 8 shows the relationship between the month of calving and the length of the associated preceding calving intervals for 1521 records of cows at maturity (4th to 6th lactations). It will be observed that there was a tendency for the intervals prior to calvings from January to April to be shorter than those prior to calvings from May to December. This could probably be attributed to the higher conception rate exhibited by cows during the pasture season than at any other time of the year. But the correlation was not so pronounced as to warrant the necessity of adopting suitable corrections to meet it.

Table 8

Relation between month of calving and the length of the preceding calving intervals of the 4th to 6th lactations

Month of calving	Number of cows	Length of preceding calving interval (days)
January	180	386.8
February	333	379.7
March	317	385.0
April	171	385.4
May	76	396.3
June	39	391.9
July	36	393.7
August	36	399.1
September	49	390.6
October	90	386.1
November	88	397.4
December	106	399.1
Total and average	1521	387.3

(iv) Relationship between age and the length of the calving interval

It was shown in Table 5 that the calving interval associated with the first lactation was on the average about 30 days longer than subsequent ones. It has also been possible to study the distribution of the first three calving intervals in relation to the age at first calving, and the results of this study are presented in Table 9. It will be observed that there was no significant trend in this respect, in the present data.

Table 9

Relation between the age at first calving and the length of the first three calving intervals

Age at first calving (months)	No. of cows	Length of calving interval (days)		
		1st calving interval	2nd calving interval	3rd calving interval
31 and under	108	415.5	386.6	392.9
32 to 35	196	420.5	387.7	383.3
36 and over	73	414.6	390.9	383.1
Total and average	377	417.9	388.0	386.0

The relationship between successive calving intervals was also investigated by the correlation method. Two different analyses were made for this purpose. The first was based on 614 cows, records of whose first and second calving intervals were available.

The results are summarised in Table 10. The correlation -0.022 ± 0.040 between the two calving intervals was not significant, showing that the calving interval associated with one lactation was practically independent of the next. This point was further elucidated by a study of the variance of the calving interval between cows within herds. Table 11 shows the results of this analysis. It was based on 377 cows from 12 herds, with each cow having complete records for the first three calving intervals. The results supported the conclusion drawn from the first analysis, that there was little or no tendency for a cow to repeat the length of her calving interval in successive lactations. The coefficient of intra-cow correlation within herds after elimination of the variance due to age was only -0.024, and was not significant.

Table 10

Correlation between the calving intervals of the first and second lactations of 614 cows.

Average length of first calving interval	=	419.5 days
Average length of second calving interval	=	391.9 days
Correlation coefficient r	=	-0.022 ± 0.040

Table 11

Analysis of variance of the first three calving intervals of 377 cows from 12 herds

Source	d.f.	Mean square	Composition of mean square	Variance component
Between lactations	2	120,642	$\sigma_W^2+377\sigma_L^2+n_o\sigma_{HL}^2$	305.7
Between herds	11	7,578	$\sigma_W^2+3\sigma_C^2+n_o\sigma_{HL}^2+n_1\sigma_H^2$	37.1
Herd lactation interaction	22	4,396	$\sigma_W^2+n_o\sigma_{HL}^2$	46.2
Between cows within herds	365	2,778	$\sigma_W^2+3\sigma_C^2$	-70.0
Remainder	730	2,988	σ_W^2	2,988.0

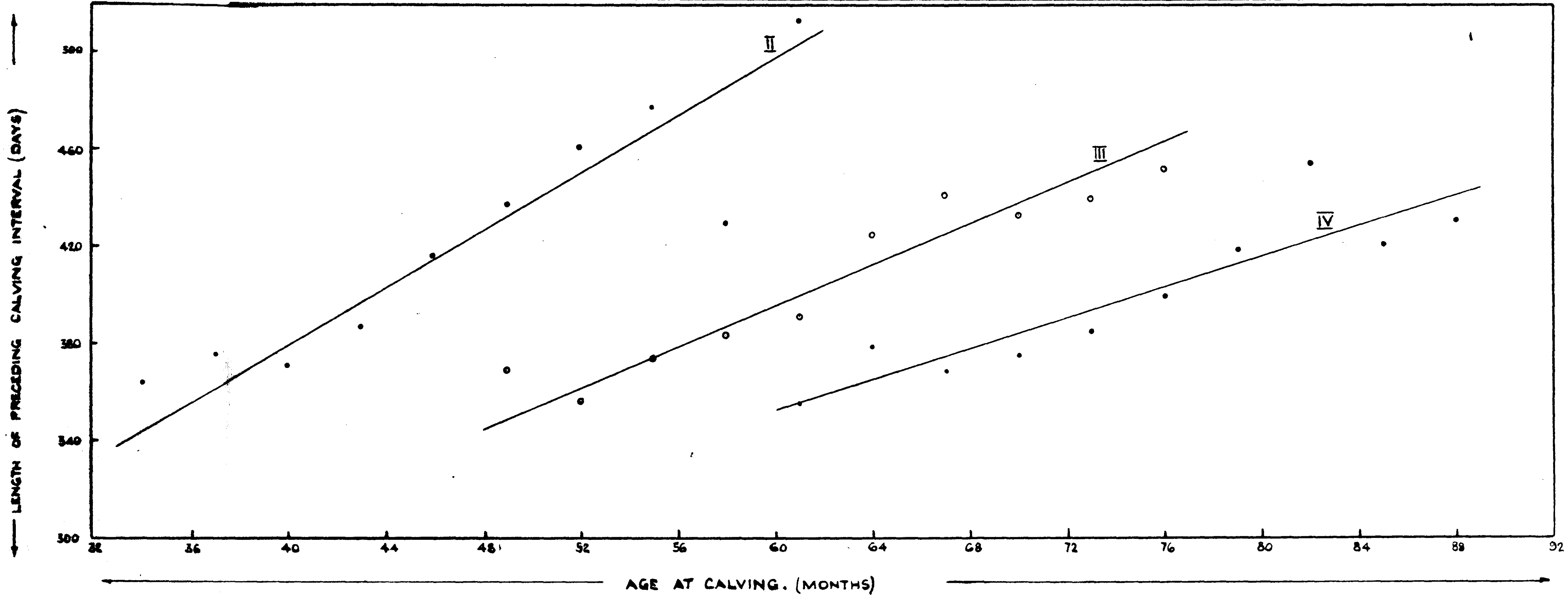
Inter-cow correlation within herds after elimination of variance due to age $= \frac{\sigma_C^2}{\sigma_W^2+\sigma_C^2}$

$= -0.024$

A highly significant correlation however was found to exist within lactations, between the age of the cow in months and the length of the preceding calving interval. The intensity of this relationship will be shown in a subsequent section by means of appropriate correlation and regression coefficients. For the present purpose of indicating the natyre of this relationship, the regression of preceding calving in-

FIG 7.

REGRESSION OF LENGTH OF PRECEDING CALVING INTERVAL ON AGE AT CALVING IN THE 2ND, 3RD, AND 4TH LACTATIONS.



terval on age is shown graphically in Fig. 7 for the second, third and fourth lactations. The regressions were linear. When the age at calving increased by one day, the length of the preceding calving interval increased by 0.11 to 0.20 days; so that, cows which calved for the second time at 3 years 7 months, had an average preceding calving interval of 397 days, but if the second calving was at 3 years 2 months, the average preceding calving interval was 368 days. This relationship between age and preceding calving interval must therefore be taken into consideration in arriving at suitable corrections for the influence of these variables on production.

It is evident from the above analyses of the inter-relationships of age, month of calving and length of calving interval, that there are two significant correlations which are relevant to the present study of the non-genetic causes of variation in milk yield. The first is due to the change in seasonal distribution of calvings from young to mature cows. The second is the correlation within lactations, between the age of the cow and the length of the preceding calving interval. It is necessary to make due allowance for these relationships in analysing the influence of these variables on production - a point which has not been sufficiently appreciated by many previous investigators.

4. Influence of month of calving on milk yield

Although several authors have studied the influence of month of calving on milk production, their results have not been in complete agreement. This, however, is not surprising, because seasonal influences are bound to vary in their effects from one locality to another and from one farm to another according to variations in the nature of the food supply and other external factors of management. This is revealed even within the confines of the present investigation. The 12 herds used in this study are all situated in the south-west region of Scotland, and are reputed to be among the best of the Ayrshire breed, with standards of nutrition and management well above the average for the country. One would therefore expect a high degree of uniformity in the effects of season of calving in these herds, but as will be shown later, this was not so.

In spite of this variation, all investigators are agreed that, generally speaking, calving in the summer months is less favourable to production than calving in winter. In the present data, the average difference in the 180 day milk yields of summer and winter calvers was about 10 per cent. In comparison, Sanders (1927) working with material from English cow-testing Associations, found differences of the order of 15 to 20 per cent., while the figure obtained in Denmark by Frederiksen and Ostergaard (1931) was only 2 to 3 per cent. - a reflection of the wide differences in management and nutritional factors obtaining in

Table 12

Relation between month of calving and initial yield

Month of calving	1st lactation			2nd lactation			Mature lactations		
	No. of cows	Initial yield (lb.)	Relative yield	No. of cows	Initial yield (lb.)	Relative yield	No. of cows	Initial yield (lb.)	Relative yield
Jan.	78	2324.8	96.0	108	2909.9	96.8	261	3159.9	97.9
Feb.	70	2417.0	99.8	131	2834.2	94.2	460	3064.1	94.9
Mar.	64	2379.8	98.3	142	3072.8	102.2	504	3246.5	100.5
Apl.	75	2500.5	103.3	72	3121.2	103.8	285	3351.1	103.8
May	58	2551.5	105.4	47	3107.1	103.3	139	3392.4	105.1
June	56	2498.9	103.2	32	3099.8	103.1	63	3393.7	105.1
July	39	2368.5	97.8	26	2915.3	96.9	59	3154.6	97.7
August	62	2430.2	100.4	32	2950.7	98.1	57	3267.6	101.2
Sept.	156	2486.7	102.7	52	2991.3	99.5	88	3326.5	103.0
Oct.	194	2479.8	102.4	88	3084.7	102.6	121	3294.1	102.0
Nov.	199	2373.0	98.0	71	3086.8	102.6	120	3234.2	100.2
Dec.	146	2300.8	95.0	94	3012.5	100.2	149	3248.4	100.6
Total & average	1,197	2421.5	100.0	895	3007.2	100.0	2,306	3229.3	100.0

Table 13

Relation between month of calving and 180 day yield

Month of calving	1st lactation			2nd lactation			Mature lactations		
	No. of cows	180 day yield (lb.)	Relative yield	No. of cows	180 day yield (lb.)	Relative yield	No. of cows	180 day yield (lb.)	Relative yield
Jan.	78	5521.0	99.0	108	6617.7	100.8	261	7168.6	99.9
Feb.	70	5839.3	104.8	131	6417.7	97.7	460	7044.0	98.1
Mar.	64	5584.5	100.2	142	6839.2	104.2	504	7323.9	102.0
Apl.	75	5453.3	97.8	72	6561.4	99.9	285	7207.9	100.4
May	58	5451.7	97.8	47	6215.9	94.7	139	7126.6	99.3
June	56	5324.5	95.5	32	6175.8	94.1	63	6983.9	97.3
July	39	5173.2	92.8	26	6237.3	95.0	59	6674.4	93.0
August	62	5470.6	98.1	32	6296.1	95.9	57	6939.7	96.7
Sept.	156	5773.9	103.6	52	6552.8	99.8	88	7325.0	102.1
Oct.	194	5728.7	102.8	88	6632.6	101.0	121	7283.8	101.5
Nov.	199	5540.4	99.4	71	6700.2	102.0	120	7187.1	100.1
Dec.	146	5454.8	97.9	94	6642.0	101.2	149	7286.7	101.5
Total & average	1,197	5574.0	100.0	895	6566.4	100.0	2,306	7177.3	100.0

different localities.

In the present work, the general trend of the variation in milk yield with month of calving was studied for the first, second, and later lactations separately. This grouping into lactations was considered necessary, firstly in view of the seasonal change in calvings from young to mature cows reported in the preceding section, and secondly owing to differences in level of production among the different lactation groups. The results for initial and 180 day yields are presented in Tables 12 and 13 together with relative values obtained by using the weighted average yield as base. They show that young and mature cows reacted in much the same way to seasonal changes. In order to present the trends more clearly, the responses to month of calving have been graphed in Fig. 8. In Fig. 9 the general trend in initial yield over all lactations (obtained by the least squares method of fitting constants which will be described later) is shown, and on this curve is superimposed another curve showing the seasonal variation in the growth rate of typical grassland herbage in this country (after Watson 1939). Comparison of these curves suggests that the variations in initial milk yield are conditioned in large measure by the prevailing conditions of food supply. The two curves of productivity - milk and grassland - each exhibit two peaks, one in May and the other in September. The first peak in initial milk yield corresponds to an ample supply of highly nutritious

FIG. 8

RELATION BETWEEN MONTH OF CALVING AND (a) 180 DAY MILK YIELD AND (b) INITIAL MILK YIELD.

(BASED ON DATA FROM 12 HERDS.)

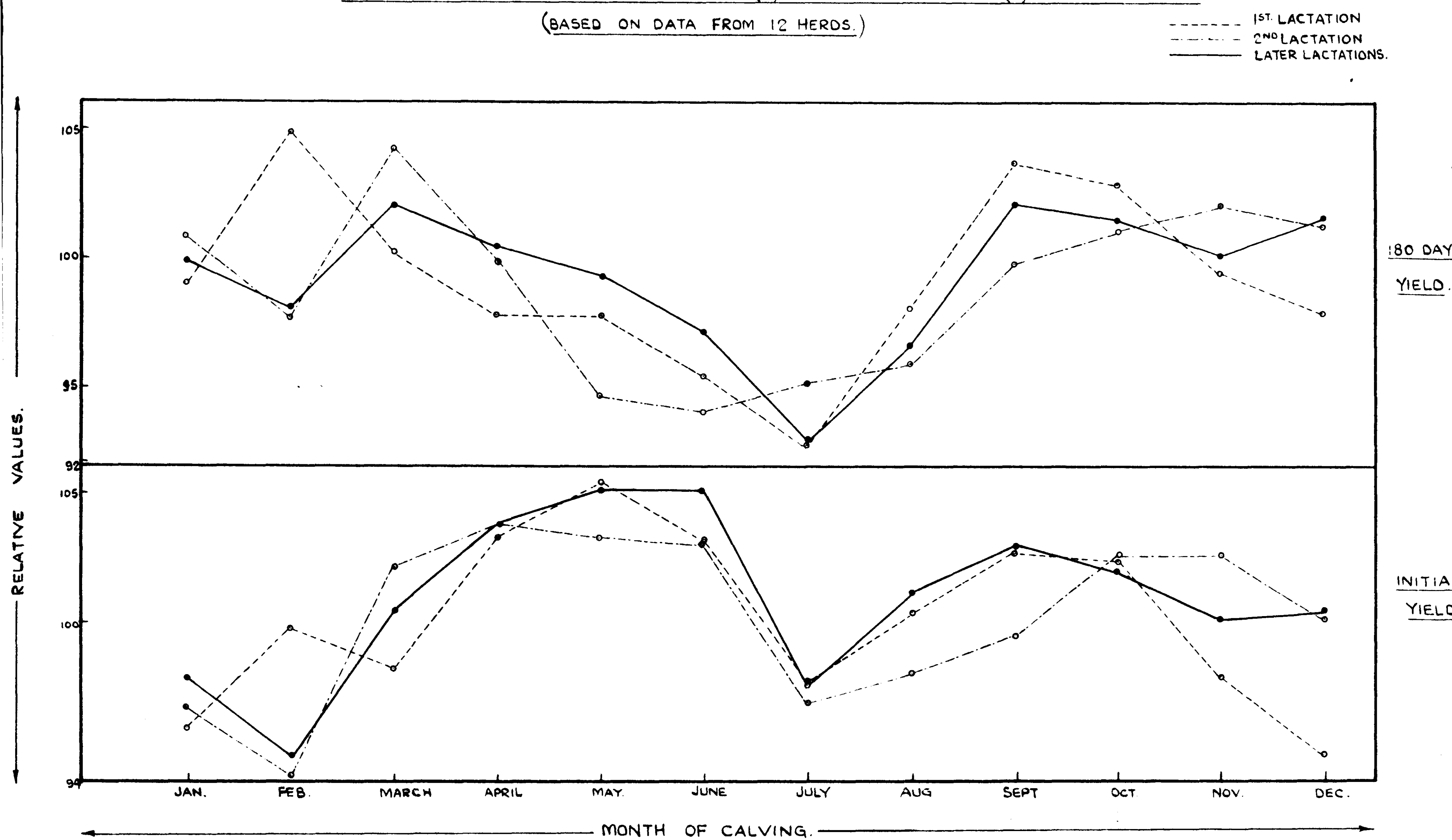
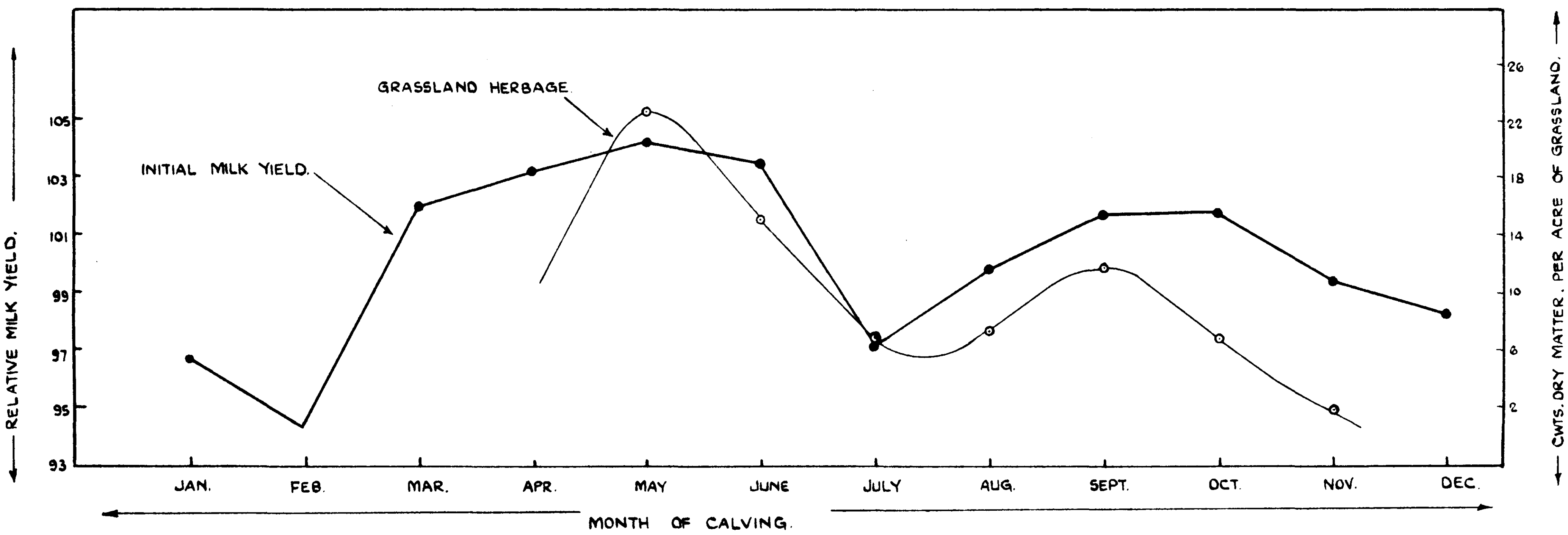


FIG 9.

SEASONAL VARIATION IN INITIAL MILK YIELD AND GRASSLAND HERBAGE.



spring grass which, for a combination of reasons, exerts a stimulating influence on milk production. With the advent of midsummer the rate of pasture growth declines, and the grass itself is of lower nutritive value. The lower initial milk yield of July calvers could perhaps be attributed to inadequate supplementary feeding at this time. A second flush of grass occurs in autumn, and this fact, coupled with the practice of "hand feeding" at this time, seems to be reflected in the initial milk yields of autumn calvers. The close similarity in the production curves for milk and grassland becomes all the more striking when it is realised that the second peak of initial milk production is lower than the first - a possible reflection of the quantity, quality and palatability of herbage available in the autumn as compared with the spring.

The trend of the 180 day yield curves might also be explained in relation to the seasonal variation in the growth curve of grass. With spring calvers, although the initial yield is high, this high level of production cannot be maintained for long, owing to the fact that the herbage available for grazing by these cows in midsummer has deteriorated. In consequence, the total yield of the cow is affected and is comparatively low. The poor production of summer calvers could again be attributed to the poor condition of pasture during the summer months, which compels the cow to draw on its body reserves for milk production, unless the grazing is adequately supplemented by stall-feeding.

This impoverishment of body reserves during the early peak period of lactation takes its toll on the entire production record, with the result that the 180 day yield is low. The comparatively high figures obtained for autumn and winter calvers could be attributed in part to stall-feeding and in part to the beneficial influence of the nutritious spring grass to which they have access in the middle of their lactations.

It is clear therefore that if the differences in production between summer and winter calvers are to be minimised and the unfavourable effects of summer calving eliminated, adequate attention must be paid by the dairy farmer to the feed requirements of summer calvers during the period when the quality of herbage on his farm is relatively poor. Adequate supplementary stall-feeding at such times and the development of better systems of grassland management are probably the only methods by which any material advance can be made in this direction.

The variance of the lactation records due to month of calving has been analysed by using the 180 day milk yields of the third and later lactations. When the data from the 12 herds were treated as a single homogeneous population, the proportion of the total variance due to differences between months of calving was only 0.69 per cent. (Table 14). But when the analysis was done for each herd separately, and the individual degrees of freedom and sums of squares totalled, the resulting variance increased to 2.74 per cent. (Table 15). This shows that 2.74 per cent. of the total variance was due to differences between months of calving within herds, and this is a better measure of the effect of month of calving on milk yield than the first. But it should be pointed out that even this analysis does not include the component due to herd month interactions. This was unavoidable owing to disproportionate numbers in the sub-classes and owing to the fact that no accurate method of analysis is available for such data.

Table 14

Analysis of variance due to month of calving

(Based on the 180 day milk yields of 2306 mature lactation records, the data from the 12 herds being treated as a single homogeneous population)

Source	d.f.	Mean square	Composition of mean square *	Variance component
Between months of calving	11	4,111,608	$\sigma_W^2 + n_o \sigma_M^2$	12,579
Within months of calving	2294	1,823,760	σ_W^2	1,823,760

Percentage of total variance due to month of calving $= \dfrac{\sigma_M^2}{\sigma_M^2 + \sigma_W^2}$

$=$ 0.69 per cent.

