

"THE HERITABILITY OF FERTILITY IN DAIRY CATTLE"

by

HARRY GORDON HUTCHISON

Veterinary Research Laboratory

Mpwapwa, Tanganyika.

A thesis submitted as part requirement for the
degree of Doctor of Philosophy of the
University of Edinburgh

June 1957.



INDEX

	<u>Page</u>
<u>Introduction</u>	1 - 6
<u>PART ONE</u>	
<u>Section 1.</u> Review of literature relating to genetic influence on the fertility of cattle	7 - 41
<u>Section 2.</u> Material used for study	42 - 52
<u>Section 3.</u> Consideration of the environmental variables to which fertility data are subject.	
Introduction	53
1. <u>Habitat</u>	
(i) Geographical	56
(ii) Meteorological	56
(iii) Nutritional	63
2. <u>Managerial practice.</u>	
(i) Age of animal at first mating	
(a) age of heifers	76
(b) age of bulls at first service	82
(ii) Service period	85
(iii) Mating practice	94
(iv) Supplementary feeding	98
3. <u>Biological limitations</u>	
(i) Age	
(a) Cows	107
(b) Bulls	119

PART ONE - Section 3 - 3. Biological limitations,
continued -

	<u>Page</u>
(ii) Disease	129
(iii) Lactation	153
4. <u>Considerations applying particularly to A.I.</u>	
(i) Technical operations at the insemination centre	135
(ii) Recognition of oestrus	147
(iii) Occurrence of oestrus during pregnancy	149
(iv) Stage of oestrus at which cow is inseminated	151
(v) Insemination technique	152
(vi) Administrative considerations.	160
5. <u>Summary of treatment of variables in preparation of data for genetic studies.</u>	170

PART TWO

THE ESTIMATION OF THE HERITABILITY OF FERTILITY

	Introduction	177
<u>Section 1.</u>	Repeatability	181
<u>Section 2.</u>	Predictability	185
<u>Section 3.</u>	Heritability	187

PART TWO - Section 3 - Heritability, continued

	<u>Page</u>
A) Correlation between daughters of a common sire	
(i) Number of services required to achieve conception	188
(ii) Conception to first two inseminations	194
B) Intra-sire regression of daughters on dams.	198
(i) Intra-sire regression. First season of daughters on first season of dams	204
(ii) Intra-farm, intra-sire regression. First season of age-corrected daughters on first season of dams	207
(iii) Intra-sire regression of daughters' fertility on fertility of their dams assessed on the records of more than one season	216
Discussion	220
C) Male fertility	229
D) Male fertility and female fertility interaction	234

PART THREE

Introduction	238
<u>Section 1.</u> Variations in the length of gestation periods.	242

PART THREE - continued

	<u>Page</u>
<u>Section 2.</u> The effect on fertility of time of insemination relative to time of observation of oestrus	252
<u>Section 3.</u> The effect of milk yield on fertility of dairy cattle	258
<u>Section 4.</u> Repeatability of the length of service period after calving	264
<u>Section 5.</u> An examination of the data relating to cows which fail to conceive to an insemination	268
<u>Section 6.</u> Repeatability and heritability of the length of post-insemination "oestrus cycles".	279

PART FOUR

Practical application of results from this study	285
Recommendations for future investigation	294
Acknowledgements	300
References	302
Appendices	324

INTRODUCTION

During this century there has been growing interest among livestock farmers in the possibilities of improvement of their animals by selective breeding, and the tendency has been to select for all criteria which happen to command the interest of the individual breeder in the foggy belief that almost anything can be achieved by selection.

With greater understanding of genetic principles has come the realisation that some characteristics are susceptible to more rapid improvement by selection than others, and the progressive breeder now seeks information on the heritability of characters which he wishes to improve before committing his resources to a selective breeding programme.

During a visit to the United States of America in 1955, the view was expressed to the author, on more than one occasion, by well informed authorities, that low breeding efficiency was the cause of more culling from American dairy herds than all other causes together, except for low yield.

Much of such culling would be in respect of diagnosed reproductive disease, and most of the other animals culled for breeding inefficiency would probably be culled as an interaction of such inefficiency and their productive level, but these opinions do, at least, suggest that the American dairy farmers at present pay considerable attention to fertility when they decide which animals to cull.

This study aims to assist the dairy cattle breeder in deciding to what extent he is justified in selecting for increased fertility among his animals.

Fertility is a term which is often ambiguous even in scientific usage. Fundamentally it is clear that fertility relates to the ability to produce offspring. The ambiguity has arisen by reason of the gestation period of higher animals, and the tendency for the offspring to be recognised as a member of the next generation only when it commences to lead an independent, or semi-independent life.

The difficulty which man experiences in recognising fertility in cattle as measured by the

production of a normal zygote, contrasted with the simplicity of recognising fertility as measured by the production of a calf, justifies common acceptance of the latter criterion when the fertility of cattle is discussed.

A statistical investigation, unco-ordinated with detailed physiological data, necessarily tends to treat fertility as a single characteristic, and it must be recognised that such an assumption may impose a very serious limitation on the value of an investigation of a process which is physiologically a resultant of complex interactions. The extent of such a limitation would largely depend on whether the whole process of reproduction were a function of a common group of genes rather than a series of physiological thresholds each influenced by an independant group of genes.

In the absence of adequate facilities for acquiring physiological records, this study is confined to an analysis of breeding records derived from artificial insemination centres in Britain, and an assessment of the influence of environmental variables upon such records.

While it is recognised that severe physiological abnormalities of cattle may result in seriously impaired fertility, or even in complete sterility, no attempt is made in this study to identify any specific physiological or pathological abnormalities which influence fertility.

Rather is this investigation aimed at elucidating more of the undefined conditions of dairy cattle which result in general sub-fertility. The sterile cow presents no problem to the breeder as it effectively culls itself, but the sub-fertile cow raises the question of whether or not the breeder should persist in breeding from such an animal if its other characteristics are satisfactory.

The very diverse nature of environmental factors which are believed to influence the fertility of cattle creates a supplementary problem in this investigation.

These factors have been very widely studied, so that an adequate review of the literature on this aspect of the investigation would confuse the review of literature which more directly pertains

to the estimation of heritability of fertility.

To reduce confusion in this respect Part One of this thesis is presented in three sections.

In Section One only the literature presenting evidence of hereditary influence of fertility in cattle, and that covering estimation of the heritability of fertility in cattle is reviewed.

In Section Two the material used for this study is described before consideration is given to the literature concerning environmental effects. This form of presentation has been adopted in the interest of conciseness, as some of the material has been used for investigations of environmental effects in Section Three.

Section Three is, then, a composite section in which possible environmental influences are catalogued and discussed in relation to such evidence as the material of this investigation offers, and in the perspective afforded by relevant literature. As this is necessarily a long section the deductions concerning each

influence are summarised, in so far as they affect this particular study, at the end of this section.

Part Two of the thesis describes the treatment of the data, and presents the estimates of heritability of fertility derived from the data, and the discussion of these results.

Part Three presents the results of a number of investigations which are supplementary to the main project and arise from aspects of preparation of data for heritability studies on fertility.

They have been grouped together as a supplement to the main study because it was considered that if they were reported in Part One, under considerations of preparation of data, they would confuse the approach to the main subject, particularly as the application of their results in this study was impracticable owing to the incompleteness of available information in respect of all animals.

In Part Four the practical application of the results of this study are discussed and some suggestions are made with regard to future investigational studies.

PART ONESECTION ONEReview of Literature relating to genetic
influence on the fertility of cattle.

- (i) Introduction.
- (ii) Bull fertility.
- (iii) Cow fertility.
 - (a) Repeatability.
 - (b) Sire-to-daughter effects.
 - (c) Dam-to-daughter effects.
- (iv) Summary.

(i) Introduction.

It is doubtful when infertility among cattle was first promoted from a farmers' grievance to the status of a problem deserving particular attention, but, as a problem, it was a concern of the veterinarian for many years before the influence of genetics was seriously considered from a scientific aspect rather than that of local beliefs or superstitions.

Perhaps the failure of Bates' "Duchess"

strain of Shorthorns marks the first recognised impact of supposition of hereditary implications, but little reference to hereditary infertility has been recorded in the literature until comparatively recent time.

It is to the credit of the veterinarians that the problem was reduced to defined proportions, and it was not until much of the obscuring influence of major reproductive diseases had been clarified that any serious assessment could be made of genetic contributions to the problem.

In 1900 Zschokke expressed the opinion that there might be a hereditary predisposition towards nymphomania among cattle. Hammond (1927) in his classical study of "The Physiology of Reproduction in the Cow" drew attention to the possibility of hereditary influence on reproductive function.

There have followed an ever-increasing spate of recorded observations and factual evidence which have left little room for doubt of the complicity of genes in the transmission of certain

conditions which adversely affect fertility of cattle.

It is natural that the early evidence of genetic influence on fertility should be largely that which concerns specific defects susceptible to direct clinical or post-mortem diagnosis.

Such defects include:-

- (i) gonadal hypoplasia;
- (ii) freemartins;
- (iii) intersexes;
- (iv) "white heifer" disease;
- (v) infantilism;
- (vi) incomplete reproductive system;
- (vii) deformities of spermatozoa;
- (viii) lethal conditions;
- (ix) severe umbilical hernia;
- (x) cryptorchidism
- (xi) impotentia coeundi;

references to which have been adequately reviewed several times within the last few years (Gilmore, 1949; De Groot, 1950; Bane, 1952; Young, 1953; and Rollinson, 1955). It would serve no useful purpose to submit a further review of the individual papers relating to these aspects of

infertility, particularly as the present investigation is not directly concerned with specific anatomical defects. It is relevant to refer to this evidence of genetic influence over fertility only in so far as it gives reason to suspect that other less obvious aspects of the infertility problem may be similarly influenced and that undiagnosed or subclinical expressions of such defects may be contributory, or absolute, causes of subfertility.

The evidence relating to genetic influence of variations in fertility and subfertility can be conveniently classified according to the relationship of the animals studied.

(ii) Bull fertility.

The conception rate achieved by bulls when their semen is used over a random sample of cows is of primary importance to insemination centres, and an examination of the statistics accumulated at such centres indicates that there is a pronounced variation between the conception rates achieved by different bulls.

The reports of the Production Division of the Milk Marketing Board of England and Wales (1948, 1949) have drawn attention to the fact that semen from the beef breeds - Hereford and Aberdeen Angus - has given better results than semen from the dairy breeds, and that, whereas conception rates achieved with Friesian and Dairy Shorthorn semen have been very similar, the performance from the Channel Island breeds has been less satisfactory.

The apparent higher fertility of beef bulls at insemination centres must, however, be accepted with reserve unless calving results have been determined to support the "conception rate" figures, as it is in the nature of certain farming practice to use beef bulls' semen on heifers, or on nurse cows, and then to turn them out onto a remote area of the farm until they "freshen". Under such husbandry it is very probable that the apparent conception rate of the bulls used will appear fictitiously high, on the basis of "non-return" records at the insemination centres, as a reflection of the infrequent observation to which heifers and nurse cows might be subject.

Mercier and Salisbury (1946) reported that, at a New York insemination centre, Friesian bulls showed a significantly higher fertility rate than Guernsey bulls, and a similar finding in respect of these two breeds was reported by Lewis (1948) from records of an artificial insemination centre in Michigan, and by Bayley (unpublished data referred to by Corley et al (1952)) in respect of inseminations in Wisconsin.

Salisbury et al (1952 a) have shown that, among bulls believed to be perfectly healthy, individuals differ significantly in the levels of assumed fertility they achieve at insemination centres when the criterion of fertility is the "non-return" rate within one month, or within five months, of the date of insemination. ⁽¹⁾ They report highly significant differences between individual bulls within breeds in the assumed early embryo mortality following use of their semen, represented

(1) The term "non-return" rate has been used in this thesis, in accordance with practice at artificial insemination centres, to mean the percentage of all inseminated animals in the groups under consideration which have not been reported to the centre as having been observed in oestrus again within a specific period of time since insemination.

by the difference between their assumed fertility levels at these two times of estimate of fertility.

McCullough et al (1951) computed the repeatability of annual conception rates of 353 bulls with 971 records from 18 insemination centres scattered over 17 States in the United States of America. Friesian, Guernsey and Jersey bulls were represented and very significant variance was detected between bulls within centres. Analysing their data within breeds they obtained repeatability estimates of :-

0.59 for 164 Friesian bulls having 467 records

0.45 for 117 Guernsey bulls having 325 records

0.51 for 72 Jersey bulls having 179 records.

These bulls represented a typical sample of "normal" and healthy bulls at insemination centres in that bulls with doubtful disease histories were excluded.

Although these studies do not constitute proof of genetic influence of bull fertility they are certainly very suggestive that heredity does exercise some influence over this characteristic, provided that one can accept that the standard of

veterinary supervision at insemination centres is sufficiently vigilant to discount the possible differential influence of disease factors.

Hignett (1950) has reported that the semen of one bull may achieve 90% conception rate in herds of high fertility whilst achieving only 20% conception rate, during the same period, in herds of low fertility, which indicates the possibility of an enormous environmental element of variability when comparative bull fertility studies are based on small or selected samples of data.

Scrutiny of the literature has failed to reveal any reported studies of genetic influence on male fertility based on either sire-to-son effects or on dam-to-son effects

Gregory et al (1951) have reported extreme infertility among five related Friesian bulls which appeared vigorous and healthy, and conception rates of 25% and 33% respectively for two other bulls related to the same group.

Both parents of each of the above five bulls were related to one or both of two bulls which were sire and son, which suggests a recessive

gene as the cause of the deficiency.

(iii) Cow fertility.

(a) Repeatability

Repeatability within an individual is a necessary requirement of any characteristic concerning which a heritability study is to be made. Low repeatability may, however, result from uncontrolled environmental influence or from unsuitable criteria of the characteristic, and does not necessarily imply, per se, that the characteristic is not subject to genetic influence.

Studies have been made of the repeatability of several criteria of fertility in cows.

Gaines & Palfrey (1931) calculated the correlation between successive calving intervals of the same cow to be 0.088, plus or minus 0.019, among a population of dairy cows which had calved ten times. Culling would have reduced variation by removal of the most infertile cows, and thus reduced the correlation coefficient, but, on the other hand, differences between different herds

would have tended to increase the overall estimate of repeatability.

Ostergaard (1942) calculated intra-cow repeatability as 0.13 for the first three calving intervals of 970 Red Dane cows.

Berge (1942) reported an intra-cow correlation of 0.213, plus or minus 0.051, for the number of services required in different seasons to achieve pregnancy among 869 cows, for 6,458 matings, in Norway; but it is not apparent from the report to what extent similarity of environment applying repeatedly to the same cow, and contrasting with that of other cows, may have emphasised this correlation, particularly in view of the time trend which is likely to have applied over the 50 year period of the data.