* n_o in this column represents the average number of lactations in each month for the whole population, and is derived from the general formula referred to in the footnotes to Tables 1 and 2.

Table 15

Analysis of variance due to month of calving

(Based on the same data as Table 14, but the analysis was done for each herd separately, and the individual degrees of freedom and sums of squares totalled to give the following results)

Source	d.f.	Mean square	Variance component
Between months of calving	128	2,217,368	43,829
Within months of calving	2166	1,554,233	1,554,233

Percentage of total variance due to month of calving with herds,

$$= \frac{43,829}{43,829 + 1,554,233} = 2.74 \text{ per cent.}$$

Correction of milk yields for month of calving

It is accepted that the determination of adequate correction factors for environmental influences is fundamental to all genetical research. The object of such correction factors is to facilitate the standardisation of the records to a common environment, so that, ultimately, a classification of the cows according to their true hereditary potentialities may be possible.

Different methods of calculating correction factors for month of calving have been used in the past, but essentially, the correction factor for any month is given by the ratio of the value of the standard month to the value of that particular month. In detail, however, the type of correction coefficient used has varied considerably in different investigations. While Sanders (1927) used the same correction factors for all cows calving in a particular month, Kruger (1934, 1937) corrected the individual lactation record on the basis of the average yield of all cows in the same herd and the same season. Kruger's correction was based on the fact that the response to season of calving varies from herd to herd. But, owing to the scarcity of cows calving in certain months of the year, he used, in fact, a "moving" six-months average as the basis of his correction. Johansson and Hansson (1940) however, have pointed out that this method suffers from the serious handicap that more than 50 per cent. of the cows may calve in two of the six months, and therefore this "moving" average cannot be very representative. They have tried to overcome this difficulty by dividing the lactation records in each herd and each year into those of summer and winter calvers, and then correcting for the difference between the averages of the two groups. Even this method has its drawbacks. One cannot expect to obtain as reliable results using two groups only - summer and winter calvers -, as when using 12 different groups according to month of calving. In fact, Johansson and Hansson themselves report that using 2 seasons, only 3.3 per cent. of the total variance was found to be due to season of calving in their material, but when monthly records were used the figure was 5.3 per cent.

It is evident from the above studies that if the correction factors are to be accurate, they should be based on month of calving, and wherever significant herd month interactions exist, they should also be calculated within herds. In the present analysis of the influence of month of calving on milk yield, it was therefore decided to test the significance of these interactions before arriving at appropriate correction factors. Statistically, a general method of analysis to elucidate such information from multiple classifications and non-orthogonal data has been developed by Yates (1933). It consists of a process of fitting constants by the method of least squares. "Tests of significance are made by fitting constants to represent all effects other than the one to be tested, evaluating the residual variance between classes after fitting has been performed, and comparing this variance with the intra-class variance." (Yates). In the present instance, in order to determine whether there is any interaction between herds and months of calving, constants representing herds and months are fitted, and the residual variance after this fitting is done, is then tested for significance against the within class variance.

The results of such an analysis of variance based on the 180 day yields of 2306 mature lactations (third and later lactations) of cows from 12 herds are given in Table 16. It shows that there were highly significant herd month interactions in milk yield, indicating thereby a differential response of different herds to months of calving. It can therefore be legitimately concluded that if the best results are to be obtained, corrections for month of calving must be done within herds. In the light of this, it is evident that the treatment of this problem by previous investigators like Sanders (1927) and Sikka (1940), has not been quite adequate. Such correction factors as they used, cannot be expected to give the most accurate results, because they have no bearing on local conditions within herds.

Table 16

Analysis of variance of herd month interactions in milk yield

Source	d.f.	Sum of squares	Mean square	F
Constants	22	619,613,933	28,164,270	
Remainder (interaction)	117	242,877,238	2,075,874	1.42**
Between classes	139	862,491,171		
Within classes	2166	3,163,070,930	1,460,328	
Total	2305	4,025,562,101		

A further consideration was necessary before arriving at the correction factors to be applied to the present data. It was, to determine whether the corrections for month of calving had to be made not only within herds, but also within years. It is a well-known fact that the summer of one year, for example, may be considerably drier than the summer of the next, and this would necessarily have a bearing on the quantity and quality of pasture available in the two years. So also the winter of one year may be milder than the next, with the result that cows may be put to grass early in the following spring. Such variations in the dryness of the summer and the severity of the winter are bound to occur from year to year for any herd, and these factors would influence the feed position and therefore milk production. It may consequently be argued that the best correction for month of calving would be one that is computed on a within herds and within years basis. But there is one serious drawback to such a correction. In the herds studied, the average number of cows in milk per year was in the region of 40 to 50; and of these, the number of calvings during certain months of the year, notably the summer months, was very small. Therefore, any attempt to correct for month of calving within years in a herd would have been subject to a high degree of chance variation due to paucity of numbers. It is only in very large herds where the basis of correction is not liable to much chance errors that such a method could be employed. In consequence, in the present analysis it was decided to correct for month of calving within herds irrespective of years. Unlike the yearly variations which are more in the nature of fluctations, the herd month interactions are of a more permanent nature and are certainly more important.

The actual method of calculating correction coefficients was in itself further designed to overcome as far as possible, the effect of small numbers in the sub-groups and the consequent likelihood of chance variation. This was accomplished by dividing the lactations in each herd into three groups (1st, 2nd, and later lactations), and then setting up the scheme for testing the interaction between months and lactations within herds. The fitted constants for months obtained from this scheme were the best estimates of the monthly averages, and were used to provide correction factors. The correction factors for the 12 herds studied are listed in Appendix Table 3.

5. Influence of age on milk yield

The variation in the milk yield of a cow with age at calving has been extensively investigated by numerous authors. There is general agreement that the milk yield increases with age up to maturity and thereafter declines. In detail, however, there is considerable variation in the findings of different investigators in regard to both the rate of increase and the period for which the rise lasts. According to some, the mature yield is attained by about the fifth or sixth lactation, while others report that it occurs at a much later period in life. It is clearly necessary therefore to investigate the reason for these differences.

The early studies on the subject (Gowen 1920, 1924, Turner 1927, and others) were based on averages calculated for all available records "lumped" together into classes according to the different age groups. The results of such studies are bound to be erroneous in so far as the later age classes would contain a selected population as compared with the early ones. The results obtained by using this method for the present data were shown in Table 5. According to this table, peak production in both initial and 180 day yields was attained only at the eighth lactation.

But, if the relationship between age and production is to be determined accurately, it is necessary in the first place to make adequate allowance for the influence of selection. The ideal method would be to base the study on a population in which no culling had taken place. This is, however, almost impossible, because the periodic weeding out of unprofitable animals is a necessary feature of normal herd practice. It is only in an experimental herd specially maintained for the purpose of research, that the ideal of an unselected population might be achieved.

In consequence, it becomes necessary to exercise some form of statistical control over the data, and make due allowance for the influence of this inevitable selection. Two possible techniques could be utilised for this purpose. One consists of restricting the data to animals that have been kept for at-least five or six lactations in the herd. For the study of Ayrshire cattle in Scotland, this method was used by Kay and McCandlish (1929). Since it is based on successive lactation yields of the same cows, it eliminates all errors resulting from selection in a normal population. A potent objection to this technique, however, is that such a restriction exercises a limiting effect on the amount of data that can be utilized for such studies. The other method of study is due to Sanders (1928), and is termed the "paired-lactation" method. It is so called because it involves the pairing together of consecutive lactation records of the same cows having two or more lactations. The first lactation figures are compared with the second for the same group, the second with the third and so on. For example, in the present data there were 822 cows whose first and second lactation records were available.

Their average 180 day yield during the first lactation was 5611.2 lb., and in the second lactation 6587.4 lb. These averages show the increase in yield due to age for the same cows from the first to the second lactation. Similarly, there were 588 cows whose second and third lactation yields for 180 days were available, and their averages were 6680.2 lb. and 7041.8 lb. respectively for the second and third lactations. The first and third lactation yields were then compared directly by correcting for the selection evidenced by the difference in second lactation yields between the 822 and the 588 cows. The average yield during the third lactation after allowance for selection is therefore given by $\frac{6587.4}{6680.2} \times 7041.8$ lb. This process is repeated for all other ages.

One important objection that could be raised against the two methods outlined in the preceding paragraph is that an error might be introduced into the computations by a gradual improvement in the environment from year to year. Any improvement in herd management or feeding would be additive to the age effect, and correction factors for age would therefore include the changes due to environmental trends. In fact, if the data under investigation had extended over a very long period of years, the degree of error could be very high indeed. But, in the present investigation, the period of years was restricted to ten and was carefully chosen so as to be fairly homogeneous. Moreover, the preliminary analysis of variance between years (Table 6) showed that there had been no significant trend in average production through the years 1930 to 1938. It seems unlikely therefore that such factors could materially affect the present investigation.

The results obtained by the study of successive lactations of the same cows and by the "paired-lactation" method are presented in Tables 17 to 20. Comparison of the results obtained by the "lumped-lactation" method (Table 5) with these, shows quite clearly the extent to which the former are fallacious. When allowance was made for the influence of selection, the peak of initial and 180 day production was attained by the fifth lactation.

Table 17

Relation between the age of the cow as measured in lactations and her initial and 180 day milk yields

(Based on 187 cows, each of which had complete records for the first 5 lactations)

Lactation number	Initial milk yield (lb.)	180 day milk yield (lb.)
1	2429.0	5733.9
2	3048.4	6763.9
3	3312.1	7304.7
4	3376.8	7486.2
5	3422.9	7592.8

Table 18

Relation between the age of the cow as measured in lactations and her initial and 180 day milk yields

(Based on 94 cows, each of which had complete records for the first 6 lactations)

Lactation number	Initial milk yield (lb.)	180 day milk yield (lb.)
1	2457.3	5785.1
2	3015.4	6712.1
3	3335.3	7389.1
4	3454.5	7670.3
5	3578.6	7934.9
6	3432.4	7514.3

Table 19

Relation between the age of the cow as measured in lactations and her initial and 180 day milk yields

(Based on 40 cows, each of which had complete records for the first 7 lactations)

Lactation number	Initial milk yield (lb.)	180 day milk yield (lb.)
1	2439.1	5723.1
2	2905.7	6641.7
3	3248.2	7312.0
4	3474.7	7784.5
5	3672.6	8250.1
6	3568.0	7736.7
7	3290.1	7245.8

Table 20

Relation between the age of the cow as measured in lactations and her initial and 180 day milk yields

"Paired-lactation" method

Lactation number	Initial milk yield (lb.)	180 day milk yield (lb.)
1	2424.7	5611.2
2	3012.5	6587.4
3	3167.8	6944.0
4	3202.4	7103.4
5	3272.8	7241.3
6	3151.9	6927.2
7	3076.8	6821.5
8	2967.2	6547.4
9	2823.3	6238.1
10	2765.9	6151.2

These figures agree in the main with the findings of previous authors who have used the "paired-lactation" method of study. The differences that exist are in the rate of increase in yield up to maturity. Sanders (1928) recorded only a small increase in milk yield in all breeds from the first to the second lactation, and in Friesians the second lactation yield was found to be even lower than the first. Johansson and Hansson (1940), working with the butterfat yields of Swedish Red and White cattle, found that production during the second lactation was lower than in the first. Sikka (1940) on the other hand, obtained results for

Ayrshire cattle which are more in line with the present findings in showing a considerable increase from the first to the second lactation. The report of the English Milk Marketing Board for the year 1947 also confirmed the latter results with "lumped" data for all breeds.

The variation in results reported in these investigations could be attributed chiefly to differences in the material studied. The figures and diagrams presented by Sanders (1928) and Johansson and Hansson (1940) show that the first dry period in their material was appreciably shorter than subsequent ones. The latter authors found that the dry period was actually 25 days shorter in the first lactation, and argued correctly that the low second lactation yield could be attributed to this fact. In the present data, however, the modal class of distribution of the first dry period and of the third to fifth dry periods was 60 to 80 days in both cases (Figs. 4 and 5), and the means were also not very different from each other. Moreover, the first calving interval was about 30 days longer than that of subsequent lactations. In contrast, the material used by Johansxon and Hansson showed not only a first dry period of only 47 days but also a first calving interval which was only 10 days longer than the following calving intervals. It is probable therefore that the variation in these two factors, dry period and calving interval, has contributed greatly to the differences in results obtained. It will also be seen from this that if low yields are to be avoided, adequate attention must be paid by the dairy farmer to the provision of a sufficiently long rest period for his cows in order that they may be in good condition for the subsequent lactation. This is particularly applicable to the early lactations when the cows are faced with the dual problem of milk secretion and bodily growth to attain maturity.

In his study of the variation in milk yield with age, Sanders (1928) stated that "it is not the number of lactations which a cow has had, which determines this variation, but the number of years she has lived". Working with Ayrshire cattle in Scotland, Kay and McCandlish (1929) and Glen and McCandlish (1930) used age in lactations as well as age in years and months for their investigations. They found that the results obtained by the two methods were comparable, and concluded that it is immaterial as to which of them is used. Subsequently, however, investigators abroad (Kruger 1934, and Johansson and Hansson 1940) stated that "the capacity of production is influenced both by the number of previous lactations and by the number of years the cow has lived". An attempt was therefore made to throw further light on this point, using the present data.

The first four lactation records of 316 cows from the 12 herds were classified into three groups according to the age at first calving. The average 180 day milk yield in each lactation was then calculated for the three groups. The results are presented in

Table 21 together with relative figures which were computed by using the highest yield in each group as the base.

Table 21

Relation between the age at first calving and the 180 day milk yields during the first four lactations

(Based on 316 cows with complete records for the first four lactations)

Lactation number	Age at first calving					
	31 months & under		32 to 35 months		36 months & over	
	Average yield (lb.)	Relative yield	Average yield (lb.)	Relative yield	Average yield (lb.)	Relative yield
1	5479.1	77.1	5766.6	77.4	6087.1	81.1
2	6490.4	91.3	6816.1	91.4	6994.0	93.1
3	7095.0	99.8	7219.4	96.9	7509.8	100.0
4	7110.6	100.0	7453.8	100.0	7439.6	99.1
Average	6543.8		6814.0		7007.6	

They show that after a late first calving, the maximum production was attained earlier, as measured in lactations, than after an early first calving. This indicates that production is influenced not only by age in lactations but also by age in years and months within lactations, and is in agreement with the findings of Johansson and Hansson (1940). There is, however, one point which may be noted, on which the results shown here for Ayrshire cattle differ from those of the latter authors for Swedish Red and White cattle. That is, in the present data, the yield of late calvers increased almost as much from the first to the second lactation as that of early calvers, indicating that the age-curves were "normal" in all three groups.

It will also be observed from Table 21 that the late calvers had a consistently higher yield than the early calvers. This was evident in the first lactation itself. But the conclusion is open to the objection that the material in the late-calving groups may have been drawn chiefly from the highest-producing herds.

In order to eliminate this possibility, it was decided to study afresh the relation between age at first calving and the first lactation yield by calculating the averages for each age-group in each herd, and then finding the unweighted means of these 12 series of averages. It is evident that by this method the possibility of high-producing herds influencing the groups disproportionately is obviated. The results of this study, using the initial and 180 day yields of 1181 first lactation cows, are shown in Table 22. The figures prove quite clearly that there was a progressive increase in production from early to late calving. This could probably be attributed to the fact that the late-calvers were in a better condition of flesh and had a greater liveweight at the time of calving than the early-calvers.

Nevertheless, it should not be concluded from this that a late age at first calving is to be recommended as good herd practice. What is suggested is that wherever early calving is practised, sufficient attention must be paid to improve the breeding condition of the heifer. It may also be noted that from an economic point of view, early calving is to be preferred to late calving, because in the latter case there is an increased cost of maintenance due to a lengthening of the unproductive period of the cow's life.

Table 22

Relation between the age at first calving and the initial and 180 day milk yields in the first lactation

(Based on the unweighted means of 12 series of averages from the 12 herds)

Age at first calving	Number of cows	Initial milk yield (lb.)	180 day milk yield (lb.)
31 months and under	433	2400.6	5499.4
32 to 35 months	520	2463.9	5687.8
36 months and over	228	2582.6	5891.1

It was shown in one of the preceding sections that there was a pronounced correlation within lactations between age and the length of the preceding calving internal. It was also pointed out that if the true relationship between age and milk yield is to be determined accurately, due allowance must be made for this correlation. The next problem therefore was the study of the inter-relationships within lactations of age, length of preceding calving interval and milk yield.

The highly significant differences that existed between levels of production in the 12 herds, and the considerable variation among these herds in regard to age at calving within lactations, showed that the different herds cannot be "lumped" together in studying these inter-relationships. For example, if a later age at calving was adopted in the low-yielding herds than in high-yielding ones, then with "lumped" data there would be a tendency for increase in age to be associated with a decrease in yield, and vice versa. It was therefore decided to overcome this difficulty of differences in herd means and calving practices by expressing the yields of the individual cows as deviations from the respective herd averages. The yields themselves had previously been corrected for month of calving within herds by using the coefficients calculated in the preceding section. This method of expressing the yields as deviations from the average of the herd to which they belong, is a modification of the original "byre average" method used by von Patow (1930). It should, however, be pointed out that von Patow's method has been severely criticised by several authors including Lush (1936) who said, "It seems unlikely that the von Patow method can ever lead to a Mendelian analysis which corresponds at all to reality." But no objection can be raised against the method adopted here when the records are used for the present purpose.

Table 23

Covariation of age at calving, length of preceding calving interval (p.c.i.), and 180 day milk yield

(Age was measured in months, p.c.i. in days and yield in lb.)

Lactation No.	Correlation coefficients *					Regression coefficients				
	Total correlation			Partial correlation		Total regression			Partial regression	
	Age-p.c.i. r_{12}	Age-yield r_{13}	p.c.i.-yield r_{23}	Age-yield $r_{13.2}$	p.c.i.-yield $r_{23.1}$	p.c.i.-age	Yield-age	Yield-p.c.i.	Yield-age	Yield-p.c.i.
1	-	0.122	-	-	-	-	29.150	-	-	-
2	0.416	0.167	0.165	0.110	0.107	0.195	41.638	2.917	29.590	2.039
3	0.356	0.138	0.128	0.100	0.085	0.141	33.639	2.625	25.803	1.851
4	0.292	0.146	0.138	0.112	0.101	0.107	35.015	3.005	27.650	2.276
5	0.360	0.081	0.161	0.002	0.142	0.136	19.640	3.432	6.371	3.224

* The standard error of the correlation coefficients was 0.027 - 0.052.

The number of cows and the averages and standard deviation for yield, age at calving and length of p.c.i. were given in Table 5.

The intensity of the inter-relationships within lactations of age, length of preceding calving interval and milk yield was studied with these data by means of correlation and regression coefficients for the first to fifth lactations. The linearity of the regressions was tested in each case, and it was found that straight lines fitted the data fairly well. The results are presented in Table 23. The first lactation had no calving interval preceding it, and in that lactation the total regression of yield on age was therefore the best measure of the relationship between these two variables. When the age at first calving increased by one month, there was a corresponding increase of 29.15 lb. in the 180 day yield of the first lactation. For the second and subsequent lactations, the **partial** correlations and regressions of yield on age with preceding calving interval held constant, and of yield on preceding calving interval with age held constant, were also calculated. The total correlation between age and yield in the second lactation was 0.167, but when the length of the preceding calving interval was held constant, it decreased to 0.110. Similarly, the total correlation between preceding calving interval and yield was 0.165, but with age at calving held constant, the correlation was 0.107. For the third and fourth lactations the value of the correlation and regression coefficients for age and yield were almost of the same order as those of the second lactation, though somewhat smaller. But by the time the fifth

FIG. 10

TOTAL AND NET REGRESSION OF YIELD ON AGE.

1ST, 2ND, 3RD, 4TH, AND 5TH LACTATIONS.

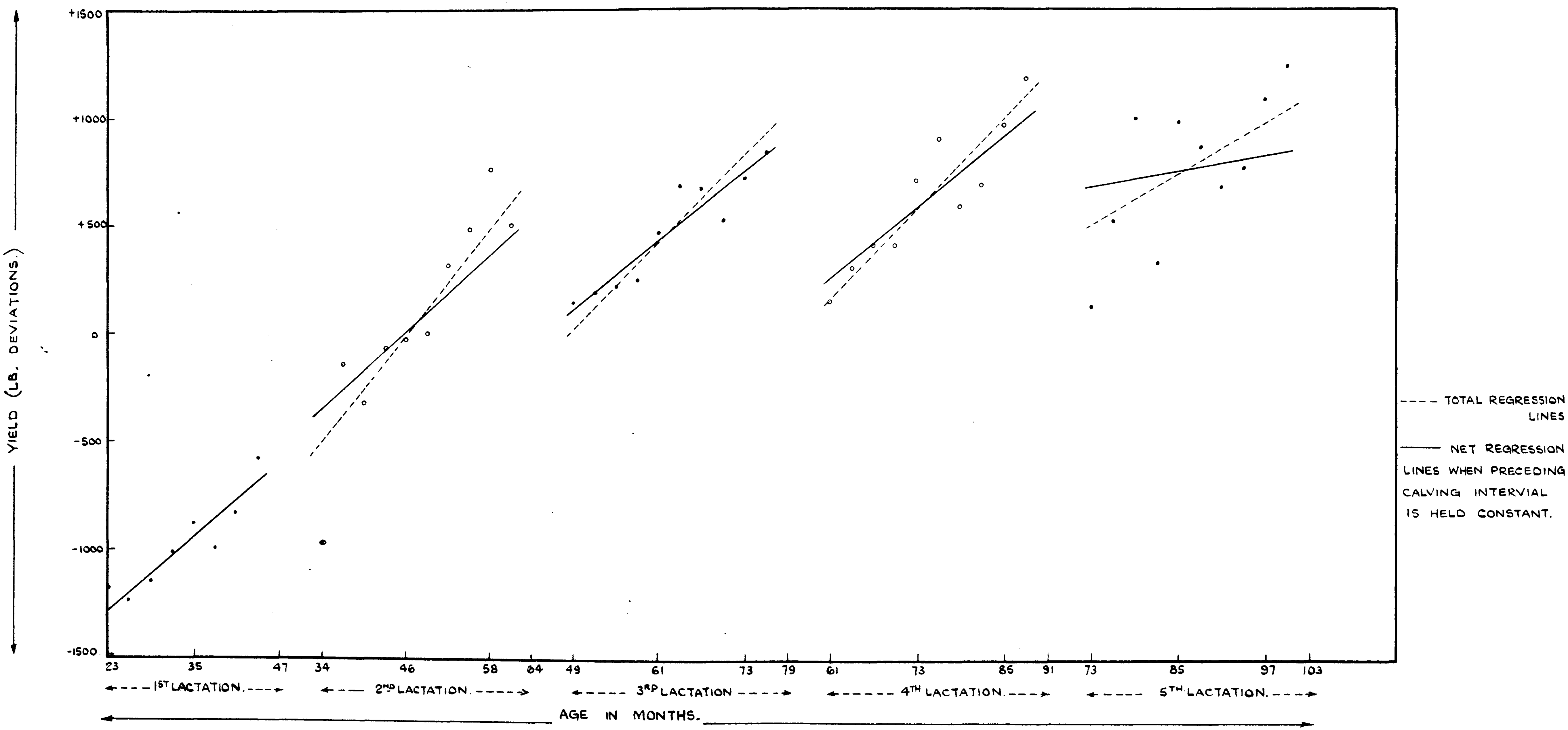


FIG. 10.

lactation was reached, yield was found to be practically independent of age at calving.

Fig. 10 shows graphically the regression of milk yield on age for the first to fifth lactations. The total and net regression lines have been drawn for the second to fifth lactations, but, for the first lactation only one line is presented as this lactation has no calving interval preceding it. The figure shows quite clearly that the yield during the first, second, third and fourth lactations increased markedly with increasing age at calving even when the length of the preceding calving interval was held constant, but the yield during the fifth lactation was practically independent of age.

These results agree in principle with the findings of Kruger (1934) and Johansson and Hansson (1940) that the milk yield of a cow is influenced both by the number of previous lactations she has had, and also by her age at calving. In the light of this, the attempts of other investigators like Sanders (1928), Kay and McCandlish (1929), Glen and McCandlish (1930) and Sikka (1940) to express yield as a function of either age in lactations or age in years and months have not been quite accurate.

Correction of milk yields for age

The standardisation of milk records for age has been attempted by several authors, and there is great diversity in the methods employed. Three main types of corrections may however be distinguished: (a) percentage corrections, (b) regression corrections and (c) addition corrections. The first of these is calculated as a ratio (on a percentage basis) of the value of the standard age to that of the given age. Thus, in order to express the first lactation record of a cow on a mature equivalent basis, it is multiplied by the ratio of the average mature yield to the average first lactation yield of the entire population. This method obviously postulates that the increase in yield with increase in age is proportional to the level of yield of the cow; in other words, the milk yield of a high-yielding cow shows a greater absolute change than that of a poor yielder. This method has, however, been questioned by several workers. Tuff (1931), for example, stated that "the increase in yield from young to full-grown age of an individual cow can neither be summarised by a constant addition nor by a percentage addition alone." He suggested instead that the regression equations expressing the relation between milk yield at the given age and at maturity, should be used for the correction of the actual yield in the first four lactations. This standpoint was also adopted by Ward and Campbell (1938) who adduced evidence "to point quite definitely to the relationship between immature and mature production being of the nature of a regression." But subsequently, several investigators (Johansson and Hansson 1940, Sikka 1940, and others) have pointed out the weakness in using regression equations as a method of standardising records for age, and since then the method has been dropped. It was shown that the regression equations included not only the effect of age but also the effect of any fluctuating or permanent environmental factors, such as changes in feeding and management, which tend to increase or decrease the lactation yield of a 2 or 3 year old cow in comparison with her yield at maturity.

The third method of standardisation for age that has been employed is the addition corrections recommended by Johansson and Hansson (1940). They argued that cows which start with a low first record show a proportionately greater increase in yield with age than cows with a high first record, and therefore percentage corrections based on the entire population would tend to undercorrect the first type of record and overcorrect the second. This has been verified with the present material, and the results shown in Table 24 agree with the findings of these authors. But, when the same cows were classified into groups on the basis of their average yield during the first four lactations, (Table 25), it was observed that cows with a high average level of production increased in yield, from one lactation to another, proportionately as much as the low-yielders. This point was also noted by the Swedish workers. Nevertheless, they argued that although the addition correction does not give good results with consistently high and consistently low yielders, yet, for cows which start with an extremely low or extremely high yield the addition correction works better than a percentage correction. They then concluded that since extreme variations in the first and subsequent lactation yields are caused mainly by environment, it is better from a genetical point of view to use addition corrections rather than percentage corrections.

Table 24

180 day milk yield in the first four lactations of 318 cows classified on the basis of their first lactation production

Lactation No.	180 day yield during the first lactation (lb.)					
	Under 5000		5000-7000		Over 7000	
	Actual yield (lb.)	Relative yield	Actual yield (lb.)	Relative yield	Actual yield (lb.)	Relative yield
1	4556.1	68.5	5824.1	78.4	7812.8	91.0
2	5955.6	89.6	6843.1	92.1	8028.8	93.5
3	6503.6	97.8	7288.7	98.1	8586.7	100.0
4	6649.1	100.0	7426.2	100.0	8438.7	98.3
No. of cows	81		201		36	

Table 25

180 day milk yield in the first four lactations of 318 cows classified on the basis of their average production during the first four lactations

Lactation No.	Average 180 day yield during the first four lactations (lb.)			
	Under 7000		7000 and over	
	Actual yield (lb.)	Relative yield	Actual yield (lb.)	Relative yield
1	5209.5	77.6	6626.1	78.5
2	6140.7	91.5	7814.4	92.6
3	6585.3	98.1	8368.2	99.1
4	6711.8	100.0	8441.8	100.0
No. of cows	202		116	

A further examination of the present data was therefore undertaken with a view to testing the validity of these conclusions. It is no doubt true that no corrections can ever be found which would suit every individual cow in a population equally well. Wherever corrections are calculated for studies in herd analysis, they are based on average results, and therefore great accuracy cannot be attained in the standardisation of individual records. But it is essential that if the correction employed is to be valid and useful, it should be one which is applicable to the population as a whole, independent of the varying level of production of the individual cows - one which is in fact not correlated with it. From the available data, 527 cows whose first three 180 day records could be obtained, were therefore used for the purpose of determining whether percentage corrections or addition corrections satisfy these requirements. The ratio of the third to the first lactation yield, and the difference, - third lactation yield minus first lactation yield, - were calculated for each of these cows. These ratios and differences were then correlated with the corresponding second lactation yields of the respective cows. The results are presented in Tables 26 and 27. The correlation between the difference and the second lactation yield was +0.155 ± 0.043, while the correlation between the ratio and the second lactation yield was +0.010 ± 0.044. This shows that the ratio of one lactation yield to another was independent of the level of production of the cow, but the difference between them was dependent on it. Therefore, it is evident that corrections for age should be proportionate, and not additive as assumed by Johansson and Hansson (1940).

Table 26

Correlation between the third lactation minus first lactation yield and the yield in the second lactation of 527 cows, (180 day yields)

Average third lactation minus first lactation yield	= 1378.09 lb.
Average second lactation yield	= 6722.4 lb.
Correlation coefficient, r =	+0.155 ± 0.043

Table 27

Correlation between the ratio of the third to the first lactation yield and the yield in the second lactation of 527 cows (180 day yields)

Average ratio of the third lactation yield to the first lactation yield	=	1.257
Average second lactation yield	=	6722.4 lb.
Correlation coefficient, r	=	+0.010 ± 0.044

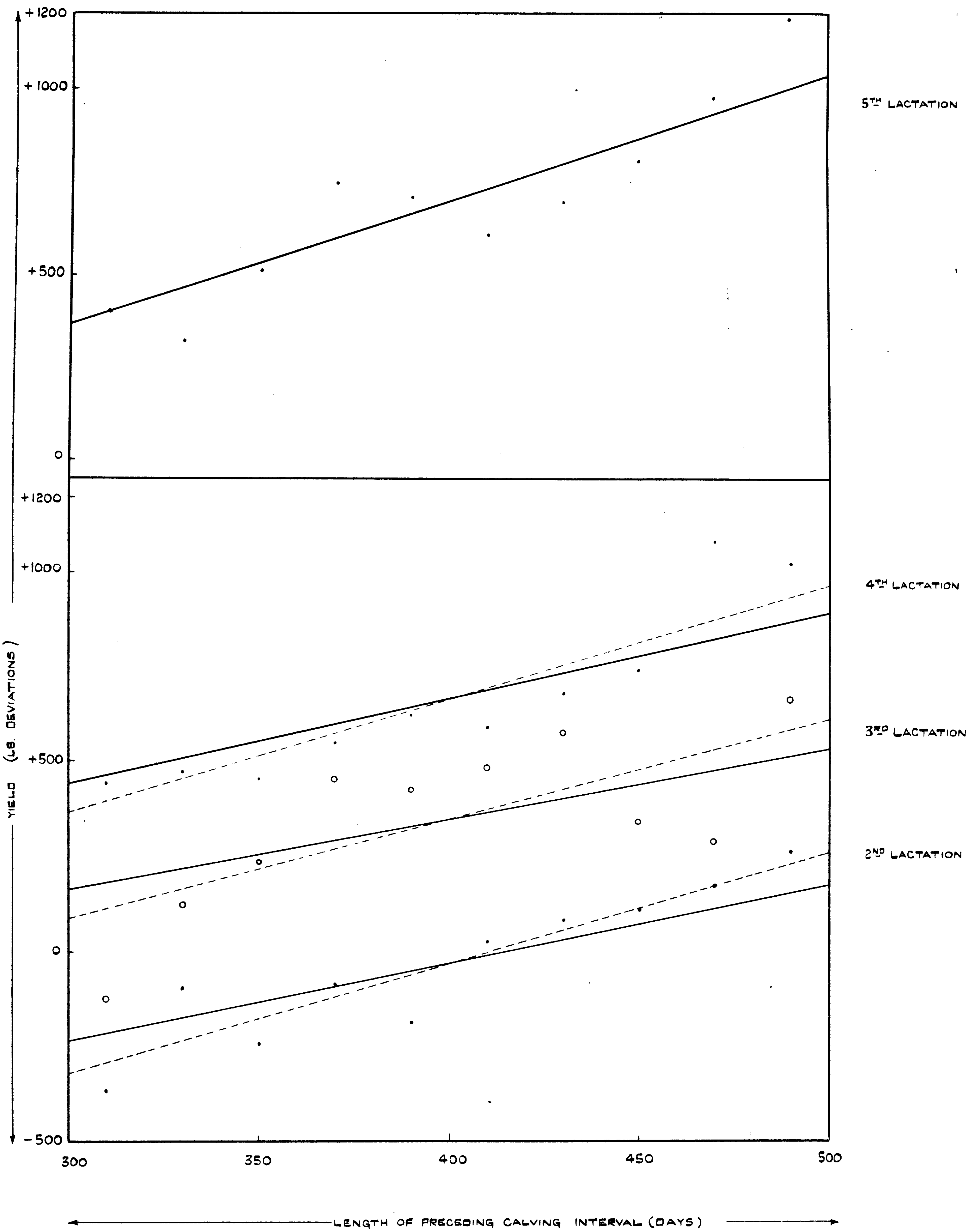
The correction factors for age used in the present investigation are shown in Appendix Table 4. They were based on yields which had previously been corrected for month of calving. The average fifth lactation yield was used as the standard for the age corrections, and the yields during the first to fourth lactations were corrected on this basis. Within lactations, the correction factors were calculated from the net regressions of yield on age with the preceding calving interval held constant. (cf. Table 23 and Fig. 10). The correction of records later than the fifth lactation was not attempted, because the paucity of cows in these groups would make the corrections liable to a high degree of chance variation. Moreover, from a practical point of view, it is better to confine one's attention to the period before the cows attain maturity, because the evaluation of the cows for purposes of selection occurs during the early lactations.

FIG. 11.

FIG. 11

TOTAL AND NET REGRESSION OF YIELD ON LENGTH OF PRECEDING CALVING INTERVAL

2ND, 3RD, 4TH AND 5TH LACTATIONS



- - - - - - - TOTAL REGRESSION LINES

——— NET REGRESSION LINES WHEN AGE IS HELD CONSTANT

6. Influence of preceding calving interval on milk yield

Adequate attention has not been paid by most investigators to the variation of milk yield with length of preceding calving interval. Among the few authors who have given any consideration to this aspect of studies in herd analysis should be mentioned the names of Matson (1929), Gaines and Palfrey (1931), Kruger (1934) and Johansson and Hansson (1940). Most of the other investigators have confined their attention to the variation of milk yield with preceding dry period (which is a part of the preceding calving interval). No attempt has, however, been made in the past to study the influence of either preceding calving interval or preceding dry period on the milk yield of Ayrshire cattle in this country.

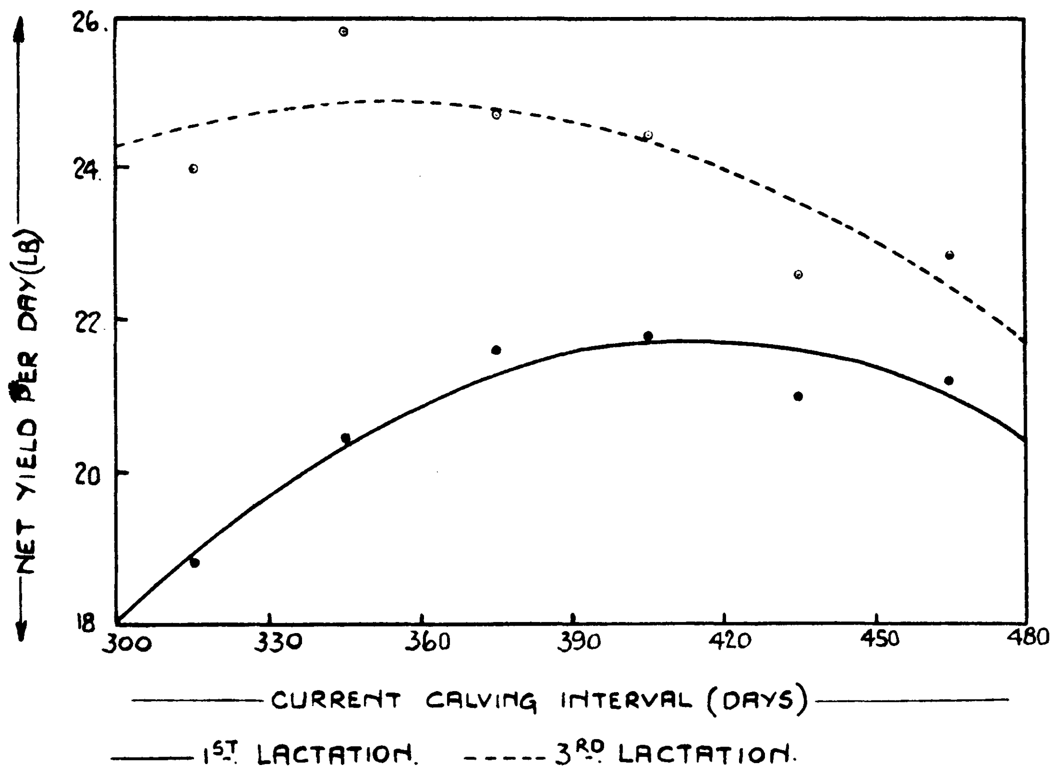
Table 23 shows the results of the analyses of variation of milk yield with preceding calving interval in the present material. It will be observed that an increase in length of the preceding calving interval by 10 days was followed by an increase of 26 to 34 lb. in the 180 day milk yield, but when the age at calving was kept constant, the net increase was 19 to 32 lb. These results are presented graphically in Fig. 11. For the second, third and fourth lactations, the total regression lines as well as the net regression lines with age at calving kept constant, are drawn. For the fifth lactation, the two lines almost coincided with one another, and therefore only one is presented.

It would appear from Table 23 and Fig. 11 that an increase in length of the preceding calving interval contributed very materially to an increased yield in the current lactation. From an economic point of view, however, there is a limit to which the length of the preceding calving interval of a cow could be profitably increased. Since the variations in length of calving interval are almost wholly environmental (the intra-cow correlation within herds was shown to be only -0.024), it should be possible to determine the optimum length of calving interval for the economic production of milk during the lifetime of a cow. Evidently, the best criterion for this purpose is the average daily yield of milk per cow during several years in succession.

Matson (1929), working in India, found that "the optimum calving interval varies directly with milking capacity and inversely with age up to maturity." Gaines and Palfrey (1931) calculated the correlation between preceding calving interval and average daily yield, and also that between current calving interval and average daily yield. They obtained values of +0.142 ± 0.018 and -0.134 ± 0.018 respectively for the two correlations, and concluded that "while there is a small gain from a short calving interval in the current lactation it is very exactly lost in the following lactation." It is obvious therefore, that if the optimum length of calving interval is to be determined accurately, attention must be paid to the effect of the calving interval not only on the current lactation yield but also on the subsequent one.

FIG. 12

RELATION BETWEEN THE LENGTH OF CURRENT CALVING INTERVAL AND THE CORRECTED DAILY YIELD OF MILK.



This was done with the present material by calculating the net effect of the calving interval on the average yield per day after allowance had been made for its effect on the subsequent lactation yield. For each lactation, the total milk yields of the cows were classified into groups according to the length of the current calving interval, using a class interval of 30 days. The yields of the cows during the subsequent lactation were also noted. Each lactation yield was then corrected for the effect of that calving interval on the next lactation, and the resulting figures used to calculate the net average daily yield during the current calving intervals. Table 28 shows the figures obtained by this process for the first, second and third lactations. The results are also presented graphically in Fig. 12 for the first and third lactations. A second degree polynomial was fitted to the actual results in order to obtain the curves. They show quite clearly that the optimum length of calving interval for the first lactation was about 400 days, while for subsequent lactations it was approximately one year. These findings show fair agreement with the practical experience of dairy farmers who calve the heifers in autumn or early winter, and the older cows thereafter in late winter or spring.

Table 28

Relation between the length of the calving interval and the net average daily yield of milk

Lact-ation No.		Length of calving interval (days)					
		301-330	331-360	361-390	391-420	421-450	451-500
1	No. of cows	28	75	192	174	139	126
	Av.daily yield (lb.)	18.82	20.48	21.62	21.82	21.03	21.22
2	No. of cows	37	133	178	105	46	43
	Av.daily yield (lb.)	21.24	21.94	24.34	24.10	23.12	21.73
3	No. of cows	27	118	146	76	25	20
	Av.daily yield (lb.)	24.02	25.85	24.75	24.45	22.67	22.97

The method used here was also employed by Johansson and Hansson (1940) for Swedish Red and White cattle. They found that in their material, the optimum length of calving interval for the first lactation was about 420 days, for the second lactation 400 days, and for later ones about a year. They stated also that persistent milkers should be allowed longer calving intervals than cows which dry off early. This applies equally well to the present data, as illustrated by the fact that first calvers which showed a high persistency used a long calving interval more profitably than older cows.

Correction of milk yields for preceding calving interval

The question whether percentage or addition corrections should be used for the influence of the preceding calving interval on milk yield has been investigated with the present data. For this purpose, the cows were classified into three groups on the basis of their average 180 day milk yield during the first four lactations, and the regression of yield at maturity (3rd to 6th lactations) on length of preceding calving interval was determined within each group. The results are presented in Table 29.

Table 29

Regression of 180 day milk yield (lb.) on length of preceding calving interval (days) within groups of high- and low-yielding mature cows

Number of cows	Average 180 day milk yield (lb.)	Regression coefficient (yield - preceding calving interval)
207	5962.7	0.824
378	7182.8	2.265
327	8339.4	2.763

The trend of the regression coefficients shows that cows on a high level of production increased their yield with increase in length of preceding calving interval, proportionately more than low producers. Therefore, percentage corrections would be more appropriate than the use of constant additions for variations in length of calving interval; there is no justification for the method of constant additions employed by Johansson and Hansson (1940).

The actual correction coefficients used in the present investigation are shown in Appendix Table 5. The corrections for the second, third and fourth lactations were based on the net regression of yield on length of preceding calving interval with the age at calving held constant (cf. Table 23 and Fig. 11). For the fifth and later lactations, the total regressions were used because age at calving had little or no influence on these yields. The standard length of calving interval employed for the calculation of the correction factors varied from one lactation to another according to the mean for the particular population. The average yield for the whole population remained practically unchanged by this method of correction.

Table 30

Effect of corrections on the total variance in milk yield (180 days) during the first four lactations of 326 cows

Source	Mean 180 day yield (lb.)	Variance	Variance after correction to a mean yield of 6748.2 lb.	
			Corrected variance	Relative values
Uncorrected records	6748.2	1,780,930.02	1,780,930.02	100.0
Corrected for month of calving within herds	6782.4	1,746,858.89	1,729,286.38	97.1
Corrected for month of calving within herds and age in lactations	7420.0	1,616,843.72	1,337,322.44	75.1
Corrected for month of calving with herds, age in lactations and age at calving in years and months	7418.5	1,575,933.87	1,304,012.28	73.2
Corrected for month of calving within herds, age in lactations, age at calving in years and months and length of preceding calving interval.	7421.7	1,570,812.67	1,298,654.12	72.9

7. The effect of corrections for non-genetic factors on the variation in milk yield

The effect of corrections on the variation in milk yield has been studied by a comparison of the "raw" and standardised 180 day records of 326 cows, each of which had completed the first four lactations. The results of this study are summarised in Table 30.

It will be observed that an appreciable reduction in variance has been brought about by standardisation for month of calving within herds, age in lactations, age at calving in years and months within lactations, and length of preceding calving interval. The total decrease in variance was found to be 11.8 per cent., but the mean itself increased from 6748.2 lb. to 7421.7 lb. When the variance was corrected for this change in mean, the reduction in variance was 27.1 per cent. A study of each stage of standardisation separately, gives the following distribution of variances:-

	Percentage reduction of the total variance
Standardisation for month of calving within herds	2.9
Standardisation for age in lactations	22.0
Standardisation for age in years and months within lactations ...	1.9
Standardisation for length of preceding calving interval	0.3
Total	27.1

The greatest reduction in variance was brought about by standardisation for age in lactations. A smaller fraction was accounted for by the month of calving and age within lactations. But, only 0.3 per cent. of the total variance was attributable to the length of the preceding calving interval. It should, however, be pointed out that the correction for preceding calving interval was mainly effective for cows with very long or very short calving intervals preceding their lactations. These were relatively few in number, and it was therefore to be expected that the average reduction in variance for all cows in a population would be low. Nevertheless, it would still be useful for those cows which may be termed the extreme variates.