Lasley & Bogart (1945) found that among range beef cattle in Missouri, 80 cows which had a high conception rate and a high calving percentage one year, tended to have a higher than average reproductive performance in the next year, and that

40 cows which had poor reproductive efficiency one year also tended to be poor in this respect during the following year.

From an analysis of variance, Korkman (1947a) found that the permanent differences between Ayrshire cows in Southern Finland, in respect of whether or not they conceived to first service each breeding season, were very highly significant, but that they accounted for only 3.48% of the total variance in this characteristic among 4,009 cows, measured within herds and age groups, whereas the variance within cows, between seasons, accounted for 91.85% of the total variance. The intra-cow correlation within herds and age groups was 0.0483.

In a similar analysis of the same material in respect of whether or not the cow was discarded as a result of breeding difficulties, the differences between cows were also very highly significant and accounted for 11.04% of the total variance, whilst 81.31% total variance was due to variance within cows. The intra-cow correlation within herds and age groups was 0.1431.

Koort (1948) working with Swedish Red and White cattle computed an intra-cow correlation of 0.055 for number of services required per conception in different seasons, and of 0.051 for whether or not cows conceived to first or second insemination in consecutive seasons.

He found fertility markedly affected by age of cow, incidence of disease, and quality of feed, but season and level of milk yield had little effect.

Dunbar & Henderson (1950) studied first insemination records of artificially bred daughters of Friesian bulls in New York State and, from an analysis of variance, they arrived at an estimate for repeatability of conception rate to first service which would lie within a range of 0.027 to 0.051 within most herds.

Olds & Seath (1950) made a study of artificial insemination records of 6,509 dairy cattle, in Kentucky, to compare the number of services per conception required by the same cow in two consecutive seasons, and obtained a correlation of 0.084, plus or minus 0.012, between

consecutive years. These data were spread over 2,403 herds, and the repeatability which was demonstrated for average herd fertility between years would have contributed to the correlation between cows.

Pou et al (1953), from a study of the breeding records of the Beltsville Friesian and Jersey herds over a period of 30 years, calculated repeatabilities of 0.12 for the number of services required per conception, and 0.11 for the period from first service to conception each season. These estimates, made on an intra-herd basis, were corrected for seasonal and time trends, but to what extent the time trends excluded the influence of reproductive disease, which was known to be present in these herds, is open to doubt.

Inchiosa & Pfau (1954) recorded a highly significant correlation of 0.135 between calving intervals of the same cow in a study of the daughters of eight Friesian bulls, involving 538 dam-daughter comparisons, in a New Jersey herd. No indication was given of managerial trend, or other environmental contributions to this correlation, nor was there any

indication of the range of variation in the material, but in view of the very high heritability figures (0.41) for reproductive efficiency which they obtained from their data, there is need to regard their results with reserve.

In contrast to the foregoing studies, which indicate a definite, but low order, repeatability within the same cow between seasons, there have been some studies which have failed to detect any significant repeatability of reproductive efficiency between seasons of the same cow.

Trimberger & Davis (1945) made a study of the number of inseminations necessary to achieve conception in Nebraska dairy herds. They did not carry out an analysis of variance in their data, but examined the repeatability of performance of animals by grouping their data in a series of tables designed to reveal any correlation between conception rates in different seasons, and no correlation was apparent. This does not preclude the existence of a low order correlation.

Legates (1954) obtained a small negative

value for repeatability calculated as an intra-class correlation from an analysis of variance among records of the number of services required per conception for 2,443 calvings of 1,129 cows in 12 dairy herds in North Carolina. From the same material he calculated a repeatability of 0.133, plus or minus 0.026, for calving intervals.

Brown et al (1954) made a study of the calving interval of a large range herd of Aberdeen Angus cattle in Mexico. They analysed the variance of data derived from cows having three calving intervals, and five calving intervals, and obtained intra-cow correlations of 0.02, and a small negative value, respectively for the two groups of data. These data were subject to considerable variation attributable to personal ability to recognise oestrus in cows running without bulls, and the results should be treated with reserve.

Despite these few last mentioned contributions to the subject, the weight of evidence indicates that there is a slight tendency for individual cows to maintain a steady pattern of reproductive efficiency from year to year, but this

tendency is probably frequently over-ruled by year-to-year variations of environmental factors which makes the repeatability low. The fact that some estimates have indicated negative values for repeatability is not inconsistent with a true positive low value for this parameter.

(iii) (b) Sire-to-daughter effects.

Differential fertility between groups of daughters of different bulls was recognised by Wagner (1932), Kab (1937), and Lowe (1938), all of whom postulated hereditary causes for these differences, but it is not clear from the abstracts in which these works have been reviewed, what measures were taken to remove the herd influence on such sib-groups, particularly in view of the high incidence of "fertility disturbance" reported.

Trimberger & Davis (1945) demonstrated a significant difference between a group of eleven daughters of a Guernsey bull which required an average of 2.25 services per conception, and the groups of daughters of 18 other bulls which required an average of only 1.71 services per conception, but this study involved several herds and consistent

environmental influence may have contributed to this difference.

Taussig (1946) quotes an analysis of fertility in a dairy herd in New York State to indicate that the variation between fertility of different lines of breeding would justify the selection of bulls with regard to the fertility of their families.

Henle (1949), working on herd book records of three breeders' associations, found that eight Allgau bulls, out of twenty-eight studied, had depressed the fertility of their daughters, whereas five others had favourably influenced the fertility of their daughters; and, in a further study of the Allgau breed in Southern Germany, Eberle (1953) found that one bull, out of five studied, had improved the fertility and longevity of his daughters relative to their dams, whereas the remaining groups of daughters compared unfavourably with their dams on the same basis of comparison.

Gregory et al (1945 & 1951) found, and later confirmed, evidence that certain Jersey and

Friesian bulls in California were responsible for passing a gene to their daughters which caused failure of normal zygotic development in Jerseys, and abnormal oestrus in the Friesians. Mead et al (1946) estimated that the frequency of the recessive gene responsible for this failure in the Jersey breed was very high within certain strains, and that the combined frequencies of genes for both types of sterility were such that, if they were segregating independantly in a population mating at random, they could account for most of the sterility found in apparently healthy herds in their area.

Kidwell et al (1954), in Nevada, subsequently identified 31 sterile Friesian heifers, spread over seven generations, of which 28 could be traced to a single foundation bull through their sire and dam. The other three were first generation heifers which may have obtained similar genes from other sources.

The case for genetic cause of this condition is strengthened by the fact that the Friesian bull identified by Gregory et al (1945) as responsible for the Friesian type of sterility was a son of the foundation sire used in the

Nevada herd.

Whilst this evidence is strictly outwith the consideration of sub-fertility it has a place within the scope of this discussion in that it accounts for a form of reproductive failure in apparently normal animals which would defy normal clinical diagnosis, and although the expression of the gene in the form of sterility could be readily detected from a scrutiny of herd records, the same, or similar, genes may be responsible for less extreme influence on the reproductive processes under different conditions.

Further evidence of very significant sire-effect on average calving interval was produced by Inchiosa & Pfau (1954) from a study of eight groups of daughters by different Friesian bulls in one large dairy herd in New Jersey. Correlations of 0.135 between recurrent records of the same cow, and of 0.176 between paternal half-sisters, were both highly significant in these data. This information is presented in a summary report which provides inadequate information on which to assess its value, but higher correlations between half-sisters than between recurrent records of the same

cow suggest that there is an environmental bias influencing these results.

Korkman (1947a), in a detailed statistical study of 33 Ayrshire herds and daughters of 634 bulls in Southern Finland, determined that, whilst sire-to-daughter effects in respect of whether or not a cow conceived to first service in any given reproductive season were highly significant, they accounted for only 1.18% of the total variance in this characteristic and provided an estimate of heritability of 0.047. Similarly, in an analysis of whether or not a cow was culled on account of reproductive faults, using the same material, Korkman found very highly significant differences between paternal half-sib groups but they accounted for only 2.54% of the total variance in this characteristic, which provided an estimate of heritability of 0.102.

In this study Korkman found very significant herd and age effects on the temporary infertility of cows, but they accounted for only 1.92% and 1.57% respectively of total variance; and age accounted for 5.11% of total variance in respect of culling

for reproductive faults, but there was no significant difference between herds in this respect.

Olds et al (1949), from a study of natural breeding records of dairy cattle in Kentucky, were unable to detect any significant correlation between the fertility of bulls and their daughters, but they observed an unusually high frequency of cystic ovaries among the daughters of two bulls, of infantile genitalia among the daughters of a third bull, and of slowness to conceive as heifers among the daughters of another bull.

Dunbar & Henderson (1950 & 1953) made a statistical study of the fertility of 1,015 Friesian cows in New York State, which were bred artificially, were the progeny of 57 different bulls, and spread over 281 farms.

They considered two criteria :-

- (i) whether or not the cow was reported in oestrus again within 180 days of the time of her first insemination in any one breeding season; and
- (ii) calving interval between first and second calvings only.

They found that the variance between groups of paternal half-sibs accounted for only 0.1% of the total variance in respect of non-returns to first service, and made no contribution to the variance in respect of calving intervals.

Tabler et al (1951) made a detailed study of 401 Ayrshire cows in a single herd in West Virginia, using an analysis of variance to examine four criteria of fertility :-

- (i) percentage "reproductive efficiency"
 - being the total number of months of pregnancy plus three months for each calving period, expressed as a percentage of the total number of possible "reproductive months" spent by each cow in the herd. The number of possible reproductive months was assessed as the number of months from first mating as a heifer, to 3 months after the last calving date, or 3 months past the next calculated calving date if the cow was in the second half of diagnosed gestation

when called from the herd;

- (ii) length of interval between first service and conception in respect of each calving period (excluding heifers);
- (iii) length of interval between calving and first subsequent service; and
- (iv) the number of services required per conception during the second breeding period.

Highly significant differences were found between groups of paternal half-sibs in respect of all these criteria, but the authors point out that this component of variance will have included a considerable environmental effect in this study, which covers a long period of time.

Brown et al (1954) have conducted an examination of the components of variance in calving interval in a herd of Aberdeen Angus range beef cattle in New Mexico, which were individually mated as soon as they were observed in oestrus after each calving.

No significant difference was detected

between paternal half-sib groups among the progeny of 10 bulls whose daughters had three calving intervals each, nor among 7 of the bulls whose daughters had five calving intervals each. Seasonal and age effects were demonstrated in these data, but no attempt was made to correct for them; also, the fact that the occurrence of oestrus in the cows depended on recognition without the aid of bulls, may have introduced a considerable margin of human error into these data. These results must therefore be treated with reserve.

(iii) (c) Dam-to-daughter effects.

Kab (1937) was able to identify 35 cow families of the Yellow Franconian breed which maintained a relatively high fertility from generation to generation, and which contrasted with 11 other cow families whose fertility was consistently below average from generation to generation.

It is not clear in the abstracted form of this work to what extent these differences might have been explained by herd nutritional and disease environments.

Lowe (1938) noted differences between cow families in level of fertility which he considered must be of an hereditary nature, and Fetscher (1940) also expressed the opinion that hereditary causes might be responsible for the fact that a lower incidence of sterility was found among calves derived from families of high average fertility than among calves derived from families of low average fertility.

Wegscheider (1939), in a study of 45 families recorded in the herdbook of the Lower Bavarian Spotted Breed, concluded that heredity was influencing fertility levels, and in a further examination of 50,000 animals of this breed Fett (1951) drew a similar conclusion, particularly with respect to an effect of premature senility which appeared to limit certain cows to a maximum of four calvings only. No indication is given in these studies that variance between farms had been discounted before their conclusions were drawn.

Fohrman & Graves (1939) drew attention to the fact that, among the Beltsville Friesian herd

there was some evidence of dam-to-daughter transmission of fertility level, as exemplified by 9 very fertile dams which produced very fertile daughters, and 7 dams of poor fertility which produced daughters of low fertility.

Spielman & Jones (1939) examined the Oregon State College dairy herd in respect of fertility, using a reproductive efficiency "index" very similar to that already quoted as having been developed by Tabler et al (1951), which had been derived by modification of the index used by Spielman & Jones. The Spielman & Jones index allowed each cow 12 months for each calving, and the total of months to the cow's credit in this respect were expressed as a proportion of the number of months since the cow attained the specific age considered optimum for her particular breed to commence first pregnancy. Pregnant cows leaving the herd were credited with the number of months they had been pregnant before leaving.

By applying this index to cow families they found a correlation of 0.546, plus or minus 0.118, between reproductive index of foundation cows

and the mean reproductive index of their female descendants, but this correlation was probably biased upwards by breed differences which they reported in their data.

Jones et al (1941), in a more general study of reproductive performance among dairy cattle in Oregon, attribute much of the infertility in certain breeds and families to the inheritance of low fertility, and to close breeding for some character other than good fertility. They do not attempt to assess heritability.

In a general study of the Louisiana State University dairy herd, Seath et al (1943) reported that the daughter-groups of dams having three or more daughters varied in the proportion of successful services in each group from 40.6% to 92.3%, but no test of significance of differences between groups was reported.

In a similar general study of 8 years artificial insemination results in Nebraska, Trimberger & Davis (1945) found very little indication of heritability or repeatability of conception rates, but consideration of 20 cow

families which had five or more female representatives, revealed one family of five which required very significantly more services per conception (2.92), and two families, of eight and sixteen cows respectively, which required very significantly fewer services per conception (1.00 and 1.22 respectively) than average, but these figures exclude two sterile animals in the family of eight and one in the family of sixteen, and the possibility of undiagnosed disease or nutritional factors influencing the results cannot be excluded.

Koort (1948) determined that between fifteen and twenty per cent of the variation in the number of services required to achieve conception in a herd of Swedish Red and White cattle was attributable to hereditary causes.

Henle (1949), working with records from three breeders' associations, found that 53 of 132 families of Allgau cattle had good average fertility, whereas 35 families had poor average fertility. An incidence of 16.17% reproductive disorders was reported in his material, excluding cases of temporary infertility.

Chance & Mather (1949) considered the evidence available from six dairy herds, which included 882 cows in 89 families, and detected only one family which differed significantly in reproductive efficiency from the others.

Haussermann (1952) concluded that genetic factors must be responsible for the differences between 14 families of low fertility and 9 families of good fertility among a population of 578 Wurttemberg Spotted Mountain cattle which had been subjected to severe culling for sterility.

Mack (1953) also recorded considerable differences in fertility level of 11 cow families in which he studied the number of services required per conception, and percentage of cows calving to each service, and concluded that they were attributable to hereditary factors.

Pou et al (1953), using the records of dams and daughters in the Jersey and Friesian herds at Beltsville, calculated a heritability of 0.07 for both the average number of services required per conception, and for the average period from first service to conception.