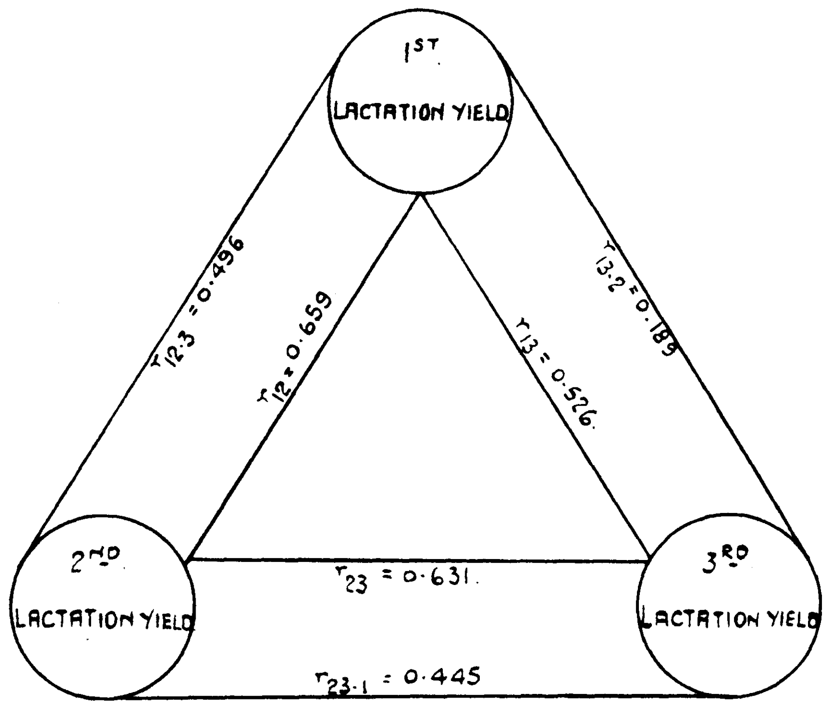
8. Relative value of different records for estimating producing ability

From their study of the relative usefulness of the first three lactation records as indicators of the cow's real producing ability, Johansson and Hansson (1940) concluded that the second lactation record is the least dependable of the three, and that it should consistently be excluded from any estimates of a cow's production capacity. An extensive study of this question was made in relation to the present data, and the results outlined below showed on the other hand that there were no significant differences among the first three records in their ability to reflect the cow's hereditary type for milk yield.

Table 31 shows the variance of the first three lactation records (180 days) before and after correction for the differences in mean yield. The relative values of the corrected variance are given for purposes of comparison, and it will be observed that they showed very little variation from the first to the third lactation. In Johansson and Hansson's material, the variance of the first lactation yield was found to be about 18 per cent. lower, and that of the second lactation 18 per cent. higher than the variance of the third lactation. It should, however, be noted that their second lactation records were rather abnormal in that the dry period preceding that lactation was on the average 25 days shorter than in other lactations.

FIG. 13

CORRELATION BETWEEN THE 180 DAY MILK YIELDS OF THE FIRST THREE LACTATIONS. (AFTER CORRECTION)



(THE STANDARD ERROR OF THE PRIMARY CORRELATION COEFFICIENTS IS 0·025 - 0·032)

Table 31

The variance of the first three lactation records (180 days) before and after correction for differences in mean yield

Lactation No.	No. of cows	Mean 180 day yield (lb.)	Variance	Variance after correction to a mean yield of 7000 lb.	
				Corrected variance	Relative values
1	1211	5571.8	972,590.4	1,535,094.2	99.8
2	915	6553.9	1,306,449.0	1,490,352.2	96.9
3	688	6994.1	1,535,616.6	1,538,208.5	100.0

The relative usefulness of the first three records was also studied by the correlation method. The first, second and third lactation records (180 days) of 513 cows which had previously been corrected for month of calving, age and length of preceding calving interval, were used for this purpose. All the possible correlations between the first three records were calculated, and the results are presented in Fig. 13. They show that the correlations between the second lactation on the one hand, and the first and third lactations on the other, were very similar. The comparatively low correlation between the first and third records was of course to be expected, because the environmental factors and the condition of the cow would be less similar when the records were further apart in time than when they were close together. The partial correlation coefficients which are presented in the same figure, also point quite clearly to the fact that the correlation between non-consecutive lactations was definitely poorer than between consecutive lactations. The high total and partial correlations shown by the second lactation yield with the first and third indicate that the second record would be quite satisfactory for estimating a cow's producing ability.

In Table 32, the results obtained by correlating each of the first, second and third lactation yields of 187 cows with their average yields during the fourth and fifth lactations, are presented. The total and within herds correlations were determined for both "raw" and corrected 180 day yields. The trend of the correlation coefficients shows once again that their value increased gradually as the records approached each other in time. The values of the coefficients for the second lactation showed no evident deviation from this general trend, and it can therefore be concluded from these data that the second lactation record would be as reliable as any other in evaluating the cow's genotype for milk yield.

Certain other information presented in Table 32 may now be considered. This table contains in addition to the correlations reported in the preceding paragraph, two further sets of correlations. These were obtained by correlating the average of the fourth and fifth lactation yields of each cow with the average of the first and second, and with the average of the first, second and third lactation yields of the same cows. It will be observed that these correlations were of the same order as the corresponding ones obtained by correlating the average of the fourth and fifth lactation yields with each of the second and third lactation yields; - in most cases they were even slightly smaller than the latter. This means that the probable yield of a cow at maturity (fourth or fifth lactation) can be predicted as accurately from the third lactation as from the first three lactations together. In other words, as Sikka (1940) also concluded, "where the yield of the preceding lactation is known, there is little gain in considering the production of any of the other past lactations to estimate the probable yield in a future lactation."

Table 32

Correlation between the 180 day yield of each of the first three lactations and their averages, and the 180 day yield at maturity

Lactation No.	Raw 180 day yield		Corrected 180 day yield	
	Total correlation	Within herds correlation	Total correlation	Within herds correlation
1	+ 0.453	+ 0.385	+ 0.469	+ 0.392
2	+ 0.554	+ 0.476	+ 0.599	+ 0.507
3	+ 0.712	+ 0.641	+ 0.702	+ 0.617
Av. 1 & 2	+ 0.551	+ 0.480	+ 0.583	+ 0.505
Av.1,2 & 3	+ 0.653	+ 0.587	+ 0.670	+ 0.597

9. Variance of milk yields due to differences between herds and years

It was shown in a preliminary analysis of variance of the average 180 day milk yields of each herd in each year from 1930 to 1938, that there was no evidence of a permanent change in yield through the nine years studied. On the other hand, the differences in herd means were found to be highly significant. It was pointed out, however, that since the analysis was based on average figures, the results might not agree completely with those obtained from detailed analyses using the individual yields of cows. The present section is therefore devoted to a detailed study of the variance of milk yields due to differences between herds and years.

The analysis reported here was based on 1138 first lactation records of cows from the 12 herds over a period of nine years (1930 to 1938). It was evident at the outset, that owing to unequal numbers in the subclasses the estimates of the population variance obtained by straightforward statistical methods would not all be independent. The following method of overcoming this difficulty was therefore suggested by Dr R.A. Robb, and was adopted.

An estimate of the variance within each subsample was first made by considering the data as being classified one-way into 108 subsamples. This estimate would be independent of any estimate based on the means of subsamples, and has accordingly been used throughout as the best estimate of the population variance. The results of this analysis are summarised in Table 33.

Table 33

Analysis of variance

Source	d.f.	Sum of squares	Estimated variance
Between subsamples	107	354,959,500	
Residual	1030	773,739,932	750,233
Total	1137	1,127,699,432	

The other independent estimates of the population variance that had still to be obtained were :-

(i) an estimate based on the mean yields of the herds over the whole period,

(ii) an estimate based on the mean yields in different years of all herds, and

(iii) an estimate based on the mean yields of particular herds in particular years, i.e. on the mean yields of subsamples.

The method adopted to obtain these was founded on empirical evidence and gave sufficiently accurate results. It consisted of replacing the actual numbers in each subsample by proportionate numbers, altering the original data accordingly, and finding the estimates (i), (ii) and (iii) from these adjusted data in the usual way. This method is applicable only where the actual numbers are not too disproportionate. The fact that it was applicable to the present data was therefore verified by using the chi-square test for the actual and theoretical proportionate numbers. It was found that the hypothesis of proportionality in the population was acceptable, and therefore the empirical method was used in the analysis of variance. The results are summarised in Table 34.

Table 34

Analysis of variance

Source	d.f.	Sum of squares	Estimated variance
Between herds	11	208,238,744	18,930,795 (i)
Between years	8	32,945,849	4,118,231 (ii)
Interaction	88	99,660,063	1,132,501 (iii)
Between sub-samples	107	340,844,656	

Comparison of estimate (iii) of the population variance with the original best estimate showed significant interaction. Comparison of estimate (i) with estimate (iii) gave a significant difference. Similarly estimate (ii) was significantly different from estimate (iii) (on the 1 per cent. level).

The following conclusions emerge from this analysis :-

(1) There was a significant difference between the yields of different herds.

(2) There were significant differences between years applicable to all herds.

(3) There were significant herd year interactions, i.e. the yields of different herds tended to change at different rates over the period.

From a genetical point of view, the question now arises, what proportion of these differences between herds and years was due to environmental causes, and what proportion could be attributed to differences in heredity? If it were possible to estimate the magnitude of the environmental fraction, then obviously a more accurate evaluation of the inherent differences between cows could be obtained after elimination of the environmental differences. But unfortunately, no satisfactory method of estimating the two components separately has hitherto been discovered. In fact, it seems almost impossible with the present type of data to arrive at any satiwfactory conclusions in regard to this matter. However, with the increasing use of the same bulls in different herds by artificial insemination, it should be possible in the future to obtain an adequate basis for estimating genetic differences in levels of production between herds. The little evidence that has hitherto been collected along these lines (Rendel and Robertwon - private communication) suggests that the greater part of the differences between herds is due to management. Until more data are forthcoming, it will be well to refrain from any further discussion of this point.

10. Study of the genetic improvement in milk yields achieved by selection

It is a well known fact that in the breeding of any population, there is an inevitable selection of certain individuals over others on the basis of their phenotypic qualities. These qualities naturally vary from one population to another. However, in the breeding of dairy cattle in this country, the yield of milk appears to form the main basis for the selection that has been practised by herd owners up to the present day. It seems desirable therefore to determine what effect this selection has probably had on the productive level of different herds of dairy cattle during a given time.

The original methods employed for this purpose by Ryde (1936), Lortscher (1937), and Nelson (1943) were based on the assumption that if changes due to age are allowed for, the difference in the yields of the same cows in successive years is due to environment. The genetic change in the whole population for the period under study, could then be determined by subtracting the environmental fraction calculated above, from the total. But owing to the fact that it is impossible to segregate fully the effect of a more or less continuous improvement in environment from the effect of the change in age of the cows, the conclusions drawn from such studies cannot be considered satisfactory. In 1944, Dickerson and Hazel, in their paper on the effectiveness of selection on progeny performance, suggested a method of estimating the rate of genetic improvement for a known selection programme. The application of this method to milk yield data has been extensively developed by Rendel and Robertson (1949), and it is this method which is employed here.

The performance of a cow is generally judged by the dairy farmer on the basis of the total milk yield during one or more lactations. It was therefore decided that for this study on selection, it would be preferable to use total lactation yields rather than figures based on a partial lactation period of 180 days. The intensity of selection practised in the 12 herds was then calculated in terms of selection differentials, i.e. the difference between the average yield of the animals chosen as parents and the average of their own generation. For this purpose, the cows were classified into six groups of contemporaries, and the phenotypic selection differential was calculated within each group by weighting the first lactation record of each cow according to the number of daughters she left in the herd, and comparing the average yield obtained by this process with the average of all first lactations in the group. This apparent phenotypic selection differential was converted to a genetic measure by multiplying it by the appropriate figure for heritability - the effective heritability being taken as 0.25 for the present data (see Part V). The results are summarised in the third column of Table 35 under the heading, "genetic superiority of dams based on first lactation."

Table 35

Estimation of selection differential from culling practised

Period	Selection differential on 1st lactation * (gallons)	Genetic superiority of dams		Number of daughters in herds
		based on 1st lactation (gallons)	based on 1st to 4th lactations (gallons)	
1	+ 10.6	+ 12.4	+ 33.4	147
2	+ 25.5	+ 0.9	+ 19.0	112
3	+ 41.3	+ 23.5	+ 28.0	135
4	+ 14.4	+ 13.9	+ 21.3	148
5	+ 29.6	+ 20.3	+ 25.7	153
6	+ 24.0	+ 9.9	+ 23.2	135
Total	+ 24.1	+ 14.1	+ 25.4	830

* Mean of first lactations of cows having second lactations minus mean of all first lactations.

However, in the breeding of dairy cattle it is found that not all the selection takes place on the basis of the first lactation itself. The actual amount of culling on first lactation can, in fact, be calculated* by comparing the first lactation yield of cows that also have a second lactation, with the average first lactation yield for the whole group. The results obtained from this calculation are presented in the second column of the same table. As Rendel and Robertson (1949) have pointed out in their paper on the estimation of genetic gain in a closed herd of dairy cattle, "the lack of correspondence between the two columns (the second and third columns in this case) is a reflection of the degree to which parenthood was independent of culling." If all the culling had taken place on the first lactation and none of the culled stock left any progeny in the herds, then it is evident that the figures in the third column would be one quarter of those in the second. The fact that this was not so in the present data shows that the genetic superiority of the cows chosen to be parents of the next generation of females, should be calculated on the basis of all available records. This is given by the following formula arrived at by Rendel and Robertson (1949):-

$$I_{CC} = \Sigma\, nh_1^2\,(Y_1 - \bar{Y})$$

where I_{CC} is the genetic superiority, h_1^2 is heritability based on 1 lactations, $\bar{Y}$ is the mean of the first lactations of the whole group, Y_1 is the mean of the lactations (corrected to first lactation) and n the number of daughters, for each cow. The figures obtained by this process are shown in the fourth column of Table 35 and give a total of 25.4 gallons.

Dickerson and Hazel (1944) have pointed out, however, that the best criterion of the efficiency of any breeding programme is the genetic improvement per year rather than per generation. Therefore, the value of 25.4 obtained above, must be divided by the total generation length in order to obtain the annual improvement. It has been shown by Rendel and Robertson (1949) that the total generation length, ΣL, for dairy cattle can be calculated as the sum of the four components L_{CC}, L_{CB}, L_{BC} and L_{BB}, where L_{CC} is the mean age of the dams when the heifer calves are born, L_{CB} is the mean age of the dams when the bull calves are born, and so on. The generation lengths for the 12 herds of dairy cattle used in the present study were found to be as follows :-

$$L_{CC} = 63 \text{ months}$$
$$L_{CB} = 78 \text{ months}$$
$$L_{BC} = 46 \text{ months}$$
$$L_{BB} = 47 \text{ months}$$
$$\Sigma L = 19.5 \text{ years}$$

Therefore, the genetic improvement per year through the selection of dams of cows is given by $\frac{25.4}{19.5} = 1.3$ gallons. Since the average yield per cow in the whole population studied was around 1000 gallons, this means a rate of genetic improvement of 0.13 per cent. per year.

The rate of improvement calculated above was due to the selection of dams of cows. The same method could be applied to determine the improvement achieved through the selection of dams of bulls as well. The sum of these two results would give the total improvement achieved by selection in the 12 herds, since no selection is practised on the male side (unless progeny-testing is adopted). However, with the present data, it was not possible to calculate the improvement due to the selection of dams of bulls, because most of the sires used were bought in from other herds, and the data relating to these herds were not available for study.

A detailed analysis has been made of the genetic improvement attained through the selection of dams of cows in each of the 12 herds, and the results are presented in Appendix Tables 6 and 7. They are self-explanatory. The final figures for the improvement per year were, however, found to be a little smaller than the actual values presented in Appendix Table 7, when allowance was made for the fact that some breeding stock was occasionally bought into the herds from outside. In fact, an overall value of 0.11 to 0.12 was obtained for the effective genetic improvement by multiplying the calculated values by the proportion of home-bred heifers.

These results for Ayrshire cattle show fair agreement with those obtained by Rendel and Robertson for Kerry (private communication). It would appear from this that the actual improvement attained in most herds through the selection of dams of cows is, on the average, only about one gallon in a thousand gallons per year. Comparison of this figure with the theoretical estimates made by Rendel and Robertson of the maximum possible improvement by this method, shows that only one half of the possible improvement was attained by these herds. The fact that in certain herds, i.e. Herds B and C, values of the order 0.22 and 0.27 were obtained could be attributed chiefly to sampling errors arising from a skewness in the population.

There are many reasons why the rate of improvement actually attained in most herds is only about one half of the maximum possible value. In the first place, all the selection is not directed towards milk yield only; there may be selection for other characteristics such as type and conformation, and this would tend to lower the selection differential on yield. Secondly, there is the fact that selection as practised in most herds, is very often incomplete, in that the offspring of cows which are themselves culled for low production are frequently incorporated into the herd. In consequence, what is effectively a cull becomes part of the breeding stock for the next generation. These, and numerous other factors, show that the breeding of dairy cattle by mass selection can only be a very slow process, and the results obtained from the present study of 12 leading herds of Ayrshire cattle prove that it cannot be expected to bring very satisfactory results.

PART III

Studies in Persistency of Lactation

Part III

Studies in Persistency of Lactation

1. Measures of persistency

Previous investigations into the shape of the lactation curve have drawn considerable attention to its importance in dairy cattle breeding. For example, Bonnier (1935) adduced evidence which pointed to the conclusion that the shape of the lactation curve is "constitutionally determined", and he emphasised the necessity of "seriously studying the question as to the possible hereditary nature of the shape of the lactation curve." Other investigators, notably Gaines (1927, 1931), Gooch (1935), Sikka (1940) and Johansson and Hansson (1940) have probed further into this problem, and although their results are not in complete agreement, most of them show that the shape of the lactation curve exerts a fair measure of influence on the total lactation yield. The present investigation on persistency of lactation was undertaken in order to obtain further information on this subject.

Part of the variation in results obtained by previous investigators could be attributed to differences in the techniques employed to analyse the shape of the lactation curve. An attempt was therefore made at the commencement of this investigation to apply some of these methods to the present data and determine the nature of the results obtained. The first method employed consisted of finding a mathematical interpretation to the shape of the lactation curve. It may be noted in this connection that Gaines (1927, 1931) and Gooch (1935) fitted exponential curves to milk yield data, while Sikka (1940) worked with parabolic exponential curves as well. In the present instance, the search for a representative mathematical curve was extended to cover in addition orthogonal polynomial regression curves of higher degrees. The Kirkhill herd belonging to the Hannah Institute was used for this purpose, and in order to ensure greatest accuracy, both monthly and weekly records of cows were studied. But the varying results that were finally obtained showed that these attempts were beset with numerous pitfalls and would hardly compensate for all the work. For example, it was found in some cases that the third and fourth degree terms brought highly significant reductions in the errors of estimate, while in others they were not significant at all. This meant that the cows in the present study would have to be classified into different groups on the basis of the best-fitting orthogonal polynomial, and this in turn would have led to the highly questionable position of making between-group comparisons of this type. This was obviously very unsatisfactory, and therefore the fitting of orthogonal polynomial regression curves was abandoned.

A measure based on the linear regression of yield on time was then tested as a means of describing the shape of the lactation curve. This measure was also used by Bonnier (1935) and Kronacher <u>et al</u>. (1936) with slight differences in detail, but they obtained rather unsatisfactory results, probably on account of the fact that the time of maximum yield and the commencement of drying-off, between which periods they measured the regression, varied naturally from one cow to another. In the present study, the length of time was fixed as the period between the 30th and 300th day, and the results were then more consistent. Nevertheless, this method was not adopted for the rest of the study, because it was found that the shape of individual lactation curves was far too variable to be represented by any rigid mathematical curve.

Moreover, any attempt to measure the shape of the lactation curve should take into consideration the two segments that are typically characteristic of it - the rising segment and the declining segment. The rising segment is that phase of production following parturition, during which the milk yield of a cow increases. Individual cows differ considerably in regard to the period for which this rise lasts; some show a rise for only a few days after calving, but in others the increasing phase in production lasts for several weeks. On the average however, almost all cows reach their peak within the first ten weeks of calving. Thereafter, the rate of secretion begins to decline, and here again individual cows differ considerably. Some decline in yield very rapidly after the period of peak production, while others more or less maintain their initial level of production over a considerable period, and show little or no decline. The former are termed non-persistent, and the latter, persistent cows. Persistency therefore is a measure of the shape of the lactation curve, and it determines the degree to which the milk yield in early lactation is maintained by a cow during the rest of her lactation. A numerical expression of persistency can therefore be obtained by comparing the yield after the period of peak production with the initial yield. Such a figure has been used throughout the present investigation, and is given by the formula :-

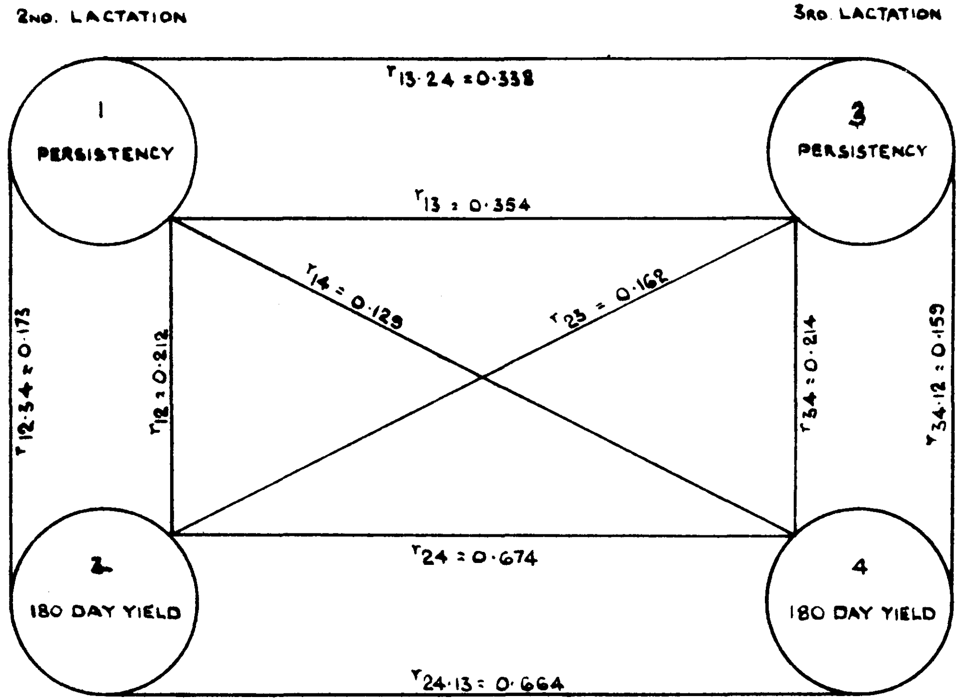
$$\text{Persistency} = \frac{A-B}{B},$$

where A is the yield during the first 180 days and B is the yield during the first 10 weeks.