Inchiosa & Pfau (1954) arrived at a much higher estimate of heritability of calving intervals from a study of a Friesian herd in New Jersey in which the correlation between dams and daughters was 0.203. The report of this work has been seen in summary form only, but higher estimates of genetic correlations between relatives than repeatability within individuals (0.135) suggest that some uncorrected bias affected the data.

This weight of evidence, which supports the view that some degree of dam-to-daughter effect does exist in respect of fertility, is not without contrary findings.

Olds et al studied the Jersey and Friesian herds at the Kentucky Agricultural Experiment Station and recorded a non-significant daughter-dam correlation of minus 0.013 in respect of the number of services required per conception, and could find no significant correlation between this characteristic in 11 foundation cows and the mean of their female-descendant groups (ranging from 3 to 70 descendants).

Tabler et al (1951), in their study of 19

families of Ayrshire cattle, found greater variance within cow families than between them in respect of services per conception and period from first service to conception, and, in the case of their reproductive efficiency "index", the variance was not significantly greater between families than within them. In this study the individuals in the family had an average coefficient-of-relationship of only 15 per cent, so that reduction of intra-family variance would not be large on this account.

Legates (1954) calculated intra-sire regressions of daughters on dams (expressed on the basis of single observations for the dams) in respect of services per conception and calving interval, and obtained values of 0.013 and minus 0.018 respectively, from a study of fertile cows only, in twelve North Carolina dairy herds. The heritability of 0.026 for services per conception is not significantly different from zero in these data.

Brown et al (1954) also calculated intra-sire regressions of daughters on dams, in respect of

first calving interval only, from records of natural, but individual, services in a Mexican herd of Aberdeen Angus cattle.

They used 64 dam-daughter pairs and obtained a regression of minus 0.18. In these data calving interval was significantly affected by season and age effects for which no adjustments were made, and the method of identifying oestrus was subject to human errors.

(iv) Summary and Discussion.

The concensus of informed opinion resulting from studies of genetic effect on fertility of cattle is that such an effect exists, and can sometimes be demonstrated, but it is of low degree and subject to major modification by environmental influences.

In some studies long time trends have been involved, and the influence of reproductive diseases, whose diagnosis is not always easy, will probably have distorted correlations in many studies, but particularly in those covering periods during which the veterinarians have organised contagious abortion campaigns.

It is not difficult to criticise the tendency to disregard such influences as disease, time trends, and inter-farm variance, but when investigators have to make use of available data rather than data derived from planned experimentation they are often faced with making the best of inadequate material.

The analyses of variance made by Korkman (1947a), Koort (1948) and by Dunbar & Henderson (1953) have all dealt with an "all-or-none" characteristic - whether or not a cow conceives to a specific number of services - which has a binomial distribution. As the variance is related to the mean in a binomial distribution it does not seem valid to apply the technique of analysis of variance to this type of raw data. On the other hand, Robertson & Lerner (1949) have argued that where the genotype variance is small it is permissible to utilise raw data, and this condition is satisfied in these analyses.

Summary of Repeatabilities and Heritabilities
estimated in literature reviewed.

Repeatability			
Criterion	Estimate	Author	Method
Calving interval	0.088	Gaines & Palfrey (1951)	Correlation
do.	± 0.019	Ostergaard (1942)	do.
do.	0.13	Brown et al (1954)	do.
do.	0.02	Inchiosa & Pfau (1954)	do.
do.	0.135	Legates (1954)	Analysis of variance
do.	0.133 ± 0.026		
No. of services/ conception	0.213	Berge (1942)	Correlation
do.	± 0.051	Olds & Seath (1950)	do.
do.	0.084 ± 0.012	Pou et al (1953)	Analysis of variance
do.	0.12	Koort (1948)	do.
Conception at 1st service	0.0483	Korkman (1947a)	Analysis of variance
do.	0.027 to 0.051	Dunbar & Henderson (1950)	do.
Period from 1st service to conception	0.11	Pou et al (1953)	Analysis of variance
Whether or not cow culled for breeding troubles	0.143	Korkman (1947a)	Analysis of variance

Heritability			
Criterion	Estimate	Author	Method
Calving interval	0.704	Inchiosa & Pfau (1954)	Paternal $\frac{1}{2}$ sisters
do.	0.406	do.	Dams-daughters
do.	Nil	Dunbar & Henderson (1953)	Paternal $\frac{1}{2}$ sisters
do.	Nil	Brown et al (1954)	do.
do.	minus 0.36	do.	Dams-daughters
do.	minus 0.036	Legates (1954)	do.
No. of services/ conception	minus 0.026	Olds et al (1949)	Dams-daughters
do.	0.026	Legates (1954)	do.
do.	0.07	Pou et al (1953)	do.
Conception at 1st service	0.047	Korkman (1947a)	Paternal $\frac{1}{2}$ sisters.
do.	0.001	Dunbar & Henderson (1953)	do.
Period from 1st service to conceptn.	0.07	Pou et al (1953)	Dams-daughters
Whether or not cow culled for breeding troubles	0.102	Korkman (1947a)	Paternal $\frac{1}{2}$ sibs

SECTION TWO.MATERIAL USED FOR STUDY

Records of inseminations carried out from six artificial insemination centres, and one sub-centre, were used in this investigation.

The following centres co-operated in this project:-

Dumfriesshire Cattle Breeders' Association Ltd.,
Cambridge Cattle Breeding Centre,
Reading Artificial Insemination Centre,
Somerset Cattle Breeding Centre,
Hampshire Cattle Breeders' Society, Ltd.,
Mid-Worcestershire Artificial Insemination
Centre, Ltd., Bromsgrove, and their
sub-centre at Bromyard, Herefordshire.

These centres are widely scattered over England and southern Scotland, and the herds of their members offer a reasonable sample of the commercial dairy cattle of Britain.

Time and financial limitations dictated that the investigation should depend very largely on data already collected by the centres during the course of their normal operations, and, as each

centre is independant of the others, the records, although basically similar, vary in detail between centres, and it was not always possible to pool data from different centres in seeking an answer to a common enquiry.

At the Dumfriesshire centre, which was visited first, an attempt was made to secure additional details of individual animals and descriptions of managerial practice and environment at individual farms by distributing questionnaires to 270 farms. The value of the response from those farmers who replied was very varied, and it was evident that the amount of additional information obtained was not adequate to justify further attempts to collect data in this manner.

Visits were made to the co-operating centres during the period from October 1950 to June 1951, and extracts were made from their records onto analysis cards which had been designed for this project. A specimen of the analysis card used is shewn in Figure 1. One card was used for the data derived from a single insemination, but the calf disposal summary was not used.

Specimen
Analysis Card
used for the
investigation
of factors
influencing
fertility of
cows served
by artificial
insemination.

[illegible]

This card was designed for this investigation by the author and is produced by Messrs. Copeland-Chatterson Co. Ltd., 50 Wellington Street, Glasgow C.2, under reference 51. cc. 79115 c.

The aim at each centre was to identify as many dam-daughter pairs of cows on which there was hope of obtaining full insemination data for at least one complete breeding season, and to extract the complete "lifetime" record of inseminations given to each animal in such pairs.

In addition to dam-daughter pairs it was possible in some cases to identify further daughters of bulls which had stood at the centre, but whose dams' records could not be positively identified among the records available at the centre, generally owing to indefinite identification, or duplication of identification of farm names in herds carrying transitory cow populations.

Owing to the limitation of time available in which to obtain information from the centres, all daughters of bulls at the centre were treated as potential sources of data if they had been inseminated, or were known to be due for insemination during the current season at the time of the visit to the centre, and it was hoped that the subsequent breeding history for at least one season of such daughters would be obtainable by subsequent reference to the centres concerned.

On this basis 2,092 potentially useful dam-daughter pairs were identified, and an additional 180 daughters of bulls from the Dumfriesshire and Hampshire centres whose dams could not be paired with them owing to various uncertainties.

In addition to dam-daughter data an extract was made of several thousand inseminations carried out at the Dumfriesshire centre, representing the complete insemination history of every cow which had been notified to the centre as having given birth to a female calf before 1950 as a result of an insemination.

Of the potentially useful material collected a very large proportion eventually had to be discarded as it often proved impossible to obtain the necessary additional information through the channels available. Two centres to which direct enquiries were addressed were able to provide much of the missing information, although a considerable wastage resulted from lack of confirmation of results from the farms to the centre, and one of the centres had completely altered their recording system during the interval between the original visit and the subsequent request for information, so that

it was not possible to identify positively all the animals concerned in the later enquiry.

As a result of these various wastages, the effective data available have been reduced to 1,251 dam-daughter pairs, and 1,287 daughters of bulls who sired at least four daughters which had completed a breeding season. The distribution of these data is tabulated in Tables 1 and 2, but the whole of these data could not be used in each treatment of the data owing to individual facts having been omitted from the available records.

At each centre details of the monthly conception rates classified by bulls and by inseminators were extracted in whatever form such records were maintained at the centre.

Detailed information of results of inseminations had been collected over a sample period at the Somerset centre, and these data, which had been the subject of an analysis by Clarke (1949), were extracted in detail.

Similar information was extracted from the records of the Dumfries centre, and was augmented by replies to the circulated questionnaires and by personal enquiries at farms.

Pedigrees of all bulls used at the six centres were classified in detail to the grand-parental generation in an attempt to identify all related individuals standing at any of the co-operating centres.

Meteorological data were very kindly provided by the Meteorological Officer at the Royal Air Force station at Silloth, Cumberland, which offer a meteorological pattern closely similar to that which applies over much of the area in which the Dumfriesshire insemination centre operates, and similar data were obtained from the Meteorological Office of the Air Ministry (through the kind assistance of Mr. R.S. Marshall, Adviser on Animal Health to the Secretary of State for the Colonies) in respect of their stations at Collumpton and Cambridge, which were considered likely to offer a reasonably representative meteorological pattern for the Somerset and Cambridge areas respectively.

During the preliminary handling of the data it became apparent that a great deal of time would be consumed in calculations of intervals between various recorded dates, and in order to reduce this time a slide rule scale was devised to enable

intervals to be read directly from a calendar scale.

The prototype of this scale was mounted by the

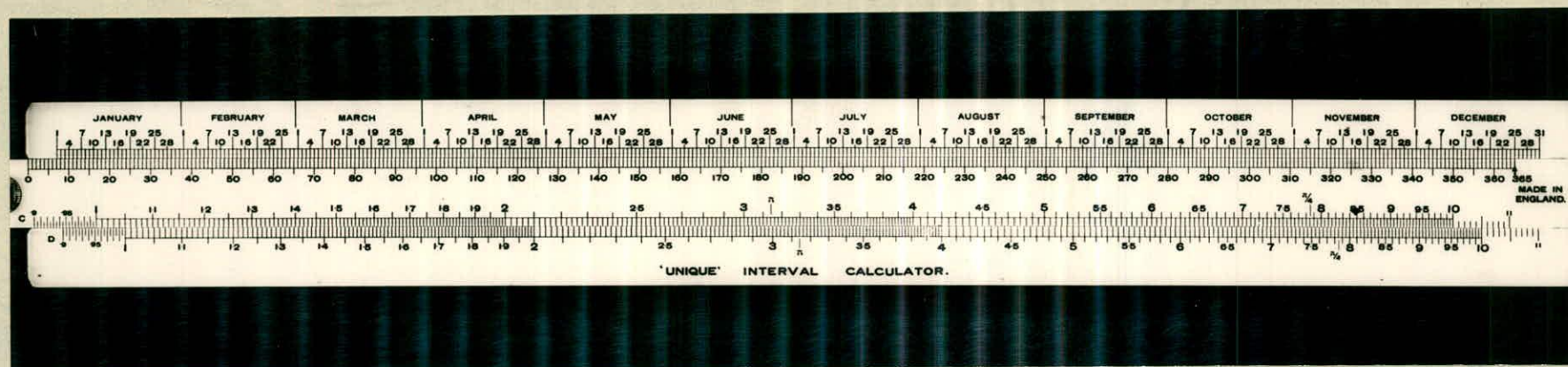
Unique Slide Rule Company Limited, who later

produced the scale as a commercial "Interval

Calculator", a photograph of which is shown in

Figure 2.

Figure 2. An "Interval Calculator". Designed by the author for use in this research, and manufactured by The Unique Slide Rule Co. of Brighton, Sussex.



The upper scale is used to determine the number of days interval between any calendar dates - in the photograph it is set to measure the interval from the 25th of December to any date in the following year. The lower scale is an ordinary logarithmic scale which adds to the versatility of the instrument when the intervals are being used to estimate rates of change - e.g. liveweight gains.

Table No.1. Distribution of daughter-dam pairs available for heritability study, classified by centre, and breed of sire of daughters.

	Somerset		Cambridge		Reading		Dumfries		Hampshire		Worcester		Total	
	Dr.- dams	Sires	Dr.- dams	Sires	Dr.- dams	Sires	Dr.- dams	Sires	Dr.- dams	Sires	Dr.- dams	Sires	Dr.- dams	Sires
Shorthorn	293	9	119	7	96	6	-	-	31	4	30	2	569	28
Friesian	198	6	100	3	15	1	-	-	-	-	33	2	346	12
Guernsey	47	2	-	-	64	3	-	-	44	3	-	-	155	9
Ayrshire	-	-	-	-	-	-	147	6	-	-	14	2	161	8
TOTAL	538	17	219	10	175	10	147	6	75	7	77	6	1251	57



Table No.2

Distribution of daughters available for heritability study
grouped by centres and breed of sire.

	Somerset		Cambridge		Reading		Dumfries		Hampshire		Worcester		Total	
	Bulls	Dtrs	Bulls	Dtrs	Bulls	Dtrs	Bulls	Dtrs	Bulls	Dtrs	Bulls	Dtrs	Bulls	Dtrs
Shorthorn	9	293	7	119	6	99	-	-	4	43	2	30	28	584
Friesian	6	198	3	100	1	15	-	-	-	-	2	33	12	346
Guernsey	2	47	-	-	4	66	-	-	3	53	-	-	9	166
Ayrshire	-	-	-	-	-	-	6	177	-	-	2	14	8	191
Total	17	538	10	219	11	180	6	177	7	96	6	77	57	1287

Daughters of bulls having fewer than five daughters have been omitted from the data.

SECTION THREE

CONSIDERATION OF THE ENVIRONMENTAL VARIABLES TO WHICH FERTILITY DATA ARE SUBJECT

Introduction

The available knowledge on the fertility of dairy cattle indicates that it is a characteristic which is very sensitive to environmental influences.

The value of a heritability study is not prejudiced by a variable environment, provided that environment is adequately defined, although the degree of heritability will necessarily be reduced by every increase in environmental variability. To be of use to the farmer or breeder of cattle, a heritability estimate must be applicable in an environment with which he is familiar, and not in a hypothetical environment in which most of the variables which he accepts have been standardised out of existence.

It is, however, of the utmost importance to approach such a study with a thorough understanding of the various environmental influences which are liable to bias fertility data, in order that a balanced appreciation of any data or results may

be made.

Before proceeding to an analysis of the data collected for this study a review of the possible influences of general and local environments - in the broadest sense - will be presented in this Section with particular reference to the data available for this study.

To systematise the approach to an exceedingly broad subject, the environment has been considered under the headings and sub-headings listed below.

1. HABITAT.

- (i) Geographical.
- (ii) Meteorological.
- (iii) Nutritional.

2. MANAGERIAL PRACTICE (Within the limits of normal good husbandry)

- (i) Age of animal at first mating.
- (ii) Service period (the period between parturition and first subsequent service).
- (iii) Mating practice.
- (iv) Supplementary feeding.

3. BIOLOGICAL LIMITATIONS (Within normally developed individuals)

- (i) Age
- (ii) Disease
- (iii) Lactation.

4. CONSIDERATIONS APPLYING PARTICULARLY TO ARTIFICIAL INSEMINATION

- (i) Technical operations at the insemination centre
- (ii) Recognition of oestrus
- (iii) Occurrence of oestrus during pregnancy
- (iv) Stage of oestrus at which the cow is inseminated
- (v) Insemination technique
- (vi) Administrative considerations.

5. SUMMARY OF EFFECTS OF ENVIRONMENTAL INFLUENCES ON FERTILITY STUDIES.

1. HABITAT.

1. (i) Geographical habitat

Although it must be recognised that the geographical location and geological formation of the habitat in which an animal lives may radically affect the physiological processes of the animal, particularly where a species or breed is transferred from the area of its evolution to some contrasting habitat, in practice it is impracticable to separate the location and geological effects, and under conditions of field experimentation these effects are normally confounded with more variable effects which tend to conceal any real effect of geographical influence.

In this study no attempt can be made to isolate geographical effects as they are confounded with other variables, but as the whole area of Britain is small in terms of geographical measure it is unlikely that any major influence will have been overlooked on this account.

1. (ii) Meteorological habitat

The effect of meteorological factors on fertility of livestock has been discussed by many

authors, and conflicting evidence has been produced in different areas, which suggests that there may be a considerable meteorological-geographical interaction and possibly also a meteorological-nutritional interaction, and perhaps a three way interaction as well.

Under field conditions there is little hope of separating the real effects, if any, of constituents of the general meteorological environment, and it tends to be a matter of surmise whether apparent effects are due to variations in light intensity, periodicity of sunshine, temperature variations, indirect effects of rainfall, humidity variations, or to interactions between such factors, within a small geographical area such as Britain.

A great deal of attention has been paid to photoperiodicity effects on other species of livestock, but there has been no clear evidence of direct effects of light variation on cattle comparable to the studies of Yeates (1949), and Hafez (1952), on sheep. Quinlan & Roux (1936) found that fewer services were required to achieve conception in heifers which received unrestricted sunlight and exercise, in South Africa, relative to

others which were restricted to shade, but Olson (1938), in South Dakota, reared four Friesian heifers from birth to maturity under conditions which excluded all sunlight, and found no difference between them and a control group in reproductive behaviour.

In view of the conflicting evidence of seasonal effects on fertility when comparisons are made between results derived from widely separated areas - as in the case of the findings of depressed summer-season fertility among cattle in the southern areas of the United States (personal discussions) as well as in some of the hot and humid inland states, such as Indiana (Erb, 1955), which contrasts with the findings of Canadian studies, and those of the New York workers (Hilder et al, 1944; Mercier & Salisbury, 1947a, 1947b), in which summer fertility is good - it seems desirable that meteorological effects should only be discussed in relation to the particular locality which is the subject of study.

In Britain Hammond (1927) noted that oestrus tended to be rather longer among cattle in the summer. Phillips et al (1949) postulated that climatic conditions might be partly responsible for the uneven

distribution of calving in Britain owing to shorter, or less pronounced, oestrus during winter exercising restriction on autumn calving, and they also tentatively discussed the possibility of the rain pattern being the cause of the trend for autumn calving to increase from west to east across Britain. Their arguments do not appear very convincing since rain pattern is confounded with the very obvious economic pressure towards autumn calving in the more populated eastern areas, but the transition towards arable farming, which interacts with the economic effect towards greater autumn calving if cattle food must be purchased in any case, may be regarded as an indirect effect of rainfall pattern. From the point of view of actual conception rates to inseminations the records of the Milk Marketing Board (1949) have shewn a very slight drop in the April to June quarter, but this was not significant.

To examine the question of meteorological effects on the data of this study, curves were plotted of variations in mean maximum monthly temperatures, mean minimum monthly temperatures, mean monthly hours of sunshine, and monthly rainfall and mean monthly hours of daylight for the Dumfries,

Somerset and Cambridge centres - representing the extremes of meteorological variation among the centres co-operating in this study. The mean overall three-month "non-return" figures for first inseminations at each centre were then plotted on transparent sectional paper, on a similar scale, so that these curves could be superimposed over the various meteorological curves, and could be examined for any apparent correlations, either as immediate correlations or as "lagged" correlations (correlations between meteorological conditions one month and conception rate in a subsequent month, allowing for a time lag for the meteorological variation to produce a physiological reaction). In the case of "hours of day-light" the greatest correlation with conception rate appeared to be that between hours of day-light in a given month and conception rate four months later. This finding is in general agreement with the findings of Yeates (1949) and Hafez (1952) in respect of sheep, that the sexual periodicity effect tended to follow the initiating changes of light by about three to four months.

The correlations between conception rates

and the meteorological variables examined in this study are tabulated in Table No.3.

The correlations in Table No.3 do not support the case made out by Abrams (1952) that sunlight exerts a significant effect on bovine reproductive efficiency in Britain, although it seems reasonable to suppose that sunlight is normally beneficial and that the apparent effect is insignificant because the degree of variation in amount and intensity of sunlight in Britain is seldom such as to impose a threshold with respect to reproductive efficiency so long as acceptable husbandry methods are practised to preclude serious Vitamin D deficiency.

The same interpretation probably applies also to the temperature variable, and comparisons between the reproductive efficiency of the same animals when living in the tropics, in temperate latitudes, and in arctic latitudes might well demonstrate significant meteorological effects.

Table No.3

Meteorological data	Correlation of assumed conception rate 3 months post-insemination with					
	Same month meteorological data			Preceding month meteorological data		
	Dumfries	Somerset	Cambridge	Dumfries	Somerset	Cambridge
Mean maximum temperature	- 0.2143 ^{NS}	- 0.0813 ^{NS}	+ 0.1534 ^{NS}	- 0.0286 ^{NS}	+ 0.0131 ^{NS}	+ 0.0618 ^{NS}
Mean minimum temperature	- 0.1449 ^{NS}	- 0.0932 ^{NS}	+ 0.1907 ^{NS}	+ 0.0618 ^{NS}	+ 0.0035 ^{NS}	+ 0.0863 ^{NS}
Mean hours of sunshine	- 0.2439 ^{NS}	+ 0.0320 ^{NS}	- 0.1161 ^{NS}	- 0.0502 ^{NS}	+ 0.0695 ^{NS}	+ 0.0741 ^{NS}
Monthly rainfall total	+ 0.1576 ^{NS}	- 0.0287 ^{NS}	- 0.0067 ^{NS}	+ 0.1836 ^{NS}	- 0.1107 ^{NS}	+ 0.1947 ^{NS}
Mean hours of daylight	- 0.2298 ^{NS}	- 0.1932 ^{NS}		Hours of daylight 4 months previously		
				+ 0.2566 ^{NS}	+ 0.1354 ^{NS}	

1. (iii) Nutritional habitat.

In temperate countries, which enjoy a well distributed rainfall and are not frequently exposed for prolonged periods to extreme cold, one would not expect the pronounced cycle of fertility such as cattle in tropical areas develop when subsisting in a natural nutritional environment which swings from extreme to extreme. There is, however, a considerable body of opinion among farmers and other livestock workers in Britain, that seasonal variations in fertility of cattle occur regularly as a result of either the meteorological or nutritional conditions associated with seasonal changes.

The more detailed aspects of nutritional environment are considered under the heading of "Managerial Practice", but the broader aspect of the influence of nutritional environment of a grazing animal may be reflected in seasonal variations in gross fertility statistics.

To examine this point in relation to the data of the present study, the overall monthly mean conception rate figures for all first inseminations carried out at the main centre of

each of the four principal co-operating centres during the period covered by this investigation, were analysed for calendar month, season quarters, and annual trends. The tabulated data in respect of each centre are presented in Appendices 1 to 4, and the analysis of variance in respect of each centre is given below.

Table No. 4.

Analysis of variance among monthly mean conception rates at the Somerset centre during the period from February 1946 to September 1950 (excluding December 1949, for which month no statistics were available)

Source of Variance	d.f.	s.s.	m.s.	F
Total	54	895		
Between years	4	239	59.75	4.52 XX
Between quarters	3	59	19.67	1.42 NS
Between months	11	99	9.00	0.65 NS
Within months	36	498	13.83	

Table No. 5.

Analysis of variance among monthly mean conception rates at the Cambridge centre during the period from June 1944, to September 1950 (excluding September and October 1945, for which statistics were not available).

Source of variance	d.f.	s.s.	m.s.	F
Total	73	2711		
Between years	6	1129	188.17	8.67 ^{XX}
Between quarters	3	117	39.00	1.80 ^{NS}
Between months	11	315	28.64	1.32 ^{NS}
Within months	53	1150	21.70	

Table No. 6.

Analysis of variance among monthly mean conception rates at the Reading Centre during the period from October 1944, to September 1950.

Source of Variance	d.f.	s.s.	m.s.	F
Total	71	1777.80		
Between years	5	437.43	87.486	4.22 ^{XX}
Between quarters	3	69.87	19.917	0.96 ^{NS}
Between months	11	201.97	18.352	0.88 ^{NS}
Within months	52	1078.63	20.74	

Table No. 7.

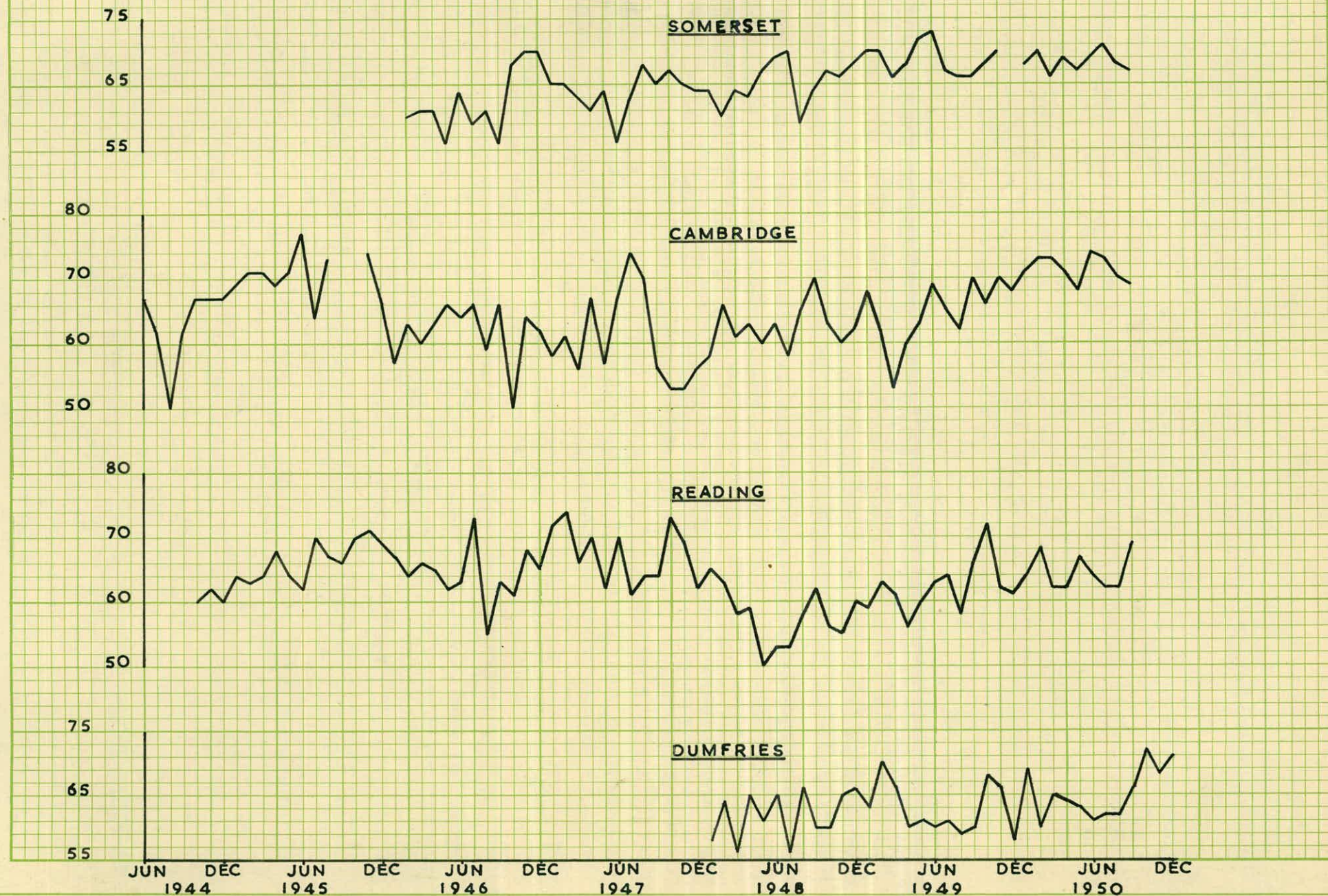
Analysis of variance among monthly mean conception rates at the Dumfries centre during the period from January 1948, to December 1950.

Source of variance	d.f.	s.s.	m.s.	F
Total	35	557.97		
Between years	2	79.03	39.515	3.18 NS
Between quarters	3	106.20	35.400	2.85 NS
Between months	11	136.43	12.403	1.00 NS
Within months	19	236.31	12.437	

A graphical indication of the month-to-month variation in overall conception rates at each of these centres is presented in Figure No.3, which leaves no room for wonder at the insignificant results of analysis for seasonal effects. It should be noted that direct comparisons of the actual level of conception between centres cannot be made with these data owing to differing criteria of conception at some centres. This point will be discussed later.