The concept underlying this numerical measure of persistency is in essence, the same as the "shape-figure" used notably by Johansson and Hansson (1940) and also by other investigators. Johansson and Hansson split up the lactation period of each cow into 100-day periods, and used the ratios between the butterfat yields in the different periods as measures of persistency. The chief drawback to their method is that the first 100-day period which is taken to represent the time of maximum physiological activity of the cow, includes a considerable portion of the declining segment of the lactation curve; and therefore it does not provide a sufficiently sensitive measure of persistency when it is compared with the second 100-day period. Among later workers, Ludwick and Petersen (1943) have evolved a formula for persistency which is based on "a summation of the ratios obtained by comparing production in each of a number of subdivisions of the lactation period with the preceding one." But, in their computations they have omitted the yield during the first seven weeks of production - a step for which there is little justification in the light of present-day knowledge on the physiology of lactation.

FIG 14.

CORRELATION BETWEEN THE PERSISTENCY AND 180 DAY YIELD OF THE SECOND AND THIRD LACTATIONS.

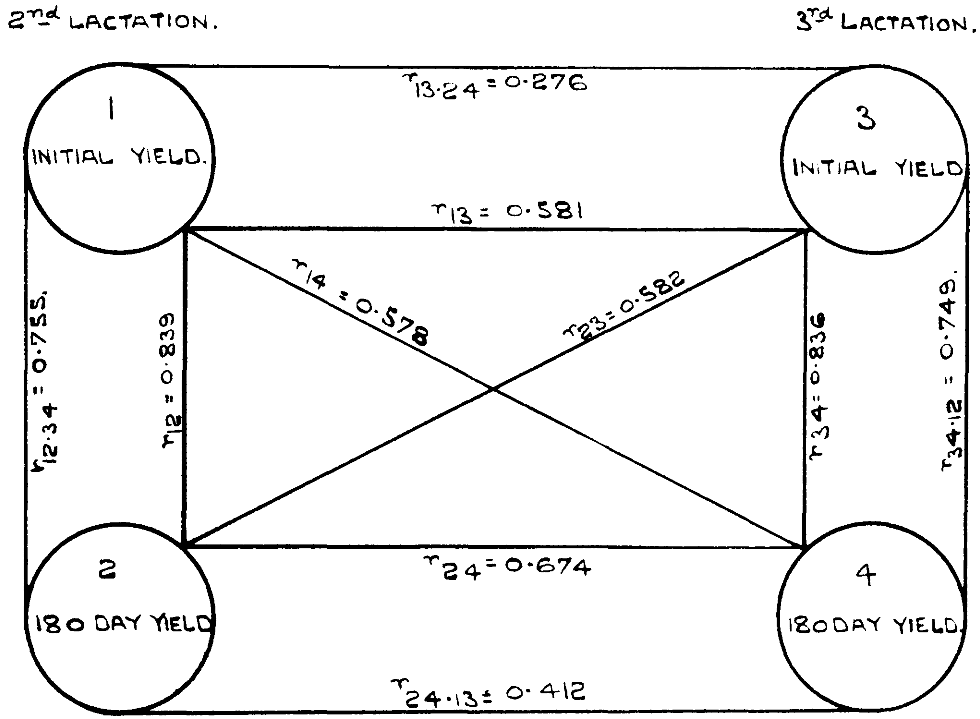


(THE STANDARD ERROR OF THE PRIMARY CORRELATION COEFFICIENTS IS 0·019 - 0·035)

FIG. 15.

CORRELATION BETWEEN THE INITIAL AND 180 DAY YIELDS.

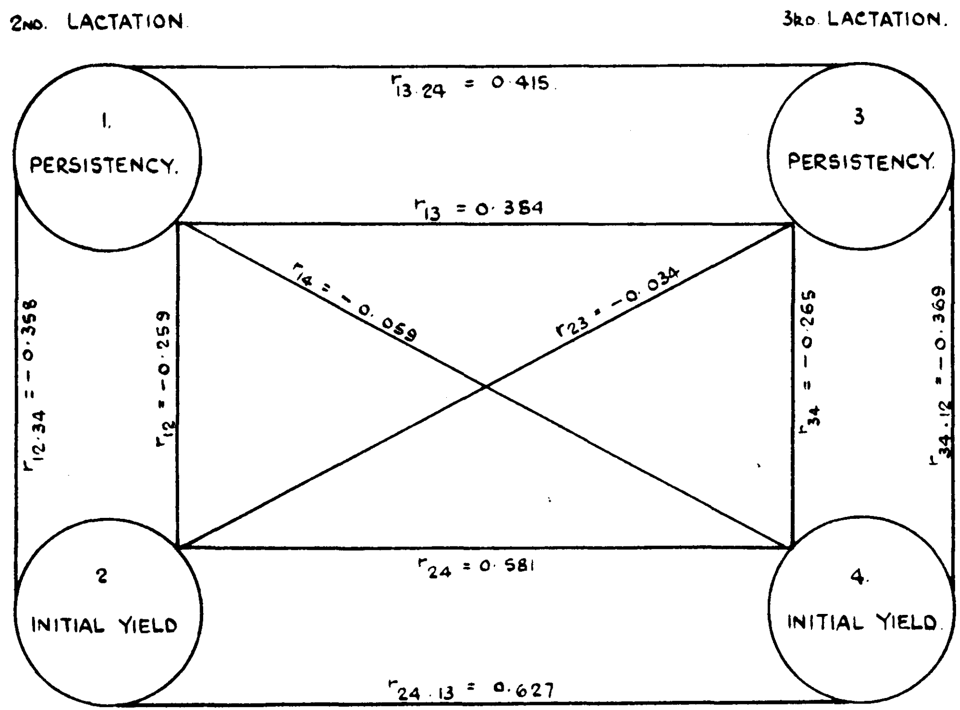
OF THE SECOND AND THIRD LACTATIONS.



(THE STANDARD ERROR OF THE PRIMARY CORRELATION COEFFICIENTS IS 0·010 – 0·024.)

FIG 16.

CORRELATION BETWEEN THE PERSISTENCY AND INITIAL YIELD OF THE SECOND AND THIRD LACTATIONS.



(THE STANDARD ERROR OF THE PRIMARY CORRELATION COEFFICIENTS IS 0·023 - 0·035)

2. Relationship between persistency and yield

The average values of persistency during the years 1930 to 1938 for each of the 12 herds studied, are summarised in Appendix Table 8. Comparison of these figures with the corresponding ones for initial and 180 day milk yields (Appendix Tables 1 and 2), shows that in some herds, a combination of high persistency and high initial and 180 day milk yields was achieved to a fair extent; in others, only one or two of these three characteristics seem to have been incorporated to any great degree. A study of the inter-relationships of these three variables in milk production was therefore undertaken in order to determine how far they are compatible with each other.

For this purpose the second and third lactation figures of 588 cows from the 12 herds were employed, and all the possible correlations among the variables were calculated (Figs. 14, 15 and 16). The correlation between the 180 day milk yield and persistency of the second lactation was found to be 0.212, and the corresponding coefficient for the third lactation was 0.214. The regression of the 180 day milk yield on persistency was 1219.0 and 1221.6 for the second and third lactations respectively. Persistency therefore contributes to a high total yield (as measured by the 180 day period). However, the latter seems to be more closely correlated with initial yield than with persistency - the correlations between initial and 180 day yields being 0.839 and 0.836 for the second and third lactations respectively.

While the above-mentioned correlations were all positive, it was found that the correlations between persistency and initial yield were negative. The observed correlations for these two characteristics were of the order -0.259 and -0.265 respectively for the second and third lactations. However, in interpreting these correlations it should be remembered that they are all compound values derived by lumping together the records of cows belonging to 12 different herds. In order to elucidate the true relationship between cows it is therefore necessary to determine separately the contribution of the different components - "between herds", "between cows within herds" and "within cows" - to the total correlation. The desirability of obtaining such information is important particularly in regard to the relationship between persistency and initial yield, because if the persistency and initial yield of different cows are found to be truly negatively correlated, it will show that it would be difficult to combine in one and the same cow the two desirable characteristics, high persistency and high initial yield.

It may be noted in this connection that most studies in the past (Gaines 1927, Sanders 1930 and Gooch 1935) have not taken this into account. Sikka (1940) seems to be the only author who has paid some attention to this problem, but he has not considered fully the difficulties of application of the analysis of variance and covariance to binomial data.

The results of the present study based on the third, fourth and fifth lactation records of 263 cows from 12 herds are detailed below.

(a) Relationship between persistency and initial yield

The total correlation between the persistency and initial yield of the 789 lactations from this data as shown in Table 36, was -0.202 ± 0.034. This means that there was a significant negative relationship between these two variates when the data were taken as a whole.

Table 36

Covariation between persistency and initial milk yield *

Source	d.f.	Variance		Covariance	Correlation coefficient ∅
		Persistency	Initial yield		
Total	788	0.0374	353,578.95	-23.258	-0.202±0.034
Between herds	11	0.0034	66,758.51	- 6.315	-0.419±0.248
Between cows within herds	251	0.0101	121,790.88	+ 8.175	+0.233±0.060
Within cows	526	0.0239	165,029.56	-25.118	-0.400±0.037

* Cf. Hazel, Baker and Reinmiller (1943) for the method employed to partition the variance and covariance.

∅ The standard errors of the first three correlation coefficients are slightly underestimated by this method of analysis.

After elimination of the differences between herds this correlation was split up into a correlation between cows in the same herd, r = +0.233, and another "within cows", r = -0.400. The between herds value was -0.419. This correlation based on 11 degrees

Table 37

Covariation between persistency and 180 day milk yield*

Source	d.f.	Variance		Covar-iance	Correlation coefficient ∅
		Persis-tency	180 day yield		
Total	788	0.0374	1,806,670.73	+62.610	+0.241±0.034
Between herds	11	0.0034	277,936.22	- 3.580	-0.116±0.297
Between cows within herds	251	0.0101	824,580.89	+48.655	+0.533±0.045
Within cows	526	0.0239	704,153.62	+17.535	+0.135±0.043

* Cf. Hazel, Baker and Reinmiller (1943) for the method employed to partition the variance and covariance.

∅ The standard errors of the first three correlation coefficients are slightly underestimated by this method of analysis.

of freedom was not significant, and it therefore suggests that between herds the persistency was independent of the initial yield. The correlation between cows within herds, however, was positive and highly significant, while the intra-cow correlation also attained a highly significant value but was negative. This means that the persistency of different cows was really positively correlated with their initial levels of production, and the negative relationship between persistency and initial yield observed in the total data was actually due to the pronounced "within cows" effect. It should therefore be quite feasible to combine in any one cow the two desirable characteristics, high persistency and high initial yield. But the capacity of any one cow for each of these qualities would appear to be fixed for life, so that if the initial yield rises above her optimum level, the persistency is diminished and vice versa.

These results suggest that the negative correlations between maximum yield and persistency reported by Gaines (1927), Sanders (1930) and Gooch (1935) were really due to the contribution of the "within cows" component.

(b) <u>Relationship between persistency and 180 day yield</u>
It will be observed from Table 37 that all the correlations except that "between herds" were highly significant. The correlation between cows was the highest, while the lowest value was obtained within cows. This low intra-cow correlation between persistency and 180 day yield could be attributed to the negative intra-cow

Table 38

Covariation between initial and 180 day milk yields *

Source	d.f.	Variance		Coveriance	Correlation coefficient ⌀
		Initial yield	180 day yield		
Total	788	353,578.95	1,806,670.73	+717,808.78	+0.898±0.007
Between herds	11	66,758.51	277,936.22	+129,419.89	+0.950±0.029
Between cows within herds	251	121,790.88	824,580.89	+299,877.76	+0.946±0.007
Within cows	526	165,029.56	704,153.62	+288,511.13	+0.846±0.012

* Cf. Hazel, Baker and Reinmiller (1943) for the method employed to partition the variance and covariance.

⌀ The standard errors of the first three correlation coefficients are slightly underestimated by this method of analysis.

correlation between persistency and initial yield reported in the preceding paragraph.

These results differ from the findings of Gooch (1935) who observed no evidence of any correlation between persistency and total yield ($r = -0.050 \pm 0.026$). They agree however, with the results of Gaines (1927), Sanders (1930) and Sikka (1940), who obtained significant positive correlations between persistency and total yield.

(c) Relationship between initial yield and 180 day yield

All the correlations between initial and 180 day yields presented in Table 38 were positive and highly significant, and in every case the coefficients were higher than the corresponding values obtained for persistency and 180 day yield. This shows once more that the total yield of a cow is more closely correlated with initial yield than with persistency.

These conclusions are in accord with those of Gaines (1927), Sanders (1930), Gooch (1935) and Sikka (1940), who have all reported similar high correlations between these variates.

All the foregoing analyses bear out the conclusion that increased total milk production can be attained by breeding for high initial milk yield combined with high persistency. But it should also be noted that these characteristics can be modified very considerably by such environmental influences as feeding and management, as shown by the extent to which the coefficients of intra-cow correlation in Figs. 14, 15 and 16 deviate from unity. This is particularly so for persistency which shows the lowest repeatability.

Table 39

Relation between month of calving and persistency

Month of calving	1st lactation			2nd lactation			Mature lactations		
	No. of cows	Persistency	Relative value	No. of cows	Persistency	Relative value	No. of cows	Persistency	Relative value
January	78	1.3758	105.2	108	1.2911	108.6	261	1.2795	103.9
February	70	1.4343	109.7	131	1.2670	106.5	460	1.3099	106.4
March	64	1.3641	104.3	142	1.2323	103.6	504	1.2640	102.6
April	75	1.1860	90.7	72	1.1043	92.8	285	1.1522	93.6
May	58	1.1364	86.9	47	0.9952	83.7	139	1.1045	89.7
June	56	1.1330	86.6	32	0.9923	83.4	63	1.0543	85.6
July	39	1.1862	90.7	26	1.1363	95.5	59	1.1187	90.8
August	62	1.2583	96.2	32	1.1318	95.2	57	1.1295	91.7
September	156	1.3218	101.1	52	1.1881	99.9	88	1.2039	97.8
October	194	1.3111	100.3	88	1.1543	97.0	121	1.2137	98.6
November	199	1.3380	102.3	71	1.1758	98.9	120	1.2273	99.7
December	146	1.3758	105.2	94	1.2070	101.5	149	1.2581	102.2
Total & average	1,197	1.3077	100.0	895	1.1894	100.0	2,306	1.2315	100.0

3. Influence of month of calving on persistency

The relationship between month of calving and persistency was studied for the first, second, and later lactations separately, and the results are presented in Table 39 together with relative values obtained by using the weighted average in each group as base. Fig. 17 shows these results graphically. It will be observed that young and mature cows responded in practically the same manner to variations in month of calving. The highest persistency was attained by cows calving in the winter months, while the lowest values were attributable to summer calvers. Comparison of Fig. 17 with the corresponding figure for 180 day milk yield (Fig. 8) indicates a close similarity in the trend of these curves. It would appear therefore that the monthly variation in persistency could be explained on the same basis as the variation in 180 day milk yield, and could be attributed in large measure to differences in the prevailing conditions of food supply in different months of the year.

An analysis of the response of individual herds to month of calving was carried out to determine whether there were any significant differences between herds in this respect. Yates' least square method of fitting constants was applied to the persistency figures of 2306 mature lactations (3rd and later), and the results of this study are presented in Table 40:-

FIG. 17.

RELATION BETWEEN MONTH OF CALVING AND PERSISTENCY

(BASED ON DATA FROM 12 HERDS)

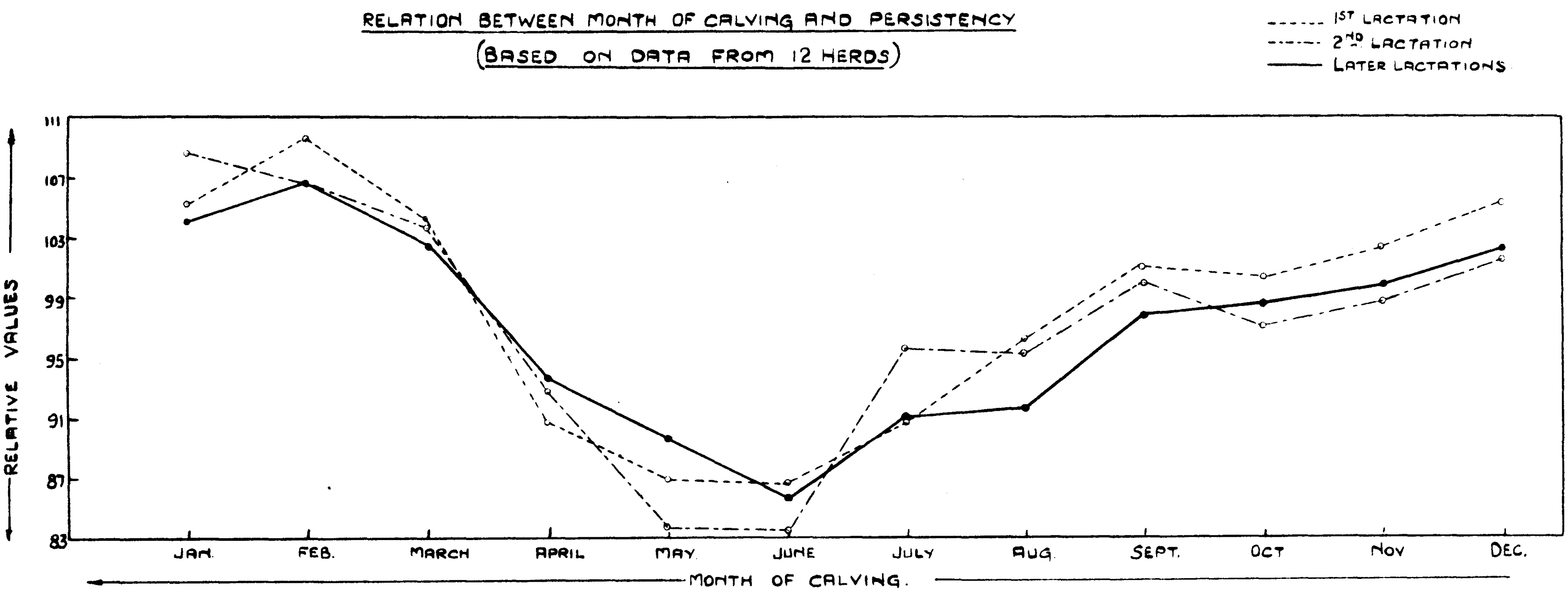


FIG. 18.

RELATION BETWEEN MONTH OF CALVING AND THE SHAPE OF THE LACTATION CURVE UP TO 180 DAYS FROM CALVING

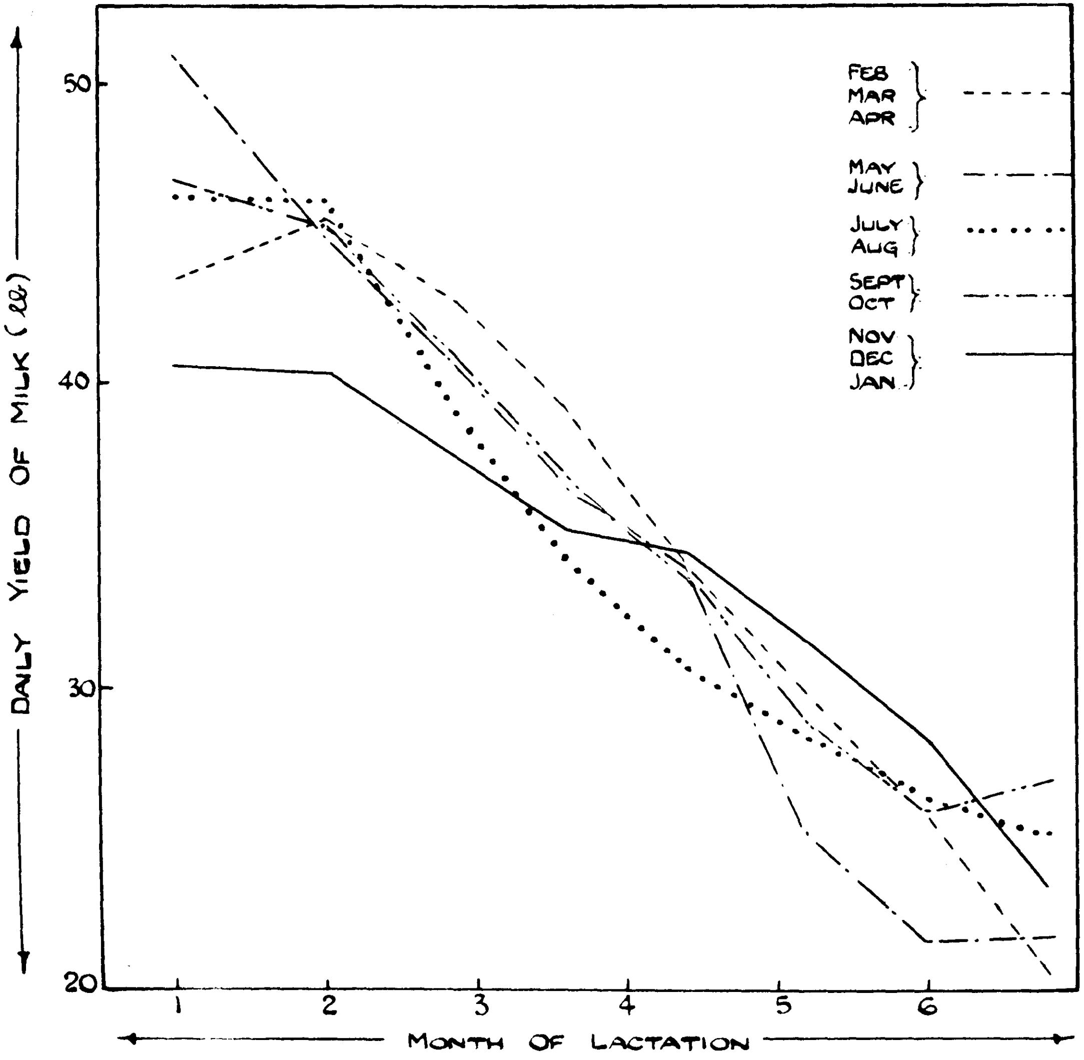


Table 40

Analysis of variance of herd month interactions in persistency

Source	d.f.	Sum of squares	Mean square	F	Significance
Constants	22	18.6418	0.8474		
Remainder (interaction)	117	5.9460	0.0508	1.48	xx
Between classes	139	24.5878			
Within classes	2166	74.3753	0.0343		
Total	2305	98.9631			

The analysis shows that as in the milk yield data, there were significant herd month interactions in persistency. It is evident therefore that a study of persistency in relation to month of calving can be accurate only when it is done on a within-herds basis.