FIGURE NO. 3

OVERALL MONTHLY NON-RETURN RATES TO FIRST INSEMINATIONS AT FOUR PRINCIPAL CENTRES



These results are in general agreement with those of Holt (1952), for a Devon artificial insemination centre, which revealed no significant difference between overall mean conception rates for calendar months over a period of five years. They are also in agreement with the data presented by Cembrowicz (1952), and derived from the complete overall mean conception rates for the Somerset centre and sub-centres, although they are not in accord with the expressed result of his examination which appears to have been upset by a clerical error in placing the decimal point in the figure derived for the mean square of variance between months. As the figures are presented there is clearly a mathematical error and if this is corrected the variance between months becomes insignificant.

Stewart (1950) produced evidence from one year's operations indicating a lower mean conception rate at the Reading centre during the summer months, and he observed that an accentuated drop in conception rates at sub-centres during the summer months was attributed to inadequate precautions during transportation of semen at the hotter time of year.

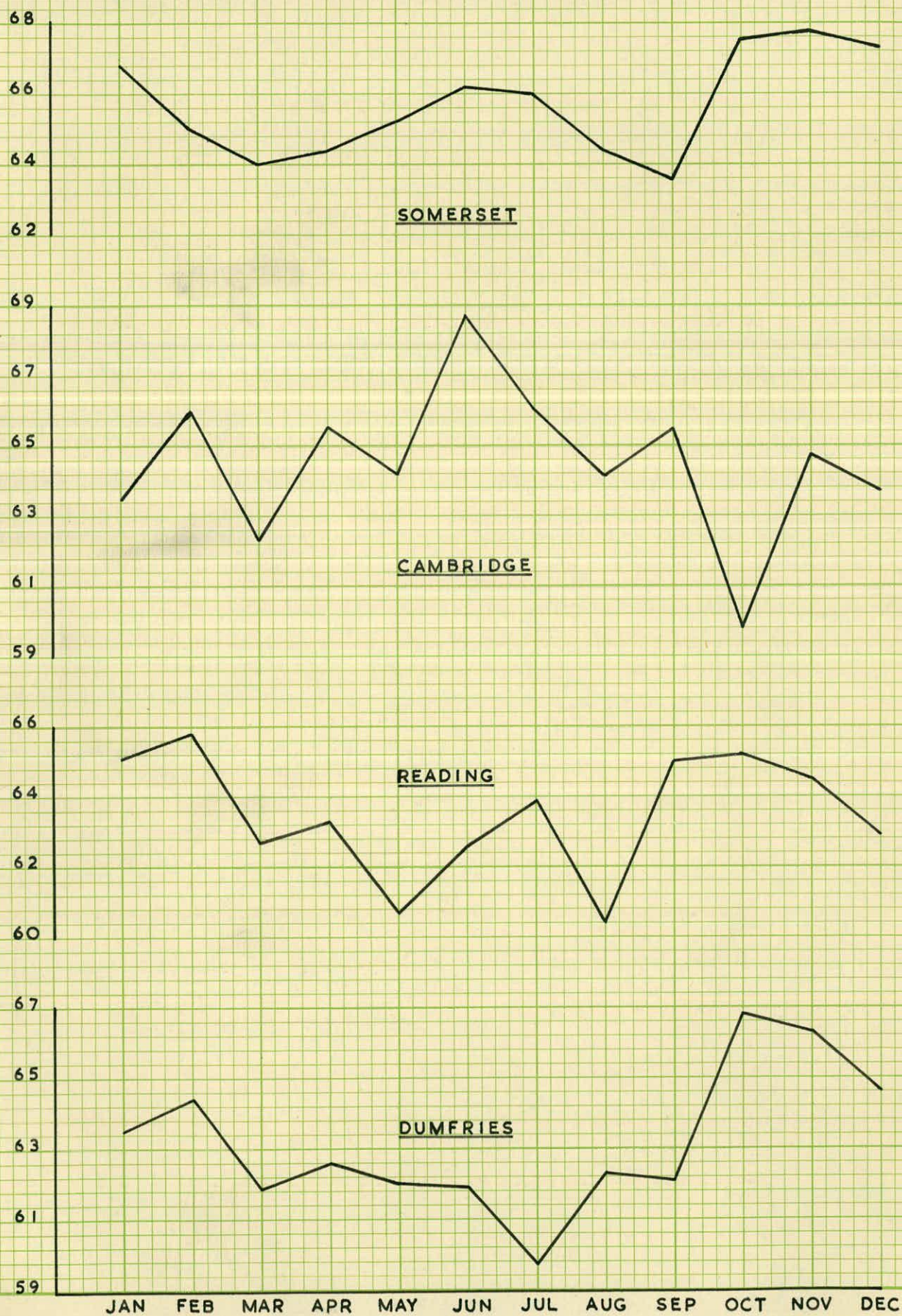
In spite of the lack of significance in these data there is a general trend towards improved fertility in the winter months at all centres, except Cambridge. These trends can be seen more clearly in Figure No. 4, in which the overall mean conception rates for each calendar month, averaged over the period, have been plotted.

The October trough in the Cambridge data is probably over-emphasised by the chance that prevented inclusion of the October conception rates for the years 1945 and 1950, which were both years of outstandingly high conception rates at Cambridge. The high summer conception rate at Cambridge is a peculiarity of this centre, although there is a secondary mode in the Somerset data during the summer months, but since these indications have been shewn to be insignificant in these data there is little purpose in postulating theories to explain them.

In view of the possibility that seasonal changes were being obscured in the bulked data of each centre by the advent and culling of individual bulls which, if popular, could very markedly weight an overall monthly mean conception rate at a centre,

FIGURE NO.4

MEAN OVERALL NON-RETURNS RATE TO FIRST INSEMINATIONS DURING
EACH CALENDAR MONTH AT FOUR PRINCIPAL A.I. CENTRES



sample data were used to examine seasonal trends on a "constant-bull" basis.

From the Somerset data an extract was made of the monthly mean conception rates of twelve of their most popular bulls (5 Shorthorns, 5 Friesians, and 2 Guernseys) which were in consistent service during the period from October 1947, to September 1948. These data are tabulated in Appendix 5, and their analysis of variance is given below.

Table No.8.

Analysis of variance of monthly mean conception rates of 12 consistently used popular bulls at the Somerset centre during the period from October 1947, to September 1948.

Source of Variance	d.f.	s.s.	m.s.	F.
Total	142	5740.73		
Between Breeds	2	85.51	42.655	1.16 ^{NS}
Between bulls	11	466.56	42.415	1.15 ^{NS}
Between quarters	3	269.25	89.750	2.43 ^{NS}
Between months	11	674.94	61.358	1.66 ^{NS}
Error	115	4244.67	36.910	

These bulls bear out the impression of higher

winter fertility, although the variance between quarters does not attain the level of significance. Their overall quarter mean conception rates were:-

January - March 65.1%

April - June 65.5%

July - September 64.7%

October - December 67.5%

The Reading data were also treated, with a view to reducing the possible influence of changes in the bull population on seasonal trends, by extracting conception rates each month in respect of only those bulls whose semen had been used for a minimum of 10 first inseminations during the month and during the succeeding month. Thus two mean conception rates were calculated in respect of each month (except the first and last months of the period) - one being the mean of the month-means of those bulls which qualified during the current and preceding months, and the other being the mean of the month-means of those bulls which qualified during the current and succeeding months. The differences between the means of adjacent

months assessed on identical groups of bulls in the two months were then determined, and these differences were analysed in respect of seasonal trends.

These data are presented in Table.No.9, and the analysis of variance is given below.

Table No.9.

Month-to-month changes in the mean conception rate (first insemination, 16 week non-returns) of all bulls having a minimum of 10 first services in each pair of consecutive months at Reading.

Year		Oct-Nov.	Nov-Dec.	Dec-Jan.	Jan-Feb.	Feb-Mar.	Mar-Apr.	Apr-May	May-Jun.	Jun-Jul.	Jul-Aug.	Aug-Sep.	Sep-Oct.	Total difference	Ann. mean difference
1944-45	No. of bulls	5	5	8	8	5	5	3	5	3	4	4	5		
	Mean CRs.	52.0 50.3	49.9 55.3	60.9 64.7	65.5 60.3	64.1 64.2	64.2 75.0	69.3 67.3	62.4 62.3	59.9 77.8	73.9 64.0	64.0 66.2	64.5 70.3	+ 27.1	+ 2.3
	Difference	- 1.7	+ 5.4	+ 3.8	- 5.2	+ 0.1	+ 10.8	- 2.0	- 0.1	+ 17.9	- 9.9	+ 2.2	+ 5.8		
1945-46	No. of bulls	4	6	8	7	9	7	6	7	4	3	7	9		
	Mean CRs.	72.0 69.3	74.0 70.9	69.6 65.1	65.5 64.5	65.6 68.9	67.0 66.5	64.0 61.7	62.8 63.8	61.1 68.8	75.4 63.9	55.3 66.6	61.3 56.8	- 6.8	- 0.6
	Difference	- 2.7	- 3.1	- 4.5	- 1.0	+ 3.3	- 0.5	- 2.3	+ 1.0	+ 7.7	- 11.5	+ 11.3	- 4.5		
1946-47	No. of bulls	9	11	11	7	7	9	9	9	8	5	5	9		
	Mean CR	56.8 67.1	68.7 61.5	61.5 73.6	73.8 73.8	73.8 66.8	69.0 70.3	70.3 60.3	58.4 66.8	67.2 61.7	63.7 62.7	62.7 65.1	64.3 73.1	+ 12.6	+ 1.1
	Difference	+ 10.3	- 7.2	+ 12.1	-	- 7.0	+ 1.3	- 10.0	+ 8.4	- 5.5	+ 1.0	+ 2.4	+ 8.8		
1947-48	No. of bulls	9	8	9	10	10	10	10	11	11	9	8	9		
	Mean CR.	73.1 68.0	69.6 66.1	65.6 63.2	65.0 61.9	61.9 58.7	58.7 56.2	57.2 48.3	49.1 45.1	45.9 51.6	50.6 52.6	52.2 58.8	58.2 50.3	- 27.3	- 2.3
	Difference	- 5.1	- 3.5	- 2.4	- 4.1	- 3.2	- 2.5	- 8.9	- 4.0	+ 5.7	+ 2.0	+ 6.6	- 7.9		
1948-49	No. of bulls	8	7	9	11	11	10	10	11	10	9	8	9		
	Mean CR.	51.9 52.1	53.7 59.4	61.2 56.5	57.5 61.8	61.8 60.3	61.7 56.2	56.2 56.1	57.5 62.5	64.2 64.0	65.2 58.8	60.3 59.8	59.1 69.9	+ 7.1	+ 0.6
	Difference	+ 0.2	+ 5.7	- 4.7	+ 4.3	- 1.5	- 5.5	- 0.1	+ 5.0	- 0.2	- 6.4	- 0.5	+ 10.8		
1949-50	No. of bulls	9	11	12	9	9	10	9	9	8	6	5			
	Mean CR	72.9 65.4	62.7 63.7	64.5 61.9	60.5 65.1	65.1 64.0	65.2 63.5	67.2 65.2	67.2 66.0	67.4 63.7	65.2 66.7	63.3 70.7	-	- 7.9	- 0.7
	Difference	- 7.5	- 1.0	- 2.6	+ 4.6	- 1.1	- 1.7	- 2.0	- 1.2	- 3.7	+ 0.9	+ 7.4			
Monthly Total difference		- 6.5	- 3.7	+ 1.7	- 1.4	- 9.4	+ 1.9	- 25.3	+ 9.1	+ 21.9	- 25.9	+ 29.4	+ 15.0	+ 4.8	-
Monthly mean difference		- 1.1	- 0.6	+ 0.3	- 0.2	- 1.6	+ 0.3	- 4.2	+ 1.5	+ 3.7	- 4.5	+ 4.9	+ 2.6	-	-
Quarterly total difference			- 8.5			- 8.9			+ 5.7			+ 16.5			

Table No. 9a.

Analysis of variance of month-to-month changes in the conception rates of the same bulls (moving mean) at the Reading centre during the period from October 1944, to September 1950.

Source of variance	d.f.	s.s.	m.s.	F
Total	70	2453.34		
Between years	5	150.59	30.12	0.87 NS
Between quarters	3	25.91	8.64	0.25 NS
Between months	11	515.22	46.84	1.36 NS
Within months	51	1761.62	34.54	

These data are so variable and devoid of pattern from month-to-month, that one must conclude that conception rates at this centre have been influenced to an over-riding degree by variables other than seasonal or bull changes.

Summarising the investigation of overall "Habitat" influences on the fertility of the cattle which have contributed to this study, the conclusion is reached that variations attributable to the character of the habitat and its variations appear

to be of a relatively low order in Britain; but if the wide variation in month-to-month conception rates at any centre comes under greater control in the future, then the seasonal influences of habitat may deserve re-examination in relation to the lower "error" variation.

The different patterns of conception rates at different centres suggest that examinations of habitat influences, even in an area as small as Britain, should be examined with local, rather than pooled, data.

In this study the data will be treated on an intra-centre basis, but no attention will be paid to seasonal or meteorological variation.

2. MANAGERIAL PRACTICE.

2. (i) Age of animal at first mating.

(a) Age of heifers.

Several investigations have drawn attention to the fact that heifers tend to conceive less rapidly than older cows (Taylor, 1937; Morgan & Davis, 1938; Bowling et al, 1944; Tanabe & Salisbury, 1946; Olds et al, 1949; Milk Marketing Board, 1949).

One possible cause which suggests itself is that the physiological processes of the oestrus cycle in heifers may be less well synchronised during the early stages of puberty than in later life, and that the lower apparent fertility of heifers may reflect the tendency for farmers to serve their heifers in the earlier stages of puberty when the heifer may not be really physiologically conditioned for achieving pregnancy. On the other hand Hammond (1927), and Rice & Andrews (1951), both quote the age of puberty in cattle under normal dairy farming conditions as less than 10 months, and very few farmers would consider mating heifers under 12 months of age. But Hawk et al (1954) report that, in a Friesian herd in which all heifers were checked twice daily for oestrus from the age of 6 months, the average age at first oestrus, for a group of 67 heifers, was 397 days, with a standard deviation of 54 days, in which case it is quite possible that some farmers would be mating heifers at their first or second oestrus.

This would be likely to apply in the case of late-maturing individuals, as 15% of the heifers studied by Hawk et al failed to attain puberty until

after 455 days.

Although the difference was not significant in their data, classification of the heifers according to rate of attaining puberty revealed that the earlier maturing heifers required 2.00 services per conception compared with 2.26 services per conception for later maturing heifers, and since no heifers was served before she attained the age of 454 days, the effect of early first services will have been considerably reduced in their data.

These workers also demonstrated a significant delaying effect of scouring, and of inbreeding, on age at puberty, resulting from retarded growth rate. The average age at first oestrus of non-scouring outbred heifers was 364 days.

It is generally recognised that certain breeds, such as the Jersey and Guernsey, tend to attain puberty and to calve earlier than other breeds such as the Shorthorn and Red Poll (Milk Marketing Board, 1948), but it is reasonable to expect that within breeds the rate at which puberty is attained and at which a satisfactory level of fertility is reached will be a function of both the general and particular plane of nutrition on which the heifer is reared.

A long-term nutritional study of the effects of rearing heifers on three different planes of nutrition, representing approximately "Morrison's standard", sixty-five percent, and one hundred and forty percent of this standard, with rations that vary qualitatively as well as quantitatively, is in progress at New York State College of Agriculture. Preliminary reports on the first 24 trios of heifers (Asdell, 1952a; Mimeograph progress report by the Animal Husbandry Department of Cornell University; Reid et al, 1955) have demonstrated a very marked difference in age at first oestrus - 15 months (excluding 2 heifers still not on heat 18½ months), 11 months, and 8½ months, respectively for low, standard, and high plane feeding - as well as a tendency for depression of conception rate among the high plane heifers, when first bred at approximately 18 months of age.

The conception rate of the low plane heifers, however, compared favourably with that of the standard group when all groups were mated, as nearly as possible, at a standard age of 18 months.

To examine the possibility of differential

probabilities of conception attending inseminations given to heifers it would therefore be desirable to relate the time of insemination to the time of attaining puberty rather than to the age of the heifer.

In this study it was not practicable to obtain the necessary information for this purpose, and the compromise of relating the mean fertility levels to the age of heifers at the time of their first insemination was accepted.

The ages of all cows used in this study were not available, but the dates of birth of heifers born as a result of insemination were known.

It was not possible to determine from the available records whether or not a first insemination was in fact a first attempt at achieving conception, or whether the animal had already had a calf.

By sorting the data into age at first insemination a marked drop in frequency occurs at about thirty months of age (see Figure No. 5), and this age was therefore taken as an arbitrary point at which it was assumed that animals inseminated at later ages were second-season cows, and those inseminated at thirty months, or less, were heifers.

Datum cards were sorted into breed groups according to the breed of sire of the heifer, but of the 996 animals whose records were available at the time of this examination there were too few to give a reliable estimate of conception rates of individual breeds, and the data were heavily weighted with Dairy Shorthorns (505). The trend of conception rates to first insemination, derived from the bulked data, is superimposed on the histogram in Figure No. 5.

The conception rates achieved between the ages of fifteen to thirty months were then converted to angles (Snedecor, 1946), and a regression of angles on age was computed and found to be insignificant (Table No. 10 below).

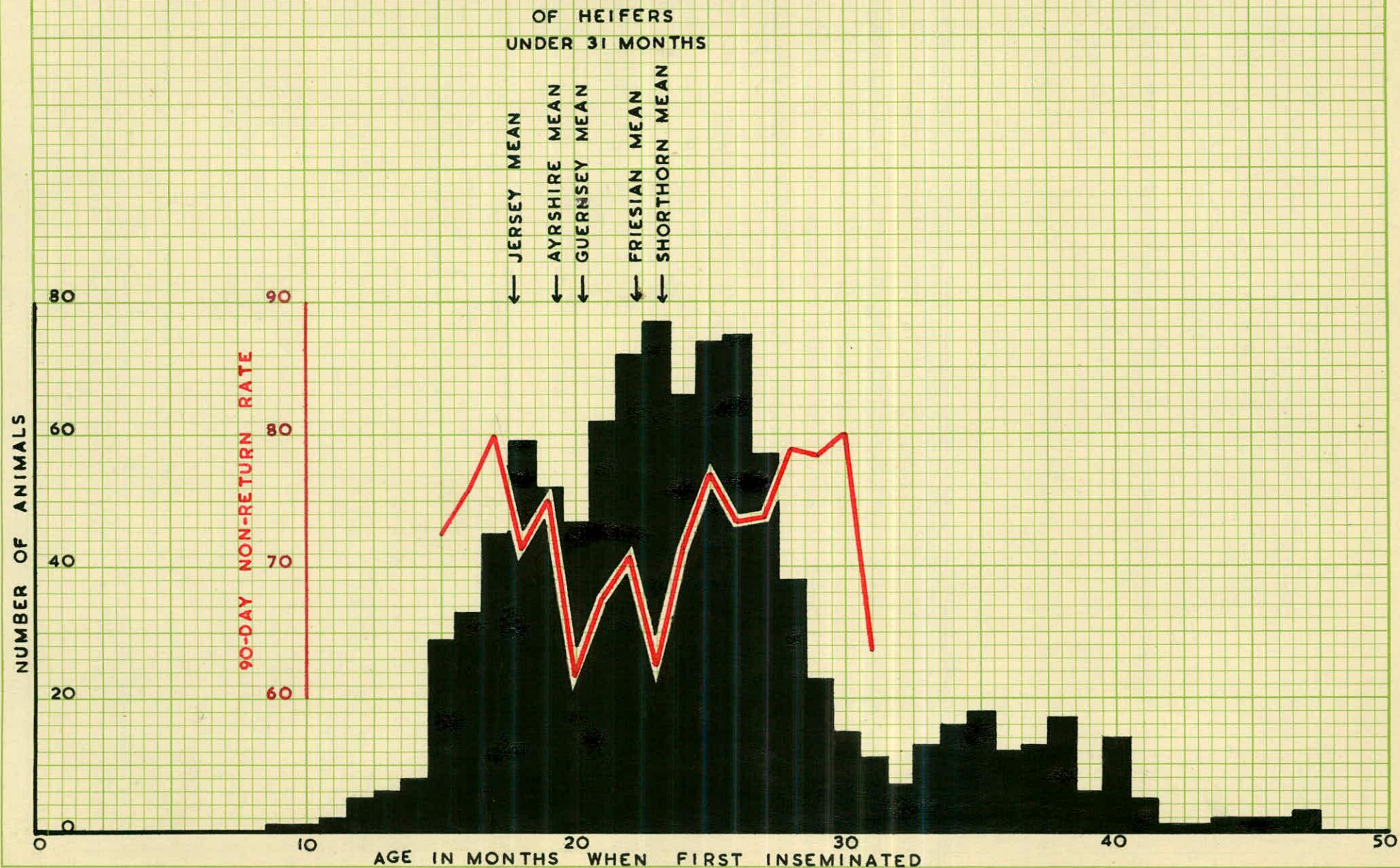
Table No. 10.

Regression of conception rate (expressed as angles) on age of heifers (under 31 months) at first insemination.

(Months)	$Sx^2 = 340.000$	$n = 16$
(CR.Angles)	$Sy^2 = 198.058$	$Sb = 0.19219$
	$Sxy = +77.100$	$t_{.05} = 2.145$
$b = + 0.2265 \pm 0.4122^{NS}$ angles per month		

FIGURE NO. 5

HISTOGRAM OF AGE OF HEIFERS OR COWS SUBMITTED FOR THEIR FIRST INSEMINATION
AND CORRESPONDING 90-DAY NON-RETURN RATES



As a point of interest it was noted that 19 out of 24 Friesian heifers and 8 out of 10 Dairy Shorthorn heifers inseminated at ages under fifteen months conceived to first insemination.

The general picture presented by these data suggests that under artificial insemination conditions in Britain heifers are very fertile and there is no consistent fertility trend within the range of ages at which heifers are usually inseminated.

In respect of age at first mating there appears to be more reluctance to mate at young ages in Britain than in the United States of America. In discussion, Dr. Kendrick, Head of the Bureau of Records of the Department of Agriculture, Washington, stated that a very small proportion of heifers of any dairy breed calve later than thirty months at present and the trend is towards earlier calving so that most heifers calve between twenty-four to twenty-seven months.

2. (i) (b) Age of bulls at first service.

Lower conception rates achieved with semen

of very young bulls have been reported by Tanabe & Salisbury (1946), the Milk Marketing Board (1949), and by Cembrowicz (1952).

This effect is probably also a function of breed, age, and plane of nutrition. The effect of plane of nutrition on which bull calves are reared on their age at first ejaculate is indicated in preliminary reports on the current long term experiment at the New York State College of Agriculture, to which reference has already been made in respect of heifer calves (Bratton, 1955; Bratton & Foote, 1955). Bull calves are similarly allocated to one of the three planes of nutrition, and those reared on the high plane (140% of Morrison standard) have produced their first ejaculate at an average age of $9\frac{1}{2}$ months, compared with ages of 12 months and 13 months for the standard and low plane bulls, respectively. The number of motile sperm per ejaculate was 3.65×10^9 , 3.0×10^9 , and 2.14×10^9 respectively, and no significant difference in the conception rates achieved with semen from each group of bulls was recorded over a sample of approximately 25,000 inseminations.

A very similar experiment is in progress at

Pennsylvania State College of Agriculture where Flipse et al (1953) have reported similar preliminary results.

With the increasing interest in progeny-testing of dairy bulls in Britain it is possible that insemination centres will in future tend to introduce a few bulls each year for testing at a very early age which might introduce a variable requiring attention in comparative fertility studies of the cows which are inseminated with their semen, but comparatively few bulls were used under two years old at the centres co-operating in this study during the period under review. The effect of age of bulls on their mean annual conception rates was examined in these data and is reported under "Biological Limitations", but it is relevant to note here that the 10 bulls "under two years old" achieved a mean conception rate of 63.95, plus or minus 3.18, percent. This was lower than the mean conception rates of other age groups up to "seven years old", but the differences were not significant.

When bulls were grouped in such a way that the same individuals were compared over pairs of consecutive years of age (moving mean), the

conception rates of eight young bulls decreased by 0.91 percentage-units from the annual mean conception rate at one year to that 2 years.

There does not seem, therefore, to be adequate reason for excluding data derived from young bulls in this study on account of excessive youth.

2. (ii) Service period.

Widespread attention has been paid to the period required by cattle to recover from parturition and to become effective breeding animals again, and there is a general agreement in the findings, from very widely scattered populations, that fertility levels of populations are depressed for about seven to eight weeks after parturition, although individual cows may conceive considerably earlier than this. (Taylor, 1937; Hofstad, 1941; Friend, 1951; Shannon et al, 1952; Trimberger, 1954).

Casida & Venzke (1936) carried out routine examinations of the reproductive tract of fifty first-or-second-calver Friesian cows. They found

that involution of the uterus occurred at 26.2, plus or minus 1.0, days post-partum, that the ovaries contained "12 mm. follicles" (about half mature size) by 28.8, plus or minus 1.3, days, and that first post-partum ovulation occurred at 40.7, plus or minus 2.1, days, although 30 cases ovulated much earlier, and in 14 cases the original follicle which started to develop later regressed, and was succeeded by a second follicle which ovulated, and this double process involved 13.0, plus or minus 4.9, days longer to ovulation than the process whereby the first developing follicle matured and ovulated.

Twenty-eight percent of the cows showed a slight purulent discharge from the uterus for one or two weeks post-partum, and this condition appeared to be associated with lack of synchronisation of oestrus and ovulation, and with a relatively poor milk yield during the first six weeks of lactation.

A similar pattern of ovarian function was reported by Trimberger (1956) who found that the mean interval from parturition to first oestrus, in a group representing four breeds of dairy cow, was 43.7 days when oestrus was defined by ripe follicles detectable in the ovaries, but 49.4 days if oestrus

was defined by external manifestations of "heat".

The distribution of his observations was :-

Interval from parturition to first "oestrus"	Percentage of animals observed falling in each interval when oestrus defined by	
	Ripe follicles	Manifestations of "heat"
1 - 30 days	30.0	25.75
31 - 60 days	51.5	43.00
61 - 90 days	15.5	24.50
over 90 days	3.0	6.75

Trimberger (1954) carried out a planned mating experiment to determine the effect of service period on apparently "normal" cows. After parturition they were randomly allocated for service or insemination at less than 61 days, 61-90 days, or over 90 days post-partum until there were 50 cows in each group, representing four dairy breeds. The same sires were used equally over each group.

The first group had an average of 0.52 oestrous periods prior to service, and 48% conceived to first service. Only 30.8% conceived to those bred within 50 days of parturition, compared with

66.7 of those bred within the period of 51-60 days post-partum.

The second group had an average of 1.18 oestrous periods before service, and 70% conceived to first service, whereas the late-bred group had an average of 3.12 oestrous periods before service, and 76% conceived to first service.

From the practical breeder's point of view the results were expressed in terms of the number of days needed from parturition to established conception in respect of cows first bred after various service periods:-

Service Period	Average interval from parturition to conception.
Less than 51 days	100.5 days
51 - 60 days	74.5 days
61 - 90 days	93.8 days

Of the early-bred cows, those which had had a previous oestrus prior to service achieved 70.6% conception to first service, compared with a conception rate of only 35.7% for early-bred cows bred at first post-partum oestrus.

To examine the application of these findings to the present study, all first inseminations which followed a parturition on a known date were extracted on the datum-cards and classified within centres, in groups of 5-day intervals, according to the service period between the preceding parturition and the date of insemination. These data are tabulated in Appendix 6 in respect of each centre separately, and bulked data grouped on 3-day intervals is given in Table No.11 below.

There was close agreement of pattern between all centres which established a very significant regression of conception rate on service period of plus 0.8769, plus or minus 0.1487, percentage-units increase per extra day service period, within the range of 21 to 71 days post-partum.

The overall mean conception rates, derived from bulked data of all centres, grouped about 3-day intervals of service period are given in Table No.11 below.

Table No. 11.

Classification of frequency and conception rates of inseminations given at various service periods post-partum (bulked data).

Service period	No. of inseminations	Conception rate percentage after 1st insemination.	Cumulative percentage of 4102 inseminations given up to specific service period.
Less than 21	59	17.95	1.01
21 - 23	54	26.47	1.92
24 - 26	80	17.50	4.02
27 - 29	74	34.49	5.92
30 - 32	95	33.69	8.44
33 - 35	115	33.91	11.44
36 - 38	94	38.30	13.90
39 - 41	112	44.64	16.82
42 - 44	135	43.70	20.34
45 - 47	149	51.01	24.22
48 - 50	175	49.14	28.77
51 - 53	171	54.97	33.22
54 - 56	163	53.37	37.46
57 - 59	142	52.11	41.16
60 - 62	134	60.53	44.65
63 - 65	130	58.46	48.04
66 - 68	130	69.23	51.43
69 - 71	135	63.70	54.93

The general effect of the service period on

conception rate is clearly evident in Figure No.6, in which are plotted the bulked data from all centres and the computed regression line within the interval from 21 to 71 days post-partum.

The prediction equation within this range of service period is

$$Y = 0.88 \text{ S.P.} + 6.00$$

where Y is the predicted conception rate to first insemination, and S.P. is the service period in days.