Fig. 18 shows the results of a study of the shape of the lactation curve as influenced by month of calving in the largest herd available in the present data. Composite lactation curves based on the third and later lactations, are presented for groups of cows calving in different, parts of the year. Lactations which commenced in two or three consecutive months are grouped together according to the similarities they exhibited. The figube shows quite clearly that the highest persistency was attained by cows calving in the winter months, while summer calvers were the poorest in this respect. These results agree with those of previous authors (Gaines 1927, Sanders 1930, Sikka 1940 and Johansson and Hansson 1940) in showing that the shape of the lactation curve is influenced by the season of calving. The degree to which season exerts its effect has varied naturally from one investigation to another, and the results presented here apply to the particular population studied.

Correction factors for eliminating the effect of month of calving on persistency were calculated on a within-herds basis by using the same technique employed for the corresponding milk yield corrections. These are detailed in Appendix Table 9.

4. Influence of age and preceding calving interval on persistency

The general effect of variations in age on the persistency of yield are shown in Table 41 which contains the results of the "lumped" and "paired" lactation methods of study.

Table 41

Relation between age in lactations and persistency

Lactation No.	No. of cows	Lumped records		Corrected for selection
		Mean	Standard deviation	Mean
1	1211	1.3080	0.1868	1.3203
2	915	1.1867	0.1979	1.1922
3	688	1.2088	0.2137	1.2001
4	548	1.2231	0.2240	1.2232
5	386	1.2303	0.2013	1.2132
6	248	1.2324	0.1828	1.2021
7	156	1.2575	0.2373	1.2195
8	105	1.2720	0.1775	1.2033
9	82	1.2949	0.1666	1.2041
10	47	1.2540	0.1705	1.2147

It will be observed that the first lactation had a rather low variability as measured by the standard deviation, when compared with the second to fifth lactations. The mean itself was highest for the first lactation. These results agree with those of previous authors (Turner 1927, Sanders 1930, Ostergaard 1931, Gooch 1935, Sikka 1940 and Johansson and Hansson 1940) in so far as the high persistency of first calvers is concerned. They differ, however, from the statement made by Pontecorvo in 1940 that the persistency of first calvers has a greater variability than that of subsequent lactations. Since no evidence was presented by Pontecorvo in support of his statement, his claim cannot be accepted in the light of present results. Moreover, Sikka (1940), using a measure of persistency rather similar to Pontecorvo's showed, in line with the present results, that the first lactation persistency has the lowest variability.

Comparison of the "paired" and "lumped" lactation results shows how selection for yield affected the persistency figures. With "lumped" data, the persistency dropped from the first to the second lactation, but thereafter increased progressively with age. After allowance was made for selection, it was observed that the average persistency of second and later calvers did not show much variation. This was confirmed by a study of the trend in persistency in the successive lactations of 187 cows, each of which had complete records for the first five lactations (Table 42).

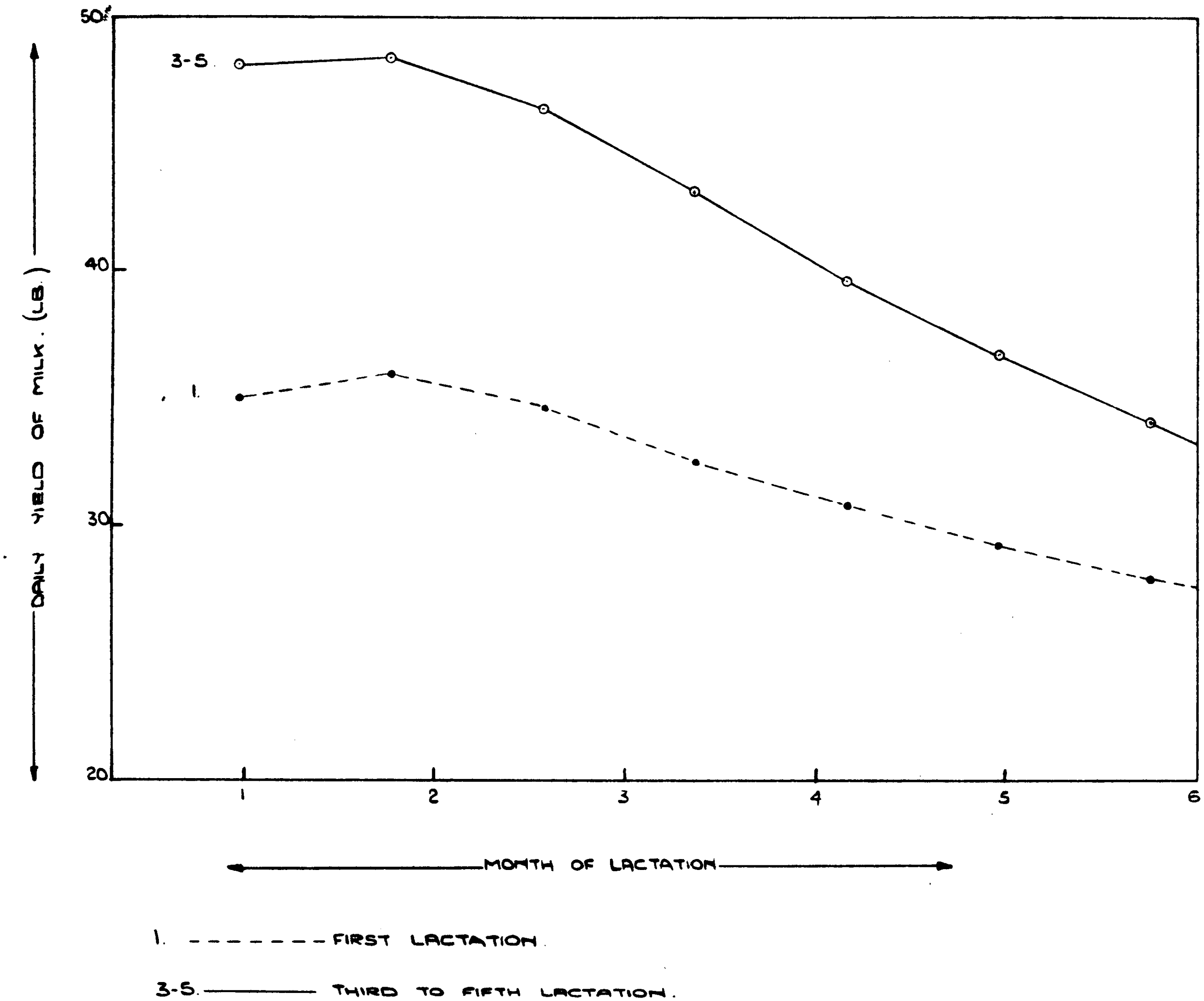
Table 42

Relation between age in lactations and persistency
(Based on 187 cows with consecutive records for the first 5 lactations)

Lactation number	Persistency
1	1.3681
2	1.2280
3	1.2129
4	1.2231
5	1.2212

FIG 19.

RELATION BETWEEN THE AGE OF THE COW AND THE SHAPE OF THE LACTATION CURVE UP TO 180 DAYS FROM CALVING.



The results shown in Tables 41 and 42 are somewhat different from those of previous investigators. Sanders (1930) and Sikka (1940) found from their studies that the persistency values decreased as the cows grew older. But, Johansson and Hansson (1940) obtained results which showed that persistency decreased with age up to about four years, and thereafter increased. It seems likely that this variation in results could be attributed largely to differences in the methods employed to measure persistency.

The effect of age in lactations on the shape of the lactation curve up to the 180th day from calving is presented graphically in Fig. 19. It is based on 536 first lactations and 527 mature lactations (3rd, 4th and 5th), and shows quite clearly that first calvers had a considerably higher persistency than older cows.

The covariation of age within lactations, length of preceding calving interval and persistency was also studied with the present data by means of correlation and regression coefficients. The results of this study for the first three lactations are summarised in Table 43. They show that the correlations between age at calving and persistency were not statistically significant. But preceding calving interval and persistency appeared to be significantly related to each other. Nevertheless the low value of the regression coefficients indicated that this relationship could be ignored for most practical purposes.

Table 43

Covariation of age at calving, length of preceding calving interval (p.c.i.) and persistency

(Age was measured in months and p.c.i. in days)

Lactation No.	Correlation coefficients*		Regression coefficients	
	Age-persistency	p.c.i.-persistency	Persistency-age	Persistency-p.c.i.
1	-0.032	-	-0.0014	-
2	0.051	0.113	0.0021	0.0003
3	0.032	0.094	0.0013	0.0003

* The standard error of the correlation coefficients was 0.029 - 0.044.

The number of cows and the averages and standard deviation for persistency, age at calving, and p.c.i. were given in Tables 5 and 41, and the correlation between age at calving and p.c.i. was given in Table 23.

It should, however, be noted in conclusion, that allowance must be made for the high persistency of first calvers when comparing cows with different lactations. This seems to be the only type of correction necessary for the influence of age on persistency.

PART IV

Studies in Butterfat Percentage

Part IV

Studies in Butterfat Percentage

Although extensive investigations on the fat content in milk have been carried out in other parts of the world, the available literature on the subject for Ayrshire cattle in this country is extremely meagre. Kay and McCandlish (1929) and Glen and McCandlish (1930) studied the influence of age on butterfat percentage by using data from Ayrshire cows which had completed at least five lactations. Asker (1949) investigated the importance of heredity in the variation of butterfat percentage in some British breeds of dairy cattle. Apart from this, very little has been done. It will therefore be interesting to examine the figures for butterfat percentage in the present data. The results reported in this section are based on the average butterfat percentage during the total lactation period.

1. Variation in butterfat percentage between herds and years

The average fat content in the milk secreted by cows in the 12 herds investigated, are presented in Appendix Table 10 for the period 1930 to 1938. The mean butterfat percentage for the whole population was 3.99 per cent. But it will be seen that there was considerable variation between herds and years in this respect. An analysis of variance based on the mean butterfat percentages of each herd in each year gave the following results (Table 44):-

Table 44

Analysis of variance of butterfat percentage between herds and years

(Based on the mean butterfat percentages of each of 12 herds in each year from 1930 to 1938)

Source	d.f.	Sum of squares	Mean square	F	Significance
Between herds	11	2.0514	0.1865	15.29	x x
Between years	8	0.2466	0.0308	2.52	x
Error	88	1.0767	0.0122		
Total	107	3.3747			

Coefficient of variation = 2.7 per cent.

This shows that the differences between herds and between years were statistically significant. In view of the relatively high values for heritability of butterfat percentage obtained in Part V of this thesis, there is reason to believe that the greater part of these differences were genetic in origin. It was therefore possible to treat the 12 herds as a single population when studying the influence of various factors on butterfat percentage.

2. Influence of month of calving on butterfat percentage

It was shown as early as 1922 by Ragsdale and Brody, and Ragsdale and Turner, that the percentage of fat in milk is influenced by environmental temperature, and that the milk produced during the summer months tends to be low in butterfat percentage. In the present study of the variation of butterfat percentage with month of calving, it was found that part of the variation might be attributed to differences in temperature as suggested by these workers, but it seemed likely that other environmental factors also played some part in determining this variation.

Table 45 shows the relationship between month of calving and butterfat percentage in the present data. The averages were obtained by the least squares method of fitting constants, as this enabled the effect of age on fat percentage to be avoided. The data was first classified for this purpose into groups according to the month of calving and the lactation number (1st, 2nd, and later lactations being treated separately). The scheme for testing interactions between months and lactations was then set up, and the fitted constants for months obtained from this scheme provided the monthly averages presented in Table 45. Relative values, calculated by using the weighted average butterfat percentage for all months as base, are also given for purposes of comparison:-

Table 45

Relation between month of calving and butterfat percentage

Month of calving	Number of cows	Average fat percentage	Relative values
January	453	3.96	99.2
February	670	3.95	99.0
March	716	3.97	99.5
April	432	3.94	98.7
May	238	3.97	99.5
June	142	3.95	99.0
July	125	4.02	100.8
August	154	4.06	101.8
September	301	4.08	102.3
October	401	4.07	102.0
November	394	4.02	100.8
December	391	3.97	99.5
Total and average	4,417	3.99	100.0

It will be observed that butterfat percentage showed a relatively small variation with month of calving as compared with the corresponding figures for milk yield and persistency (Tables 12, 13 and 29). The highest values were obtained for cows calving from July to November, and these cows produced most of their milk during the autumn and winter months. It may be possible that the low environmental temperature which would be associated with the latter period contributed in some measure to the relatively high fat content in the milk. Nevertheless, the difference in average fat percentage between cows calving in the most and least favourable months of the year was only 0.14 per cent., and could therefore be disregarded for most practical purposes.

3. Influence of age on butterfat percentage

Table 46 shows the results of studies in the variation of the fat content of milk with age from the 1st to the 10th lactations. In addition to the "lumped lactation" method of study, the "paired-lactation" method was also employed in order to obtain results that would be free from the influence of selection. However, comparison of the figures obtained by the two methods shows that hardly any selection had taken place in these herds on the basis of butterfat percentage. This is confirmed by the results from a selected population of 187 cows, each of which had completed the first five lactations. The average butterfat percentage for this group of cows was found to be only 3.98 - which was about the same as the average for the whole population.

Table 46

Relation between age and butterfat percentage

Lactation No.	No. of cows	Average fat percentage		Cows with consecutive records for the first 5 lactations	
		Lumped records	Corrected for selection	No. of cows	Average fat percentage
1	1211	4.12	4.12	187	4.10
2	908	3.98	3.99	187	3.99
3	678	3.95	3.97	187	3.98
4	547	3.90	3.92	187	3.93
5	381	3.92	3.91	187	3.90
6	245	3.89	3.89		
7	154	3.92	3.88	Average	3.98
8	105	3.92	3.91		
9	82	3.89	3.90		
10	47	3.95	3.90		

The general trend of the figures shows that there was a slight decrease in the fat content of the milk with increasing age of the cows. This is in agreement with the findings of previous investigators (Gowen 1920, 1924, Glen and McCandlish 1929, Tuff 1931 and Johansson and Hansson 1940). However, the variation with age was not so great as to recommend special corrections for it in breeding work.

4. Influence of calving intervals on butterfat percentage

The variation of butterfat percentage was studied in relation to both preceding and current calving intervals. This study was based on the 3rd and later lactations only, so that the influence of age might be avoided. The records were first calssified into groups according to the length of the preceding calving interval, using a class interval of 40 days. The butterfat percentages during the current and preceding lactation periods were noted in each case, and the averages were then calculated for each group separately. The results are presented in Table 47.

Table 47

Relation between length of calving intervals and butterfat percentage

Length of calving interval (days)	Preceding calving interval		Current calving interval	
	No. of lactations	Fat percentage	No. of lactations	Fat percentage
301-340	259	3.87	167	3.92
341-380	1006	3.91	670	3.95
381-420	565	3.93	350	3.93
421-460	205	3.93	126	3.91
461-500	89	3.95	56	3.94
501-	94	3.95	64	3.93
Total and average	2,218	3.92	1,433	3.94

The figures show that with increasing length of preceding calving interval there was a slight tendency for the butterfat percentage to increase. This could perhaps be attributed to the improved condition of cows calving after a long preceding calving interval, as suggested by Eckles (1923). With current calving intervals, however, the variation was not so marked. But in neither case was the variation of any practical importance.

5. Relationship between butterfat percentage and milk yield

It is well known that in dairy cattle, the aim of any breeding policy is to increase the production of milk and the butterfat content of that milk. It is of interest therefore, to determine whether there is any relationship between these two factors both between and within cows. The 3rd, 4th and 5th lactation records of 263 cows from the 12 herds were used in order to obtain information on this subject, and the results are presented in Table 48.

Table 48
Covariation between total milk yield and fat percentage*

Source	d.f.	Variance		Covariance	Correlation coefficient	Regression of fat % on units of 1000 lb. milk
		Milk yield	Fat percentage			
Total	788	5,169,771	0.0831	+71.38	+0.109	+0.014
Between herds	11	972,260	0.0182	+118.02	+0.887	+0.121
Between cows within herds	251	2,280,817	0.0399	-57.21	-0.190	-0.025
Within cows	526	1,916,694	0.0250	+10.57	+0.048	+0.006

* cf. Hazel, Baker and Reinmiller (1943) for the method employed to partition the variance and covariance.

The correlation between milk yield and butterfat percentage for the total data was +0.109 ± 0.035.

This indicates that there was a positive correlation between these two variates when the data were taken as a whole. The between herds correlation was +0.887 and was highly significant, which means that in the present data, herds with a high milk yield also tended to have a high fat percentage. This is borne out by Appendix Tables 5 and 13 which give the average figures for 180 day milk yield and butterfat percentage for each of the 12 herds studied. After elimination of the differences between herds, the correlation was split up into (a) the correlation between cows within herds, -0.190, and (b) the correlation within cows, +0.048. This low value of the intra-cow correlation coefficient shows that the variation in butterfat percentage between different lactations of the same cow was practically independent of the level of milk production. Between cows, the covariance was negative and statistically significant ($r = -0.190$). Nevertheless, the value of the regression coefficient was so low that when the milk yield increased by 1000 lb., the average butterfat percentage decreased by only 0.025. It may therefore be concluded that the covariation between milk yield and butterfat percentage is of little practical importance from a breeding standpoint, and that there is no cause for any pessimistic belief that an increase in the milk yield would mean an appreciable decrease in the butterfat content or vice versa.

PART V

The Role of Heredity in the Variation of Milk Yield, Persistency and Butterfat Percentage

PART V

The role of heredity in the variation of milk yield, persistency and butterfat percentage

The causes of variation in milk yield, persistency and butterfat percentage may be divided into two main groups - genetic causes and those that arise from environment. To the first group belong all differences which may be attributed to heredity, while the second comprises all the other causes of variation between as well as within individuals. With a single cow, however, it is almost impossible to decide exactly whether her variations from the average production of the herd or breed to which she belongs are due to genetical or environmental factors. But with a large number of cows, it is possible to estimate, by means of appropriate statistical methods, the relative roles of heredity and environment.

With the present material, it has been possible to study the influence of such environmental factors as month of calving, age, and length of preceding calving interval, and the results of these studies have been reported in the preceding sections. The purpose of this section is to estimate the part played by heredity in the variation of milk yield, persistency and butterfat percentage in Ayrshire cattle. This has been done partly by analyses of variations and calculation of intra-cow correlations, and partly by studies of daughter-dam correlations and regressions.

1. Intra-cow correlations

The intra-cow correlation, r, as calculated here, is a measure of the stability of the qualities examined in the individual cows. It is, in fact, a coefficient depicting the individuality of the cow, and is often referred to as the coefficient of repeatability. A high value of r means that the greater part of the variation occurs between individuals and only a small part within individuals. That is, the manifestation of the particular character varies very little from one lactation to another in the same cow. If it could be assumed therefore that all the cows used in the present investigation had lived under the same environmental conditions, the coefficient of intra-cow correlation would be a suitable measure of the total genetic variation. But this assumption would be far from correct. It has been shown in the preceding sections that there were highly significant differences between the 12 herds studied, and there is reason to believe that the greater portion of these differences were environmental. It would appear therefore that the intra-cow correlation within herds would be a better measure of the total genetic variation than that calculated on the assumption that all the cows belonged to a single homogeneous population. Even with this limitation, it should be pointed out that the differences between individuals in any one herd may very well be partly caused by environment, and therefore r cannot simply be said to show the degree of genetic variation. However, it is evident that the genetic fraction of the variance cannot be higher than that expressed by the coefficient of intra-cow correlation within herds, and

Table 49

Analysis of variance of the age-corrected 180 day milk yields of 326 cows, each of which had completed the first four lactations

Source	d.f.	Mean square	Composition of mean square	Variance component
Between herds	11	51,815,457	$\sigma_W^2+4\sigma_C^2+n_1\sigma_H^2$	470,045
Between cows within herds	314	2,799,161	$\sigma_W^2+4\sigma_C^2$	546,963
Within cows	978	611,311	σ_W^2	611,311

Intra-cow correlation within herds $= \dfrac{\sigma_C^2}{\sigma_W^2+\sigma_C^2} = 0.472$

Table 50

Analysis of variance of the persistency of 326 cows, each of which had completed the first four lactations

Source	d.f.	Mean square	Composition of mean square	Variance component
Between lactations	3	1.5991	$\sigma_W^2+326\sigma_L^2+n_o\sigma_{HL}^2$	0.0048
Between herds	11	0.5340	$\sigma_W^2+4\sigma_C^2+n_o\sigma_{HL}^2+n_1\sigma_H^2$	0.0044
Herd lactation interaction	33	0.0404	$\sigma_W^2+n_o\sigma_{HL}^2$	0.0005
Between cows within herds	314	0.0594	$\sigma_W^2+4\sigma_C^2$	0.0078
Remainder	942	0.0282	σ_W^2	0.0282

Intra-cow correlation within herds after elimination of variance due to age $= \dfrac{\sigma_C^2}{\sigma_W^2+\sigma_C^2} = 0.217$

Table 51

Analysis of variance of the butterfat percentage of 326 cows, each of which had completed the first four lactations

Source	d.f.	Mean square	Composition of mean square	Variance component
Between lactations	3	2.3024	$\sigma_W^2+326\sigma_L^2+n_o\sigma_{HL}^2$	0.0068
Between herds	11	2.0328	$\sigma_W^2+4\sigma_C^2+n_o\sigma_{HL}^2+n_1\sigma_H^2$	0.0169
Herd lactation interaction	33	0.0704	$\sigma_W^2+n_o\sigma_{HL}^2$	0.0019
Between cows within herds	314	0.2173	$\sigma_W^2+4\sigma_C^2$	0.0490
Remainder	942	0.0215	σ_W^2	0.0215

Intra-cow correlation within herds after elimination of variance due to age $= \dfrac{\sigma_C^2}{\sigma_W^2+\sigma_C^2} = 0.695$

these figures may be considered as maximum values for the percentage of the total variance which is caused by heredity. In regard to most characters pertaining to dairy cattle production, the actual figure is in fact considerably lower than this.