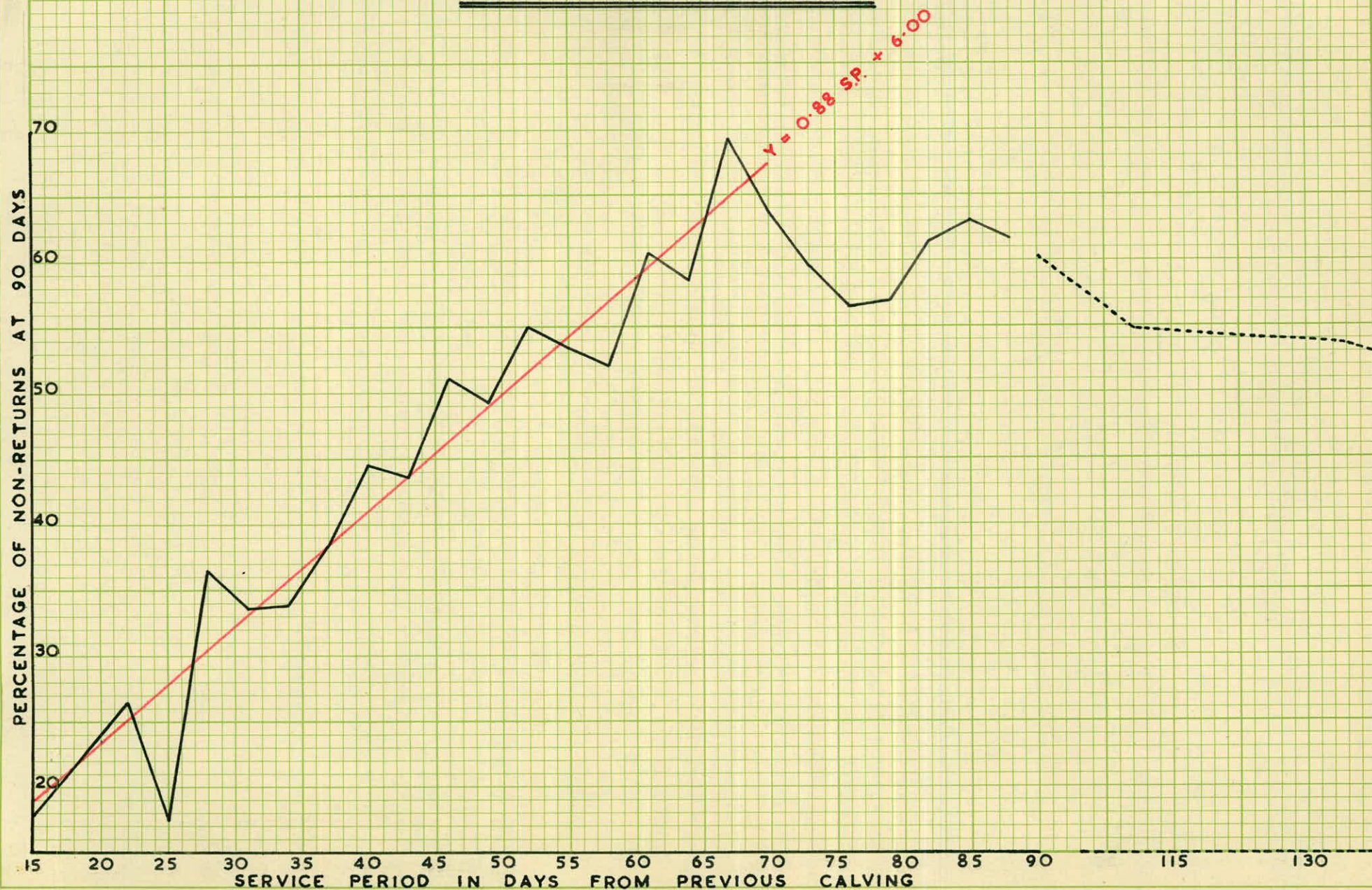
It is apparent from this examination that cows inseminated at service periods of less than fifty days are less likely to conceive than cows inseminated after longer service periods, and the importance of this fact in an investigation involving comparative fertility studies is emphasised by the high proportion of first inseminations (28.77%) which fall within the sub-optimal group. This proportion compares unfavourably with that reported from a study of 7,071 post-partum first inseminations in the United States in which only 16.1% were inseminated within fifty days of calving (Shannon et al, 1952).

It would therefore seem desirable to omit

FIGURE NO. 6

REGRESSION OF NON-RETURN RATE, AT 90 DAYS FROM FIRST INSEMINATIONS, ON SERVICE

PERIOD FROM PREVIOUS CALVING



all inseminations made within 50 days of previous calving, or to adjust the recorded fertility of each insemination given within the prescribed period to a hypothetical fertility based on the regression equation given above.

Thus an insemination given at a service period S.P. would count, not as 1, but as

$$\frac{0.88 \text{ SP} + 6}{\text{CR}}$$

where CR is the current mean conception rate for the centre.

In this particular study adjustment of the data on which the similarity of half-sibs is assessed will be desirable in order to avoid the bias which might affect small groups of daughters. It is doubtful whether any adjustment in this respect is justified in comparisons of fertility between daughters and dams unless the first breeding season of the dam is ignored in the majority of cases, because there is little pre-insemination history available about the dams used in this study.

Since most dams had several seasons of insemination records it was decided to adjust their records for the known service periods and to accept

the first insemination as unadjusted, except when the preceding calving data were known.

As a point of expediency it was decided to adjust the records by completely disregarding all inseminations made within fifty days of previous calving, regardless of whether or not it was successful.

2. (iii) Mating Practice.

Where the fertility of cows is being compared it is obviously desirable that the mating practice should be as closely standardised as possible between groups of cows under comparison.

In this study it has been assumed that the farmers who used insemination for a cow continued to have that cow reinseminated until she conceived, or at least until the farmer notified the centre that the insemination was unsatisfactory. It is known, however, that this assumption is not correct, because a proportion of farmers retained the services of bulls as well as using insemination, and they were quite likely to leave an inseminated cow or heifer with a bulling herd where it might

have been served without any notification of service to the insemination centre. Occasionally such an occurrence was reported to the centre by the farmer, but often the inseminating staff found out at a later date when the "non-return" of the cow for insemination had been credited as a "conception" in the centre's records.

There does not appear to be any satisfactory way in which this source of error can be eliminated from the present data, but it has been reduced by entering notes of all reported or detected cases of "bulling" on datum-cards and redetermining estimates of "conception" on the basis of the datum-card information rather than accepting the records at the centre. Where "bulling" occurred frequently in the records of any farm which contributed a valuable amount of data to this study the farm was visited, if possible, and the information from the centre's records was confirmed or amended in consultation with the farmer or herdsman. In cases where information seemed unreliable the data were discarded.

In discussion, at a breeders' conference, Cochrane (author of "The Dairy Cow in Britain")

suggested the possibility that denial of copulation to a cow which was persistently inseminated throughout its life might lead to depression of the cow's fertility as a reaction to an unnatural process.

If this were so, cognizance of such influence would have to be taken when comparing fertility levels of cows which had been inseminated during differing numbers of seasons.

In order to examine this possibility, in so far as the available data permitted, the histories of all cows which had been inseminated during three or more, and five or more, consecutive breeding seasons were extracted from the data, and the mean number of inseminations required to settle these cows during each of their three, and five, seasons, respectively, were computed (conception rates were standardised to 89 days non-return in view of differing criteria between centres.

These data are shewn in Table No.12, from which it can be seen that no significant trend is indicated.

This result does not necessarily refute Cochrane's suggestion, but it certainly does not

Table No.12.

Comparison of the number of services required per assumed conception by the same cow in successive seasons of artificial insemination.

Season		Somerset		Cambridge		Reading		Dumfries		Hampshire		Worcestershire		Overall mean	
Season		No. of Serv/ cows. concep.		No. of Serv/ cows. concep.		No. of Serv/ cows. concep.		No. of Serv/ cows. concep.		No. of Serv/ cows. concep.		No. of Serv/ cows. concep.		No. of Serv/ cows. concep.	
Cows having	1	468	1.455	231	1.571	197	1.594	47	1.574	59	1.474	65	1.600	1067	1.520 $\pm$ 0.055
at least	2		1.451		1.714		1.426		1.404		1.451		1.200		1.477 $\pm$ 0.053
3 A.I. seasons	3		1.448		1.825		1.547		1.510		1.448		1.400		1.563 $\pm$ 0.059
Cows	1	93	1.624	75	1.306	58	1.775	NIL		10	1.500	18	1.500	254	1.551 $\pm$ 0.107
having	2		1.576		1.480		1.500				1.600		1.111		1.425 $\pm$ 0.106
at least	3		1.570		1.680		1.293				1.900		1.277		1.531 $\pm$ 0.094
5 A.I.	4		1.420		1.627		1.604				2.200		1.721		1.575 $\pm$ 0.104
seasons	5		1.587		1.840		1.500				1.500		1.832		1.583 $\pm$ 0.112

support it, and there is no reason to take a cumulative "A.I. effect" into consideration in the treatment of these data.

2. (iv) Supplementary feeding.

Mention has already been made of the marked effect of nutritional variations on the age at which puberty is attained in cattle (Asdell, 1952a; Flipse et al, 1953; Reid et al, 1955; Bratton, 1955; Bratton & Foote, 1955).

It is relevant to a fertility investigation to estimate the extent to which nutritional variations may cause fertility levels of adult stock to vary.

As no adequate information on nutritional practices at the farms concerned in this study was economically obtainable (the questionnaire approach in the Dumfries area having failed), resort to a survey of the pertinent literature on this subject was made to obtain a perspective of probable nutritional influence.

Hignett, 1950, 1951, 1952, 1956, and Hignett & Hignett, 1951, 1952, 1953, have made a close study of the mineral requirements of cattle for achieving

and maintaining an adequate level of fertility in Britain, and they have also paid some attention to requirements of trace elements and of vitamins A and D.

Their general contention has been that more phosphorus could be fed with advantage in many herds, particularly where the intake of calcium was likely to be high, and that a ratio of 3 : 2 of CaO and P_2O_5 intake was a sound basis for good fertility provided the level of P_2O_5 was adequate - about 7g. P_2O_5 per 100 lbs. liveweight for maintenance, plus about 20g. P_2O_5 per gallon of milk yield, per day. Adequate vitamin D minimises the effect of marginal phosphorus intake.

Manganese intake can be a limiting factor to fertility if it falls below 0.04g. per 100 lbs. liveweight per day (Hignett, 1956).

Hignett (1952) expresses the opinion that implantation of the developing blastocyst is hindered where vitamin A is deficient in the ration of the cow, and abortion is more frequent, and he refers to vitamin A, copper, iodine and phosphorus as the only four nutritional factors which tend to upset reproductive function in cattle even when their

inadequacy is insufficient to induce clinical symptoms of deficiency. He would probably add manganese to this quartet since his previous review.

Quinlan et al (1941), and Joubert (1954), have also reported reproductive failures in cattle associated with low phosphorus, low protein, or generally low plane diets in South Africa; and Korkman (1947b) studied the effect of level of protein, phosphorus and calcium intakes of Ayrshire cattle in Finland, and although his material, derived from farm surveys, tended to produce confounded results, the trend of both this and the South African studies are in general agreement with the findings of Hignett & Hignett.

Korkman (1947b) also classified rations fed to the cattle in terms of "concentrated" and "green" foods, and from his investigation he found that the culling rate for infertility was higher in herds which received rations having a relatively higher concentrate : green food ratio, and that the advantage of the green food appeared to be independent of level of milk yield, and of levels of protein, phosphorus and calcium fed.

The effect of nutritional deficiencies on

the fertility of stud bulls is unlikely to apply in the present study in view of the exceptional standard of husbandry under which bulls are usually maintained at insemination centres, but in general fertility studies inadequate nutrition of bulls could have a very pronounced effect on apparent comparative fertility levels of the cows to which they were mated.

There is evidence that bulls can tolerate some fluctuation from accepted standards of feeding without depression of their fertility. Branton et al (1947) demonstrated that nutritional levels of 100%, 120% and 140% of recommended maintenance rations for dry cows of equivalent weight, and variations of protein content of the ration between 12%, 16%, and 20%, had no effect on semen production, or on apparent fertility (based on 90-day "non-return" results), of 18 bulls standing at an insemination centre.

An experiment conducted at an insemination centre by Bratton et al (1948) indicated that no impairment of fertility was detectable among six bulls which were fed a ration believed to be low in carotene, over a period of 16 months. No

clinical symptoms of vitamin A deficiency were observed, which suggests that the ration may still have offered some carotene or vitamin A. When the roughage of the ration was changed to dry beet pulp both clinical avitaminosis and impaired semen were recorded.

To sum up the position with regard to possible nutritional effects on fertility studies in Britain the following considerations should be borne in mind, in addition to consideration of the adequacy of the ration in terms of energy and protein requirements.

Vitamin A deficiency should not become a limiting factor in fertility under normal farm husbandry, although in arable districts where heifers may be fed almost exclusively on oat straw and sugar-beet pulp such a deficiency might occur. The feeding of excessive amounts of sugar-beet pulp and oil cakes in lieu of adequate pastures, which may occur in the beet-growing areas, may also lead to a deficiency in phosphorus which can be accentuated by a high calcium intake. The "inverse" conception rate pattern of the Cambridge centre, relative to other centres, during the winter might

possibly owe something to this type of nutritional influence.

Phosphorus deficiency is associated with ovarian disfunction including a tendency to increased incidence of cystic follicles and cystic corpora lutea, and to inability to maintain pregnancy. It is most likely to occur as an imbalance due to high calcium intake.

Hignett (1950) produced figures supporting the view that low herd fertility was often associated with the practice of applying heavy dressing of lime to pastures, which would tend to upset the phosphorus metabolism of the grazing animals, and the fact that in several farms following this practice the fertility of their herds was higher in the winter, when they were not grazing, than it was in the spring and summer when grazing was maximum, was interpreted to support this view.

Copper deficiency is usually a regional problem confined to grazing animals which are not receiving any supplements. Such deficiency might occur in some areas of Derbyshire, where "swayback" among lambs is not uncommon, and also on the "teart"

pastures of Somerset where the abnormality is an excess of molybdenum in the pastures which is believed to upset the copper metabolism of the grazing animal. Copper deficiency is associated with irregularity of return to oestrus after service, which suggests early embryo mortality.

Iodine deficiency is also associated with irregularity of returns to oestrus after service, and also with periods of anoestrus, with increased incidence of abortion, and with a tendency for prolonged gestation and retention of membranes after parturition. Hignett (1952) has drawn attention to the similarity of symptoms between iodine deficiency and Vibrio foetus infection.