Tables 49, 50 and 51 show the results of three analyses of variance of the milk yield, persistency and butterfat percentage of the first four lactations of 326 cows drawn from the 12 herds. Each cow had complete records for the first four lactations or more. The method of analysis is self-explanatory. The coefficients of intra-cow correlation within herds were calculated after elimination of the variance due to age. For milk yield, however, the corrected 180 day yields were used, and hence there was no age variation. It will be observed that of the qualities listed, the fat content of the milk is most and the persistency is least dependent on individuality.

Against these analyses of variation, the objection may be raised that the material was selected, in that all cows which had not completed the first four lactations were excluded. But if the variation within cows is to be studied at all, each cow must have completed at least two lactations, and since selection is effective as soon as the first record is completed it is evidently impossible to carry out the analyses on unselected material. It should nevertheless be possible to base the analyses on a less selected population than the 326 cows used in Tables 49 to 51, e.g. by taking cows which had completed only three or two lactations.

Such analyses were also made in the present study, and they were based on the following data:-

(i) 177 cows which had completed the first three lactations only.

(ii) 503 cows which had completed the first three lactations or more.

(iii) 308 cows which had completed the first two lactations only.

(iv) 811 cows which had completed the first two lactations or more.

Appendix Tables 11 to 22 show the results of these analyses. It is evident that the results presented in Tables 49, 50 and 51 together with those obtained from (i) and (iii) above, provide three sets of independent estimates of the repeatability since each of them was based on a different sample of cows drawn from the population of 12 herds. The best estimates of the intra-cow correlations for milk yield, persistency and butterfat percentage could therefore be obtained by averaging each of these three sets of values. Table 52 shows the averages which were calculated by weighting each of the individual estimates by the reciprocal of its squared standard error. This method is not without its disadvantages, but it does in general give greater weight to those estimates which were based on the greatest amount of data. By this method the average repeatability of milk yield, persistency and butterfat percentage was found to be 0.464, 0.242 and 0.691 respectively.

Table 52

Average repeatability of milk yield, persistency and butterfat percentage

Source	Intra-cow correlation within herds after elimination of variance due to age		
	Milk yield (180 days)	Persistency	Butterfat percentage
1. 326 cows which had completed the first four lactations or more.	0.472	0.217	0.695
2. 177 cows which had completed the first three lactations only	0.372	0.234	0.668
3. 308 cows which had completed the first two lactations only	0.517	0.329	0.699
Weighted average	0.464	0.242	0.691

2. Daughter-dam correlations and regressions

It has been shown by Lush (1940) that the resemblance between parents and offspring is generally the most useful for studies relating to the heritability of milk and butterfat production in dairy cattle. The general principles and application of this method of approach have been developed by Lush and his co-workers in a series of papers published in the Journal of Dairy Science and in the Proceedings of the American Society of Animal Production. The principles involved are based on the computation of the actual differences observed between individuals which are related to one another in such a way that their probable genetic differences could be estimated from the laws of inheritance.

If the observed variance between individuals in any population is denoted by σ_0^2, this can be split up into two main parts: (i) the variance due to differences in heredity σ_H^2, and (ii) the variance due to differences in environment σ_E^2. The function $\dfrac{\sigma_H^2}{\sigma_E^2}$ is then a measure of the fraction of the total variance that is due to heredity. In the case of a single parent and offspring relationship, only one half of this fraction is measured, and therefore the result has to be doubled in order to obtain the inheritance from both parents. In reality, however, the problem is rather more complicated than this brief outline would show. The total variance σ_0^2 is composed not only of σ_H^2

and σ_E^2 but also of an additional fraction σ_{HE}^2 which is due to the combined effect of heredity and environment. The fraction σ_H^2 itself may again be split up into (a) the additively genetic portion σ_g^2, (b) the variance due to dominance deviations σ_d^2 and (c) the variance due to epistatic deviations σ_i^2. An examination of these components of σ_0^2 together with the following considerations shows that figures for heritability obtained from daughter-dam studies do not actually provide an estimate of the total variance due to heredity. It is well known that in the transmission of genes from parent to offspring, only one member of a pair of genes can be passed on through one gamete. In consequence, dominance deviations are not transmitted, and the genetic fraction obtained from daughter-dam studies does not include σ_d^2. As regards epistatic deviations, only a small fraction would be included (generally about one-fourth) which would itself decrease in geometric proportion to the number of genes that need to be simultaneously present in the offspring for the manifestation of the particular character. Therefore, daughter-dam studies really provide an estimate of only the variance due to additively genetic differences and a small part of the epistatic differences. If dominance and epistatic deviations are large, then this estimate of heritability would be somewhat lower than the true value. But it is doubtful whether the variances due to dominance and epistatic deviations are important in milk and butterfat production. According to Seath and Lush (1940) they appear to be unimportant in the differences within breeds, although their data was rather scanty to be very conclusive.

The actual method of computing heritability using daughter-dam comparisons, is by calculating the correlation or regression of offspring on dam. In many kinds of data such as the present, where considerable differences in management and feeding practices exist between herds, it is necessary to restrict the analysis to an intra-sire basis. As Lush (1942) has pointed out, "Doubling the intra-sire regression of daughter's record on dam's record seems the most dependable method for estimating heritability in data like these where the sire cannot express the characteristic himself, where the dams are likely to have been a bit more highly selected than the daughters, and especially because feeding and management practices are almost certain to have differed considerably from herd to herd."

The results obtained by this method are presented after a discussion of the measures of inherent milking capacity, persistency and butterfat percentage employed in the present study.

<u>Measures of inherent milking capacity, persistency and butterfat percentage employed</u>

Many different measures have been used by investigators to denote the innate producing ability of dairy cattle in regard to milk yield, persistency and butterfat percentage. For instance, Plum (1935) used the first available record of each cow for estimating heritability. Lush and Shultz (1938) and Seath and Lush (1940) used the highest age-corrected record for some animals and the average of a number of corrected records for others. In more recent years, Putnam, Bowling and Conklin (1943) have compared the use of age-corrected first records with the average of all records in daughter-dam comparisons when proving sires, and have concluded that since the difference in the results obtained by the two methods was not significant, a real saving in labour could be made if first records only are used.

The results obtained from the above studies show that when dealing with a sufficiently large population, equally accurate estimates of heritability could be obtained on the basis of single records (first, first available, or highest), or on the basis of the average of several records provided adequate allowance is made for the number of records contributing to the average (see below). In the present study, the first available record was used always, except in the case of milk yield where, for one of the computations, the average of several records was also used.

Heritability of milk yield

(i) The material for the first study consisted of 732 mates and daughters of 65 sires, drawn from the 12 herds. The average number of daughter-dam comparisons per sire was 11, the minimum number being 5. Forty per cent. of the sires had more than 10 daughters, while about ten per cent. had more than 20. The milk production figures for both daughter and dam were the average of all normal 180 day yields that had previously been corrected for age, month of calving and length of preceding calving interval. The results are summarised in Table 53.

Table 53

Daughter-dam correlations and regressions in milk yield

Number of daughter-dam pairs	=	732
Number of sires	=	65
Average 180 day milk yield of dams	=	7231.9 lb.
Average 180 day milk yield of daughters	=	7229.2 lb.
Total correlation between milk yields of daughter and dam	=	0.362
Total regression of daughter's yield on dam's yield	=	0.411
Intra-sire daughter-dam correlation for milk yield	=	0.181
Intra-sire regression of daughter's yield on dam's yield	=	0.207

The intra-sire daughter-dam regression for milk yield was found to be 0.207, based on 667 degrees of freedom. This figure describes the relationship between the average of 3.79 lactation records per dam and 2.63 lactation records per daughter. To express it in terms of single records, Lush (1942) has suggested the following equation:-

$$b = b' \left(\frac{1+[m-1]r_{dd}}{m} + \frac{\sigma_m^2[1-r_{dd}]}{m^3} \right)$$

where b is the regression of daughter on dam when single records are used, b' is the regression when lifetime averages are used, m is the average number of lactation records per dam, r_{dd} is the repeatability and σ_m^2 is the variance of m.

The variance of m in these data was 3.87. The repeatability within herds was 0.464 as shown in the preceding section. Consequently b had a value of 0.133. Doubling this yields 0.266 for heritability.

(ii) A study of the heritability of milk production was also made on the basis of single records. The material for this investigation consisted of 903 mates and daughters of 129 sires from the 12 herds. The minimum number of daughter-dam pairs per sire in this data was 2, and the comparisons were made on the basis of the first available corrected records of daughter and dam. The results are presented in Table 54. It will be observed that the intra-sire daughter-dam regression was 0.157 in this material. This gives a value of 0.314 for the heritability of milk yield.

Table 54
Daughter-dam correlations and regressions in milk yield

Number of daughter-dam pairs	=	903
Number of sires	=	129
Average 180 day milk yield of dams	=	7240.1 lb.
Average 180 day milk yield of daughters	=	7227.0 lb.
Total correlation between milk yields of daughter and dam	=	0.307
Total regression of daughter's yield on dam's yield	=	0.323
Intra-sire daughter-dam correlation for milk yield	=	0.153
Intra-sire regression of daughter's yield on dam's yield	=	0.157

Heritability of persistency

(i) Table 55 shows the results obtained from a study of the daughter-dam correlations and regressions for persistency, from material consisting of 732 mates and daughters of 65 sires from the 12 herds. It was based on the first available records of daughter and dam. The intra-sire regression coefficient was found to be 0.068. This yields 0.136 for the heritability of persistency.

(ii) Another study of the heritability of persistency was made on the basis of the 903 daughter-dam pairs used in Table 54 for the study of milk yield. The results of this study are summarised in Table 56. They were based on the first available record for both dam and daughter. These results yield an estimate of heritability of 0.116 for persistency.

Table 55

Daughter-dam correlations and regressions in persistency

Number of daughter-dam pairs	=	732
Number of sires	=	65
Average persistency of dams	=	1.2412
Average persistency of daughters	=	1.2465
Total correlation between persistency of daughter and dam	=	0.156
Total regression of daughter's persistency on dam's persistency	=	0.178
Intra-sire daughter-dam correlation for persistency	=	0.060
Intra-sire regression of daughter's persistency on dam's persistency	=	0.068

Table 56

Daughter-dam correlations and regressions in persistency

Number of daughter-dam pairs	=	903
Number of sires	=	129
Average persistency of dams	=	1.2508
Average persistency of daughters	=	1.2559
Total correlation between persistency of daughter and dam	=	0.164
Total regression of daughter's persistency on dam's persistency	=	0.183
Intra-sire daughter-dam correlation for persistency	=	0.054
Intra-sire regression of daughter's persistency on dam's persistency	=	0.058

Heritability of butterfat percentage

The heritability of butterfat percentage was also studied with the same material as that used for milk yield and persistency. The results are summarised in Tables 57 and 58. In each case, the first available record was used as the basis of the daughter-dam comparisons. The intra-sire regression coefficients were found to be of the order 0.281 and 0.271 respectively for the two studies. Therefore the heritability of butterfat percentage could be estimated accordingly as 0.562 and 0.542.

Table 57

Daughter-dam correlations and regressions in butterfat percentage

Number of daughter-dam pairs	=	732
Number of sires	=	65
Average fat percentage of dams	=	3.95 %
Average fat percentage of daughters	=	4.07 %
Total correlation between fat percentages of daughter and dam	=	0.426
Total regression of daughter's fat percentage on dam's fat percentage	=	0.473
Intra-sire daughter-dam correlation for fat percentage	=	0.265
Intra-sire regression of daughter's fat percentage on dam's fat percentage	=	0.281

Table 58

Daughter-dam correlations and regressions in butterfat percentage

Number of daughter-dam pairs	=	903
Number of sires	=	129
Average fat percentage of dams	=	3.97%
Average fat percentage of daughters	=	4.08%
Total correlation between fat percentages of daughter and dam	=	0.396
Total regression of daughter's fat percentage on dam's fat percentage	=	0.430
Intra-sire daughter-dam correlation for fat percentage	=	0.256
Intra-sire regression of daughter's fat percentage on dam's fat percentage	=	0.271

The foregoing estimates of heritability may be summarised in the following form :-

Heritability of milk yield ....0.25 to 0.30

Heritability of persistency ....0.10 to 0.15

Heritability of butterfat percentage ....0.50 to 0.60

In non-statistical language, this means that the difference between the breeding value of any two cows was, on the average, about one quarter of the difference between their milk yields, one eighth of the difference between their persistency, and one half of the difference between their butterfat percentages.

These figures are in agreement with the results obtained by previous investigators for the heritability of milk or butterfat yield and butterfat percentage (Lush 1940, Lush, Norton and Arnold 1941, and Tyler and Hyatt 1947). They show that the major source of error in connecting an animal's phenotype with its real breeding worth lies in the environmental circumstances to which the animal is subject. The genetic fraction of the variance is such that, if cows selected to be parents of the next generation exceed the herd average by 100 gallons of milk, their daughters will exceed it by only about 12½ gallons. It may appear from this that greater progress in dairy cattle improvement can be achieved by concentrating more on environment rather than on heredity. Nevertheless, genetic differences between individuals are present on a sufficiently large scale in dairy cattle, to provide an adequate basis for substantial increases in production, over and above any which may be brought about by improved environment. However, it is only by a successful dovetailing of environmental and genetical methods that the dairy farmer can hope to derive the greatest benefits for his labours.

PART VI

General Considerations, Summary and Conclusions

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General Considerations

The problem of evaluating the breeding worth of an animal is highly important to the practical farmer who aims at improving the productive level of his stock. For most quantitative characteristics such as milk production in dairy cattle, this is rendered difficult by the apparent lack of connection between the individual's phenotype and its true breeding value. Since the production of a cow depends partly on the environment to which she is exposed and partly on her innate potentialities, any attempt to evaluate the latter would be subject to some error from mistaking the effects of environment for the effects of genes. The greater the environmental variation to which the cow is exposed, the greater will be the amount of error in judging the cow on the basis of her observed production.

In consequence it is necessary to make due allowance for the environmental effects for the proper estimation of a cow's breeding worth. This involves the correction of the observed phenotypic values to what they would probably have been if they were made under standard conditions of environment. Generally, the most important of the environmental effects for which correction should be made are those due to age and due to differences in feeding and management - if these could be estimated satisfactorily. Length of calving intervals may also need to be taken into account if they were unusually short or long, while month of calving may be important in herds where the differences in production between summer and winter calvers are considerable. If these factors are adequately allowed for, only a little gain in accuracy would be achieved by other corrections. But it is important that whatever corrections are made, they should be well founded and should be applicable to the particular population. This point was well illustrated by the corrections for month of calving used in the present study. It was found from the analyses of herd month interactions in milk yield and persistency that different herds responded differently to month of calving. This meant that if the corrections for month of calving are to be appropriate, they should be calculated on a within-herds basis so as to be truly applicable to the conditions obtaining within the particular population.

It should, however, be pointed out that corrections based on population studies do not exactly allow for the effect which a difference in environmental conditions had on all individual records. For example, an increase in length of the preceding calving interval by 10 days was found to raise the 180 day milk yield by about 20 to 30 lb., yet not all individual cows would show exactly this same response to the increased length of the preceding calving interval. This is true not only of the effect of calving interval but also of the effect of other environmental conditions to which the cows are exposed. Therefore, for practical purposes it is essential that such correction factors as are used, should be supplemented by adequate knowledge of the environment of each individual cow. The correction and interpretation of the records must be done intelligently in relation to the particular conditions under which they were made, and in relation to other factors relevant to them. It is only by this method that the dairy farmer can hope to derive the best possible results in evaluating the probable breeding worth of an individual cow. But in this connection, the note of warning given by Lush (1946) should also be remembered - "the man who works with his animals daily is, however, more likely to make too much allowance for his favourites without being aware that he is doing so."

For a knowledge of the probable breeding worth of an animal, it is also supremely important to obtain information regarding the heritability of the characteristics under consideration. In fact, the choice of an efficient breeding system is basically conditioned by knowledge of the rate of genetic improvement possible for the desired characteristics. If the characteristics are highly hereditary it would indicate that mass selection on the basis of the individual's own phenotype would be the best method of breeding that the farmer could adopt in order to attain his goal. On the other hand, if heritability is low it would point to the adoption of a system of breeding which involves the greater use of pedigree, relatives and progeny tests.

Information regarding the latter is particularly important in milk production not only on account of the low heritability of this trait, but also because of the fact that in dairy cattle only the cow can be judged on her phenotype and the bull must always be assessed on the basis of his pedigree, relatives or progeny.

The results of the present study indicated that the heritability of milk yield, persistency and butterfat percentage are of the order 0.25-0.30, 0.10-0.15 and 0.50-0.60 respectively. These figures were calculated after due allowance was made, wherever necessary, for the environmental factors - age, month of calving and calving intervals. They show therefore that even after allowance has been made for these factors, there is still a large amount of variation within herds due to chance differences in the environment. These account for about three-quarters, seven-eighths and one-half of all the differences between single records found in any one herd in milk yield, persistency and butterfat percentage respectively. In other words, if two cows differ by 100 gallons in milk yield for example, only about 25 gallons of this difference is determined by genetic causes, and when mated to the same bull the daughters of these two cows will only differ by 12.5 gallons on the average. This accounts for the host of disappointments encountered by many dairy farmers who find that the difference in yield between two animals is not a direct reflection of the observed difference between their parents.

It is, however, important to notice that all these facts apply only to average and not to individual cases. Nevertheless, they do indicate what the probabilities are for individual matings, and by using them judiciously the dairy farmer will be able to assess the probable genetic value of his stock profitably.

In conclusion, it may therefore be stated that since genetic differences between cows are overlaid by environmental ones to a very large extent, it is of the utmost importance in practical breeding to discount the latter as far as possible in order to obtain a proper estimation of the former. Well-based corrections for known environmental influences and the application of the present knowledge of heredity are two methods which every practical farmer could combine and use to his advantage.

Summary and Conclusions

1. A statistical study of the causes of variation in milk yield, persistency and butterfat percentage has been made on the basis of 5000 lactation records from 12 leading herds of Ayrshire cattle in south-west Scotland, for the period 1930-1939.

2. The unit of measurement of milk production employed was the yield during the first 180 days of the lactation period. This eliminated the effect of variations in length of current calving interval on milk yield. Persistency was measured as the ratio of A-B to B where A was the milk yield during the first 180 days and B was the initial milk yield during the first 10 weeks of lactation. For the investigations on butterfat percentage, the average butterfat percentage of the milk secreted during the total lactation period was utilised, since calving interval was found to have little or no influence on it.

3. A study of the accuracy of milk yield determinations made under the official Scottish milk recording system was carried out by using data from the Kirkhill herd belonging to the Hannah Institute. This herd was recorded on the official system since its inception, and daily records were also kept. It was found that although the yields by the official recording system were, on the average, about 5 per cent. higher than the corresponding yields obtained by daily recording, they are sufficiently accurate to be used for genetical studies.

4. Preliminary analyses of the data from the 12 herds investigated, showed an average 180 day milk yield of 6600 lb. for the total population. The mean age at first calving was 2 years and 9 months, and the calving intervals were about 30 days longer for the first lactation than for subsequent ones. Length of dry periods, however, varied very little from one lactation to another.

5. From a study of the non-genetic causes of variation in milk yield, it was concluded that the interrelations among the non-genetic variables should be considered when devising suitable corrections for their influence on milk yield. Corrections were found to be necessary for four factors; month of calving, lactation number, age at calving and length of preceding calving interval.

6. The effect of month of calving on milk yield varied significantly between herds, and it was shown that correction factors for month of calving should be calculated on a within-herds basis. The average difference in 180 day milk yield between the summer and winter calvers of all herds was about 10 per cent. in favour of winter calvers.

7. A study of the variation of milk yield with age showed that the milk yield of a cow is influenced both by the number of her previous lactations and also by her age at calving. The types of corrections for age employed by previous investigators have been

discussed, and it was shown that percentage corrections are the most satisfactory.

8. The variation of milk yield with length of preceding calving interval showed a pronounced positive trend. From an economic point of view, however, the optimum length of calving interval was found to be about 400 days for the first lactation, and about a year for subsequent ones. Corrections for length of preceding calving interval, like those for age, were most satisfactory when they were proportionate and not additive.

9. The effect of corrections for non-genetic influences on the variance in milk yields has been discussed. It was estimated that a reduction of 27.1 per cent. of the total variance was accomplished through these corrections.

10. The relative value of the first three records as indicators of the cow's real producing ability was investigated, and no significant differences were found to exist among the first three records in this respect. It was also shown that the probable performance of a cow in any lactation could be predicted as accurately from the lactation immediately preceding it, as from the average of a number of previous lactations.

11. Significant differences in milk yield were demonstrated between herds and years in the material studied. Significant herd year interactions were also noted.

12. The effect on herd improvement of selecting breeding females was investigated, and it was shown that very little genetic progress was actually attained by this method.

13. The methods employed by previous investigators for the measurement of the shape of the lactation curve have been discussed in the light of present findings.

14. The inter-relationships of persistency and initial and 180 day milk yields were studied, and it was shown that on a between-cows basis the three characteristics are compatible.

15. The influence of month of calving on persistency has been analysed, and adequate correction factors have been arrived at.

16. The variation of persistency with age and length of preceding calving interval has also been investigated. It was found that allowance must be made for the high persistency of first calvers when comparing cows with different lactations.

17. The butterfat percentage of the milk seemed to be influenced only to a very slight extent by variations in month of calving, age and length of calving intervals. The relationship between total milk yield and butterfat percentage was also studied, and it was shown that there is no cause for any pessimistic belief that breeding for higher milk yield would decrease the butterfat percentage appreciably or vice versa.

18. The role of heredity in the variation of milk yield, persistency and butterfat percentage has been analysed by means of intra-cow correlations within herds, and intra-sire daughter-dam regressions. The average repeatability of milk yield, persistency and butterfat percentage was found to be 0.46, 0.24 and 0.69 respectively, while the corresponding figures for heritability were of the order 0.25-0.30, 0.10-0.15 and 0.50-0.60 respectively.

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Appendix Tables

Appendix Table 1

Average initial milk yield (lb.) from 1930 to 1938 in 12 herds

Herd	1930	1931	1932	1933	1934	1935	1936	1937	1938
A	3000.7	3051.3	2961.9	3094.3	3127.9	2795.8	3056.1	2896.2	2954.3
B	2917.7	2835.5	3093.4	3270.1	3455.3	3462.0	3701.8	3456.0	3564.4
C	2930.9	2925.7	2942.8	2898.2	3068.2	2987.1	2821.3	2892.5	3009.7
D	2735.2	2746.9	2911.0	2542.5	2518.9	2707.2	2770.1	2776.6	2961.8
E	2680.9	2723.8	2528.1	2795.9	2677.0	2612.4	2882.1	2776.3	2924.1
F	2996.4	2998.3	3287.0	3211.2	3532.5	3623.9	3522.9	3597.1	3431.4
G	2910.1	2693.6	2829.1	2620.2	2666.3	2898.4	3408.5	3161.5	3208.8
H	2644.3	2843.1	3015.4	3220.3	3094.2	2769.5	2671.4	2723.8	2849.1
I	2689.1	2474.5	2274.2	2634.5	2528.0	2689.2	2823.6	2832.2	2712.7
J	3004.6	2734.2	2920.6	3104.2	3266.4	3496.3	3348.6	3213.3	3026.2
K	3188.6	3220.2	3211.8	3041.3	3055.3	2726.1	2923.9	3027.4	2949.3
L	3102.4	3130.8	3467.2	3659.9	3728.2	3391.5	3556.7	3608.0	2823.7
Average	2856.4	2839.1	2935.2	2933.8	2983.9	2969.7	3073.0	2999.0	3011.6

Appendix Table 2

Average 180 day milk yield (lb.) from 1930 to 1938 in 12 herds

Herd	1930	1931	1932	1933	1934	1935	1936	1937	1938
A	6784.1	7038.8	6625.2	7073.1	6991.1	6457.0	6813.0	6641.9	6583.1
B	6663.8	6625.2	7133.6	7477.5	7662.4	7711.9	8408.5	7960.6	7912.6
C	6676.2	6417.1	6762.7	6540.1	6824.8	6939.0	6406.9	6494.4	6654.0
D	5973.4	6186.2	6504.8	5985.1	5648.3	5915.8	6328.2	5997.8	6479.0
E	6021.2	6084.9	5483.4	6081.4	6027.3	5905.9	6184.0	6157.9	6381.4
F	6798.5	6761.2	7385.4	7423.5	7867.1	7723.6	7571.8	7760.6	7617.0
G	6430.2	5865.4	6453.4	5677.7	5764.5	6271.7	7148.3	6940.8	7048.6
H	5891.0	6356.3	6769.4	7121.0	6872.5	6388.4	5857.5	6142.6	6181.2
I	5961.2	5869.2	5604.9	6077.3	5917.7	6181.6	6502.5	6561.5	6451.1
J	6567.7	6200.3	6602.6	7170.9	7587.9	7576.1	7431.2	7199.7	6400.1
K	6713.4	6899.0	6913.3	6571.6	6535.4	5876.1	6011.5	6285.4	6305.3
L	7043.9	6898.5	8072.7	8325.5	8291.5	7678.2	7699.3	7637.3	6367.8
Average	6339.0	6391.1	6627.2	6680.5	6691.8	6599,7	6788.2	6630.0	6631.2

Month of calving	Herd A	Herd B	Herd C	Herd D	Herd E	Herd F	Herd G	Herd H	Herd I	Herd J	Herd K	Herd L
January	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000
February	0.990	0.961	1.012	0.984	0.923	1.030	1.004	1.033	1.027	0.918	1.034	1.073
March	1.029	1.012	0.990	0.981	0.852	0.999	1.015	0.982	1.020	0.933	0.922	0.906
April	0.994	1.028	1.040	0.988	0.882	1.053	1.051	0.936	1.050	0.924	1.056	0.983
May	-	1.000	1.019	1.018	0.834	1.073	1.044	0.994	1.078	1.005	1.094	0.849
June	1.030	1.241	1.023	1.041	0.878	1.180	1.321	1.089	1.089	0.944	1.101	0.946
July	1.083	1.185	1.170	1.052	0.935	1.063	1.122	1.134	-	0.982	1.101	0.995
August	1.022	1.103	1.085	1.021	0.970	1.123	1.172	1.096	-	1.056	1.076	0.939
September	1.058	0.952	1.073	0.948	0.945	1.038	1.121	1.049	1.105	0.989	1.096	0.919
October	1.071	1.023	1.100	0.966	0.940	1.041	1.142	1.024	0.987	0.933	0.983	0.982
November	1.071	1.019	1.058	0.993	0.951	1.064	1.052	1.044	1.002	0.870	1.015	1.020
December	1.021	1.127	1.102	0.998	0.995	0.969	1.083	0.985	0.994	1.007	0.946	0.991

Appendix Table 3

Correction factors for month of calving within herds, for 180 day milk yield

Appendix Table 4

Correction factors for age *

Age at calving		1st Lactation	2nd Lactation	3rd Lactation	4th Lactation
Years	Months				
2	0 - 2	1.329	..	..	..
	3 - 5	1.308	..	..	..
	6 - 8	1.287	..	..	..
	9 - 11	1.268	..	..	..
3	0 - 2	1.248	1.137	..	..
	3 - 5	1.230	1.122	..	..
	6 - 8	1.212	1.106	..	..
	9 - 11	1.194	1.092	..	..
4	0 - 2	1.177	1.077	1.079	..
	3 - 5	..	1.063	1.067	..
	6 - 8	..	1.049	1.055	..
	9 - 11	..	1.036	1.043	..
5	0 - 2	...	1.023	1.031	1.059
	3 - 5	..	..	1.020	1.046
	6 - 8	..	..	1.009	1.034
	9 - 11	..	..	..	1.022
6	0 - 2	..	..	..	1.010
	3 -	..	..	..	..

* Based on the net regression of yield on age, with the length of preceding calving interval held constant.

The average yield during the 5th lactation after correction for month of calving was used as the standard for the calculation of the above correction factors.

Appendix Table 5

Correction factors for length of preceding calving interval *

Preceding calving interval (days)	2nd Lact-ation	3rd Lact-ation	4th Lact-ation	5th & later lact-ations
301-320	1.034	1.023	1.024	1.039
321-340	1.028	1.017	1.017	1.029
341-360	1.021	1.011	1.011	1.019
361-380	1.015	1.005	1.004	1.009
381-400	1.008	1.000	0.998	1.000
401-420	1.002	0.995	0.992	0.991
421-440	0.996	0.990	0.985	0.982
441-460	0.990	0.985	0.979	0.973
461-480	0.984	0.979	0.972	0.964
481-500	0.978	0.974	0.966	0.955

* Based on the net regression of yield on length of preceding calving interval, with the age at calving held constant. In the case of the 5th and later lactations, however, the total regression of yield on length of preceding calving interval was used as the basis for the corrections.

The standard length of the preceding calving interval was so chosen that the average yield for the population remained practically unchanged by these corrections. The standard was therefore different for different lactations.

Appendix Table 6

Estimation of selection differential from culling practised in 12 herds

Herd	Selection differential on 1st lactation. (gallons)	Genetic superiority of dams		Number of daughters in herd
		Based on 1st lactation (gallons)	Based on 1st-4th lactations	
A	+18.4	+ 7.8	+22.1	76
B	+56.3	+20.3	+36.4	37
C	+35.6	+17.2	+57.7	39
D	+10.5	+14.8	+14.1	166
E	+10.1	+ 4.5	+12.1	43
F	+20.0	+ 1.6	+ 2.0	95
G	+48.9	+ 5.9	+31.0	56
H	+32.6	+ 7.6	+27.5	77
I	+34.2	+15.4	+37.2	65
J	+ 7.3	+27.3	+22.6	71
K	+16.3	- 4.9	-15.2	58
L	+36.4	+11.3	+35.4	47

Appendix Table 7

Estimation of genetic improvement in 12 herds

Herd	Herd average (gallons)	Total generation length (ΣL) (years)	Genetic superiority of dams (gallons)	Genetic improvement per year (gallons)	Percentage improvement per year
A	950	17.2	+22.1	+1.3	+0.14
B	1050	15.9	+36.4	+2.3	+0.22
C	950	22.0	+57.7	+2.6	+0.27
D	850	19.8	+14.1	+0.7	+0.08
E	850	20.6	+12.1	+0.6	+0.07
F	1050	19.5	+ 2.0	+0.1	+0.01
G	900	17.9	+31.0	+1.7	+0.19
H	900	18.7	+27.5	+1.5	+0.17
I	900	20.5	+37.2	+1.8	+0.20
J	1000	20.8	+22.6	+1.1	+0.11
K	900	18.8	-15.2	-0.8	-0.09
L	1100	21.8	+35.4	+1.6	+0.15

Appendix Table 8

Average persistency from 1930 to 1938 in 12 herds

Herd	1930	1931	1932	1933	1934	1935	1936	1937	1938
A	1.2672	1.3413	1.2564	1.2919	1.2425	1.3158	1.2335	1.3002	1.2195
B	1.2727	1.3435	1.3124	1.2840	1.2231	1.2288	1.2865	1.3231	1.2409
C	1.2854	1.2130	1.3107	1.2679	1.2419	1.3370	1.2707	1.2461	1.2234
D	1.2005	1.2581	1.2391	1.3606	1.2606	1.1921	1.3015	1.1656	1.2002
E	1.2636	1.2264	1.1329	1.1786	1.2581	1.2626	1.1509	1.2383	1.2094
F	1.2820	1.2658	1.2577	1.3170	1.2302	1.1373	1.1624	1.1609	1.2205
G	1.2092	1.1823	1.2833	1.1716	1.1634	1.1608	1.1015	1.2038	1.2005
H	1.2321	1.2401	1.2526	1.2168	1.2385	1.3154	1.2024	1.2658	1.1728
I	1.2262	1.3850	1.4882	1.3133	1.3645	1.3134	1.3121	1.3287	1.3805
J	1.1910	1.2864	1.2692	1.3191	1.3343	1.1814	1.2378	1.2494	1.1240
K	1.1371	1.1461	1.1562	1.1709	1.1484	1.1732	1.0621	1.0908	1.1384
L	1.2921	1.2094	1.3478	1.2948	1.2432	1.2709	1.1804	1.1177	1.2544
Average	1.2303	1.2635	1.2685	1.2859	1.2565	1.2338	1.2230	1.2206	1.2100

Month of calving	Herd A	Herd B	Herd C	Herd D	Herd E	Herd F	Herd G	Herd H	Herd I	Herd J	Herd K	Herd L
January	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000
February	0.980	1.006	0.981	1.029	0.900	0.975	0.971	0.998	0.986	0.984	0.881	0.956
March	1.050	1.064	1.066	1.112	0.990	0.959	0.976	1.011	1.026	1.013	0.912	0.921
April	1.180	1.104	1.174	1.264	1.101	1.027	1.094	1.011	1.219	1.109	0.957	1.073
May	-	1.181	1.143	1.374	1.101	1.021	1.126	1.193	1.344	1.162	1.050	1.154
June	1.160	1.349	1.145	1.366	1.168	1.126	1.280	1.210	1.413	1.118	1.093	1.202
July	1.150	1.312	1.106	1.290	1.155	0.980	1.059	1.035	-	1.065	0.985	1.038
August	1.136	1.039	1.156	1.238	1.103	1.048	1.059	1.022	-	1.122	0.963	1.352
September	1.068	1.020	1.086	1.058	1.068	0.978	1.016	1.021	1.378	1.069	0.948	1.026
October	1.050	1.022	1.079	1.072	1.011	1.036	1.056	1.029	1.204	1.033	0.966	1.054
November	1.019	1.063	1.016	1.050	1.035	1.024	1.045	1.044	1.147	1.022	0.945	1.064
December	1.068	1.030	0.945	1.050	0.905	0.985	1.055	1.035	1.086	1.006	0.924	0.978

Appendix Table 9

Correction factors for month of calving within herds for persistency

Appendix Table 10

Average butterfat percentage from 1930 to 1938 in 12 herds

Herd	1930	1931	1932	1933	1934	1935	1936	1937	1938
A	4.25	4.17	4.26	4.22	4.20	4.12	4.08	4.09	4.00
B	3.81	3.79	3.95	3.82	4.02	3.83	4.18	4.28	4.04
C	4.01	4.18	3.97	4.10	4.20	4.18	4.39	4.44	4.39
D	3.77	3.82	3.86	3.85	3.98	3.86	3.77	3.77	3.80
E	3.92	3.90	3.97	3.93	4.02	3.73	3.76	3.88	3.93
F	3.90	3.95	4.04	4.07	4.11	4.00	4.16	4.04	3.90
G	3.84	3.81	3.92	4.11	4.06	3.98	3.88	3.91	3.85
H	3.93	4.23	4.27	4.25	4.21	4.29	4.28	4.11	4.21
I	3.81	3.83	3.82	3.94	3.99	3.96	3.98	4.05	3.99
J	4.01	3.95	4.08	4.06	4.11	4.00	3.98	4.06	3.95
K	3.87	3.96	3.75	3.82	3.80	3.69	3.71	4.06	4.09
L	4.01	4.04	4.34	4.30	4.26	4.21	4.30	4.21	4.47
Average	3.91	3.97	4.02	4.02	4.07	3.98	3.99	4.01	3.99

Appendix Table 11

Analysis of variance of the age-corrected 180 day milk yields of 177 cows, each of which had completed the first three lactations only

Source	d.f.	Mean square	Composition of mean square	Variance component
Between herds	11	23,501,975	$\sigma_W^2+3\sigma_C^2+n_1\sigma_H^2$	505,736
Between cows within herds	165	2,003,151	$\sigma_W^2+3\sigma_C^2$	427,210
Within cows	354	721,522	σ_W^2	721,522

Intra-cow correlation within herds $= \dfrac{\sigma_C^2}{\sigma_W^2+\sigma_C^2} = 0.372$

Appendix Table 12

Analysis of variance of the persistency of 177 cows, each of which had completed the first three lactations only

Source	d.f.	Mean square	Composition of mean square	Variance component
Between lactations	2	0.6555	$\sigma_W^2+177\sigma_L^2+n_o\sigma_{HL}^2$	0.0034
Between herds	11	0.1299	$\sigma_W^2+3\sigma_C^2+n_o\sigma_{HL}^2+n_1\sigma_H^2$	0.0011
Herd lactation interaction	22	0.0576	$\sigma_W^2+n_o\sigma_{HL}^2$	0.0019
Between cows within herds	165	0.0578	$\sigma_W^2+3\sigma_C^2$	0.0092
Remainder	330	0.0302	σ_W^2	0.0302

Intra-cow correlation within herds after elimination of variance due to age,

$$= \frac{\sigma_C^2}{\sigma_W^2+\sigma_C^2} = 0.234$$

Appendix Table 13

Analysis of variance of the butterfat percentage of 177 cows, each of which had completed the first three lactations only

Source	d.f.	Mean square	Composition of mean square	Variance component
Between lactations	2	1.4821	$\sigma_W^2+177\sigma_L^2+n_o\sigma_{HL}^2$	0.0082
Between herds	11	1.1804	$\sigma_W^2+3\sigma_C^2+n_o\sigma_{HL}^2+n_1\sigma_H^2$	0.0236
Herd lactation interaction	22	0.0345	$\sigma_W^2+n_o\sigma_{HL}^2$	0.0008
Between cows within herds	165	0.1639	$\sigma_W^2+3\sigma_C^2$	0.0469
Remainder	330	0.0233	σ_W^2	0.0233

Intra-cow correlation within herds after elimination of variance due to age $= \dfrac{\sigma_C^2}{\sigma_W^2+\sigma_C^2} = 0.668$

Appendix Table 14

Analysis of variance of the age-corrected 180 day milk yields of 503 cows, each of which had completed the first three lactations or more

Source	d.f.	Mean square	Composition of mean square	Variance component
Between herds	11	57,344,945	$\sigma_W^2+3\sigma_C^2+n_1\sigma_H^2$	456,105
Between cows within herds	491	2,206,381	$\sigma_W^2+3\sigma_C^2$	540,121
Within cows	1006	586,017	σ_W^2	586,017

Intra-cow correlation within herds $= \dfrac{\sigma_C^2}{\sigma_W^2+\sigma_C^2} = 0.480$

Appendix Table 15

Analysis of variance of the persistency of 503 cows, each of which had completed the first three lactations or more

Source	d.f.	Mean square	Composition of mean square	Variance component
Between lactations	2	2.7342	$\sigma_W^2+503\sigma_L^2+n_o\sigma_{HL}^2$	0.0053
Between herds	11	0.5280	$\sigma_W^2+3\sigma_C^2+n_o\sigma_{HL}^2+n_1\sigma_H^2$	0.0035
Herd lactation interaction	22	0.0789	$\sigma_W^2+n_o\sigma_{HL}^2$	0.0013
Between cows within herds	491	0.0507	$\sigma_W^2+3\sigma_C^2$	0.0083
Remainder	982	0.0259	σ_W^2	0.0259

Intra-cow correlation within herds after elimination of variance due to age $= \dfrac{\sigma_C^2}{\sigma_W^2+\sigma_C^2} = 0.243$

Appendix Table 16

Analysis of variance of the butterfat percentage of 503 cows, each of which had completed the first three lactations or more

Source	d.f.	Mean square	Composition of mean square	Variance component
Between lactations	2	3.1973	$\sigma_W^2+503\sigma_L^2+n_o\sigma_{HL}^2$	0.0062
Between herds	11	2.4632	$\sigma_W^2+3\sigma_C^2+n_o\sigma_{HL}^2+n_1\sigma_H^2$	0.0184
Herd lactation interaction	22	0.0871	$\sigma_W^2+n_o\sigma_{HL}^2$	0.0016
Between cows within herds	491	0.1724	$\sigma_W^2+3\sigma_C^2$	0.0497
Remainder	982	0.0232	σ_W^2	0.0232

Intra-cow correlation within herds after elimination of variance due to age $= \dfrac{\sigma_C^2}{\sigma_W^2+\sigma_C^2} = 0.682$

Appendix Table 17

Analysis of variance of the age-corrected 180 day milk yields of 308 cows, each of which had completed the first two lactations only

Source	d.f.	Mean square	Composition of mean square	Variance component
Between herds	11	22,823,528	$\sigma_W^2+2\sigma_C^2+n_1\sigma_H^2$	416,565
Between cows within herds	296	2,070,255	$\sigma_W^2+2\sigma_C^2$	705,874
Within cows	308	658,508	σ_W^2	658,508

Intra-cow correlation within herds $= \dfrac{\sigma_C^2}{\sigma_W^2+\sigma_C^2} = 0.517$

Appendix Table 18

Analysis of variance of the persistency of 308 cows, each of which had completed the first two lactations only

Source	d.f.	Mean square	Composition of mean square	Variance component
Between lactations	1	2.4285	$\sigma_W^2+308\sigma_L^2+n_o\sigma_{HL}^2$	0.0078
Between herds	11	0.1681	$\sigma_W^2+2\sigma_C^2+n_o\sigma_{HL}^2+n_1\sigma_H^2$	0.0023
Herd lactation interaction	11	0.0303	$\sigma_W^2+n_o\sigma_{HL}^2$	0.0002
Between cows within herds	296	0.0501	$\sigma_W^2+2\sigma_C^2$	0.0124
Remainder	296	0.0253	σ_W^2	0.0253

Intra-cow correlation within herds after elimination of variance due to age $= \dfrac{\sigma_C^2}{\sigma_W^2+\sigma_C^2} = 0.329$

Appendix Table 19

Analysis of variance of the butterfat percentage of 308 cows, each of which had completed the first two lactations only

Source	d.f.	Mean square	Composition of mean square	Variance component
Between lactations	1	3.3210	$\sigma_W^2+308\sigma_L^2+n_o\sigma_{HL}^2$	0.0107
Between herds	11	1.3277	$\sigma_W^2+2\sigma_C^2+n_o\sigma_{HL}^2+n_1\sigma_H^2$	0.0236
Herd lactation interaction	11	0.0273	$\sigma_W^2+n_o\sigma_{HL}^2$	0.0000
Between cows within herds	296	0.1534	$\sigma_W^2+2\sigma_C^2$	0.0631
Remainder	296	0.0272	σ_W^2	0.0272

Intra-cow correlation within herds after elimination of variance due to age $= \dfrac{\sigma_C^2}{\sigma_W^2+\sigma_C^2} = 0.699$

Appendix Table 20

Analysis of variance of the age-corrected 180 day milk yields of 811 cows, each of which had completed the first two lactations or more

Source	d.f.	Mean square	Composition of mean square	Variance component
Between herds	11	60,296,419	$\sigma_W^2+2\sigma_C^2+n_1\sigma_H^2$	447,670
Between cows within herds	799	1,830,671	$\sigma_W^2+2\sigma_C^2$	638,705
Within cows	811	553,262	σ_W^2	553,262

Intra-cow correlation within herds $= \dfrac{\sigma_C^2}{\sigma_W^2+\sigma_C^2} = 0.536$

Appendix Table 21

Analysis of variance of the persistency of 811 cows, each of which had completed the first two lactations or more

Source	d.f.	Mean square	Composition of mean square	Variance component
Between lactations	1	6.5557	$\sigma_W^2+811\sigma_L^2+n_o\sigma_{HL}^2$	0.0080
Between herds	11	0.4644	$\sigma_W^2+2\sigma_C^2+n_o\sigma_{HL}^2+n_1\sigma_H^2$	0.0029
Herd lactation interaction	11	0.0659	$\sigma_W^2+n_o\sigma_{HL}^2$	0.0007
Between cows within herds	799	0.0425	$\sigma_W^2+2\sigma_C^2$	0.0099
Remainder	799	0.0227	σ_W^2	0.0227

Intra-cow correlation within herds after elimination of variance due to age $= \dfrac{\sigma_C^2}{\sigma_W^2+\sigma_C^2} = 0.304$

Appendix Table 22

Analysis of variance of the butterfat percentage of 811 cows, each of which had completed the first two lactations or more

Source	d.f.	Mean square	Composition of mean square	Variance component
Between lactations	1	7.0322	$\sigma_W^2+811\sigma_L^2+n_o\sigma_{HL}^2$	0.0085
Between herds	11	2.7011	$\sigma_W^2+2\sigma_C^2+n_o\sigma_{HL}^2+n_1\sigma_H^2$	0.0190
Herd lactation interaction	11	0.1016	$\sigma_W^2+n_o\sigma_{HL}^2$	0.0012
Between cows within herds	799	0.1367	$\sigma_W^2+2\sigma_C^2$	0.0573
Remainder	799	0.0222	σ_W^2	0.0222

Intra-cow correlation within herds after elimination of variance due to age $= \dfrac{\sigma_C^2}{\sigma_W^2+\sigma_C^2} = 0.721$