Physiological deficiency of iodine can occur when the ration contains adequate iodine if there is interference with normal iodine metabolism, and it is known that kale, and other brassicae, contain an abundance of goitrogenic factor in some seasons, but not in every season, which can upset the iodine metabolism of cattle if fed in large quantities. High protein feeding is also associated with disturbance of iodine metabolism, so that trouble

of this nature may be expected among very intensively managed herds, or during winters following wet summers when the cows have enjoyed abundant high protein pasture, possibly followed by prolonged kale feeding, and then by high protein silage.

As the cow is normally able to synthesise vitamin D there is unlikely to be a deficiency of this item unless cattle are kept in sheds or covered yards for prolonged periods, as may happen in some areas of Britain during the winter, and when no opportunity is afforded to such cattle to replenish their reserves of vitamin D through their rations.

The feeding of green food to cattle which are denied adequate grazing would contribute an element of insurance against depression of fertility, and additional insurance could be provided in the form of a mineral supplement, suitably compounded to meet any specific deficiencies liable to occur in a given locality.

In any planned fertility study it would therefore be desirable to define the nutritional background of the study if results are to be broadly

interpreted, and, wherever possible, the nutritional environment of animals whose fertility is being compared should be standardised with respect to those principal ingredients known to influence fertility.

In this particular study nutritional variations must be accepted as a source of unknown variation, most of which would be included in the inter-farm element of variance, and it will be estimated in this form. Nutritional variations will influence dam-daughter comparisons to a larger degree than half-sister comparisons because dams and daughters will usually feed on the one farm. If the half-sister groups are large enough, the farms, and hence nutritional effects, may be sufficiently scattered to avoid bias in comparisons of one group of half-sibs with any other such group. The possibility of bias might remain even in large samples if the nature of breed differences was such that one breed was associated with farms on a higher plane of husbandry; as might have been the case in respect of many large herds of Channel Island breeds of cattle some years ago in areas other than the south-west of Britain.

3. BIOLOGICAL INFLUENCES.

3. (i) Age. (a) Cows.

There has been a great deal of study devoted to age effects on the fertility of cows under both natural and artificial mating conditions.

The general consensus of opinion derived from such studies is that there is very little effect of age on fertility among cows until they are about ten years old, when they tend to become less fertile (Taylor, 1937; Morgan & Davis, 1938; Bowling et al., 1940; Hilder et al., 1944; Tanabe & Salisbury, 1946; Olds et al., 1949; Davis, 1951).

Miller & Graves (1932) reported that 1,109 cows over six years old required 3.83 services per conception, compared with only 2.28 services per conception for 656 cows under six years of age under natural service conditions in the Beltsville herd.

This herd had, however, an incidence of B.abortus infection which would have tended to bias the fertility of older cows which had been exposed to infection over a longer period, and although Miller & Graves restricted their study to "fertile cows" only it is probable that undiagnosed effects

of disease factors would have influenced their results.

The only report which is wholly contradictory to the above evidence, of little age effect among cows, is that of Korkman (1947b) who, in a study of Ayrshire herds in Finland detected a very significant progressive decline in fertility with age. This trend remained in a population which was being progressively culled for sterility, or breeding troubles.

The population studied by Korkman was exposed to much greater seasonal influence on fertility than applies to cattle populations in Britain and the United States, and it is possible that they may have been more exposed to reproductive disease than most of the cow populations on which other studies have been based; but it is also possible that the level of culling for reproductive troubles also contributed significantly to the apparently consistent levels of fertility of older cows in studies which report little or no depression of fertility with increasing age.

The effect of age of cow on the level of its fertility was examined in this study by sorting out all age-classified datum-cards which involved a "conception" (on the criterion of the cow not having been re-inseminated by the centre, or otherwise reported to the centre as "not conceived" within 89 days after the date of insemination) into groups, by age of cow and breed of semen used for the insemination. The number of inseminations necessary to achieve conception was then taken as an indication of level of fertility of the cow, and age was classified at the date of assumed conception.

The results of this investigation are presented in Table No.13, from which it is apparent that the only consistent trend involves the two youngest groups, under $2\frac{1}{2}$ years of age, which are very significantly more fertile than the older cows.

In order to examine the incidence of culling for reproductive faults on the population of cows used in this study the disposal records of all cows whose histories had been extracted from the records at the Somerset, Cambridge and Reading centres were classified according to the number of seasons during which the cows had been inseminated.

Table No.13.

EFFECT OF AGE OF COW ON NUMBER OF INSEMINATIONS REQUIRED TO ACCHIEVE CONCEPTION.

Age of cow in years.	Shorthorns		Friesians		Ayrshires		Guernseys		All Breeds	
	No.	Insems/concep.	No.	Insems/concep.	No.	Insems/concep.	No.	Insems/concep.	No.	Insems/concept.
Under 1½	23	1.30	15	1.20	31	1.23	27	1.07	129	1.47
1½ - 2½	306	1.33	166	1.37	142	1.33	72	1.40	906	1.43
2½ - 3½	240	1.51	121	1.60	124	1.49	48	1.50	679	1.59
3½ - 4½	156	1.55	61	1.61	111	1.39	27	1.78	423	1.54
4½ - 5½	172	1.62	93	1.62	81	1.47	17	1.59	391	1.61
5½ - 6½	147	1.61	72	1.54	75	1.37	10	1.70	311	1.54
6½ - 7½	113	1.51	52	1.44	52	1.77	8	1.75	227	1.57
7½ - 8½	70	1.63	31	1.81	42	1.45	5	1.40	151	1.60
8½ - 9½	33	1.48	17	1.41	11	1.73	4	2.00	68	1.49
9½ - 10½	27	1.67	9	1.78	17	1.47	2	1.50	55	1.62
Over 10½	19	1.37	9	1.22	14	2.43	3	1.00	45	1.64

Mean number services per conception for cows up to 2½ years old = 1.436 ± 0.074 ^{xx}

Mean number services per conception for cows over 2½ years old = 1.576 ± 0.058 ^{xx}

Note that breed classification refers to the breed of bull whose semen was used for insemination and this does not necessarily ~~xxx~~ coincide with the breed or type of cow inseminated.

The degree of selection applied to this population before their available reproductive histories began was not known. The daughters of bulls at the centres, were, however, a relatively unselected population with regard to fertility, as most had been inseminated as heifers, whereas the older cows were known to be a fertility-selected population in that they could only have appeared in the data if they had produced a living heifer calf as a result of insemination. For this reason the daughters' cards were separated from the cards of their dams and the two groups were examined as different populations.

Within each group percentages were calculated of those cows which had failed to complete specific insemination seasons, and had been classified by the farmers as "barren", or had been culled on any breeding inefficiency criterion. Additional sub-groups were also sorted out representing those cows for which there were no calving results and which had either been reported as "infertile" for the one season, or had been bulled at an interval exceeding 89 days from last insemination, or had been inseminated again in the subsequent season at an interval of less

than a normal gestation period from the last recorded insemination in the previous insemination season.

Clarke (1949) has shewn by investigation of the actual history of animals classified as "barreners" by farmers, that relatively little confidence can be placed in this classification, but in the absence of any better indication of the incidence of temporary or permanent sterility among this sample population the above classifications seemed to offer the best estimate which facilities permitted. Percentages of cows classified as "barren", or as having "failed to conceive", were calculated from the total number of animals in each group which had been inseminated for "z or more" seasons, where "z" is the number of the insemination season being examined. Thus an animal having had five insemination seasons before being classified as barren would have contributed to the data of seasons one to four as a fertile cow and to season five as a barren cow.

No season was included in these data for which inadequate time had elapsed to permit of the result being properly assessed.

Data from Somerset, Cambridge and Reading

are tabulated in Appendices 7, 8, and 9 respectively, and the pooled data from these three centres is presented in Table No. 14. Trends are illustrated in Figures Nos. 7 and 8.

The regression co-efficients for the change in percentage of these insemination failures per additional insemination season were computed on the basis of mean results for seasons represented by twenty-five, or more, cows, but significance was attained only in respect of the pooled data from the dams' group of total failures ("barren" plus "failed to conceive").

It is unfortunate that the available data in respect of the unselected cows applies only for three seasons, as there is an interesting conflict of tendencies among these data.

When only "barren" cows are considered, among the unselected "daughter" group, the proportion appears to increase with advancing seasons, although the large drop in "barren" cows at Cambridge in the third season depresses the pooled data for this season contrary to the indications at Reading and Somerset. On the other hand, when all unsuccessful

Table 14.

Estimations of incidence of insemination failures among cows submitted for insemination, classified according to the number of seasons during which the cows have been inseminated.

(Pooled data from Somerset, Cambridge and Reading).

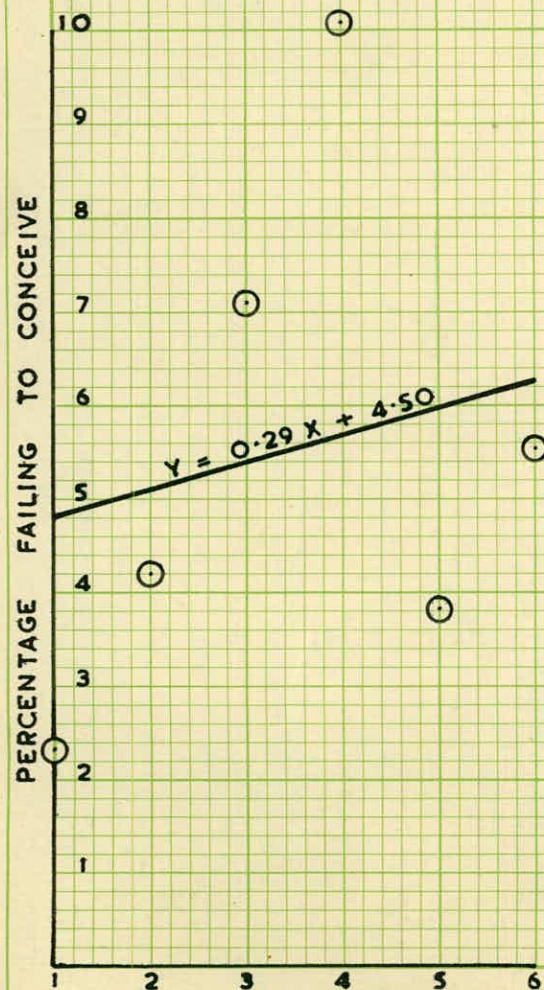
No. of insem. seasons "z"	DAM GROUP (selected breeders.)					DAUGHTER GROUP (unselected)				
	No. of cows having		% of cows having "z" or more seasons			No. of cows having		% of cows having "z" or more seasons		
	"z" seasons	"z" or more seasons	Barren	Failed to conceive	Total unsuccessful	"z" seasons	"z" or more seasons	Barren	failed to conceive	Total unsuccessful
			during season "z"					during season "z"		
1	229	1391	-	1.87	1.87	604	1045	3.44	5.16	6.60
2	343	1162	1.89	1.64	3.53	291	441	5.22	1.56	6.58
3	320	819	2.81	2.81	5.62	126	150	4.67	0.67	5.33
4	250	499	5.41	3.01	8.42	29	34	-	-	-
5	150	249	4.02	2.00	6.02	5	5	-	-	-
6	66	99	4.04	4.04	8.08					
7	22	33	9.09		9.09					
8	9	11	9.09		9.09					
Over 8	2	2	-	-	-					
Regressions of percentage barren and unsuccessful on insemination seasons			b = +1.094 ± 1.102 NS		b = + 1.113 ± 0.626 xx	b = + 0.615			b = - 0.635	

FIGURE NO. 7

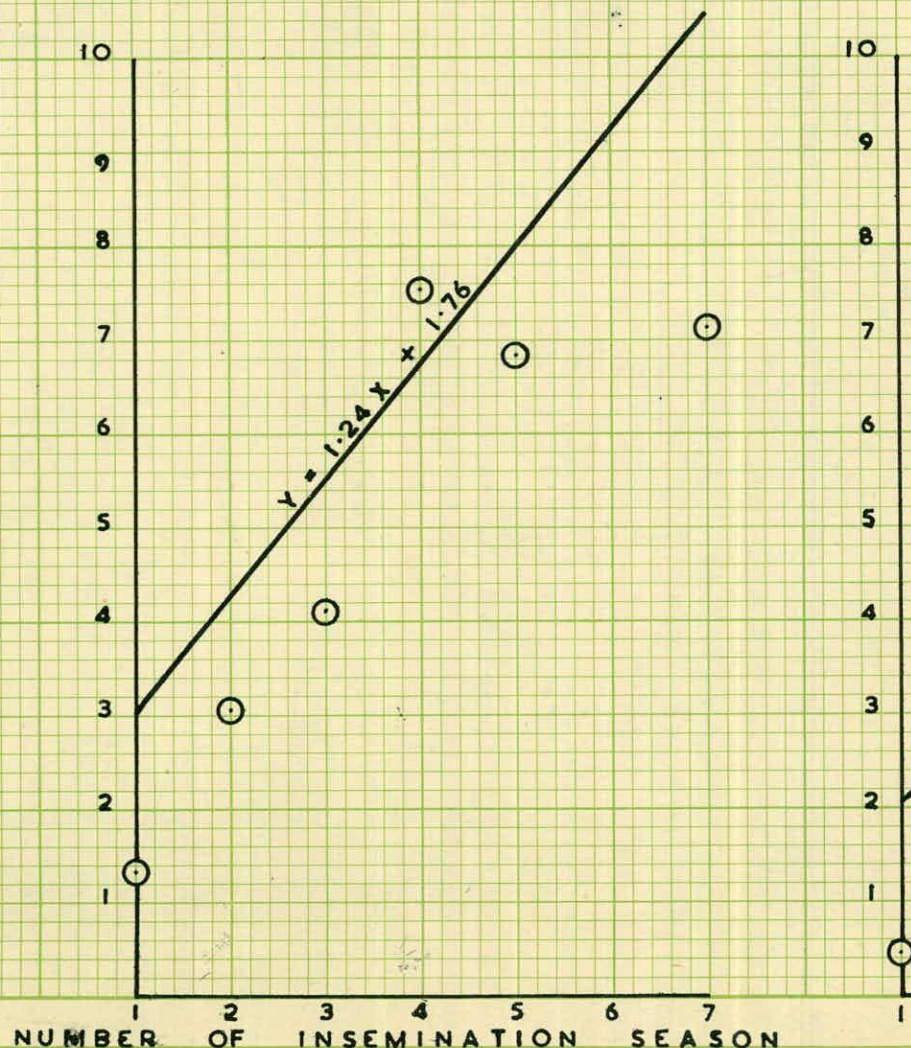
PERCENTAGE OF COWS PRESENTED FOR INSEMINATION IN SUCCESSIVE SEASONS WHICH WERE CLASSIFIED AS BARREN OR APPARENTLY FAILED TO CONCEIVE

i) DAMS OF DAUGHTERS OF A.I. BULLS AT THREE CENTRES

SOMERSET



CAMBRIDGE



READING

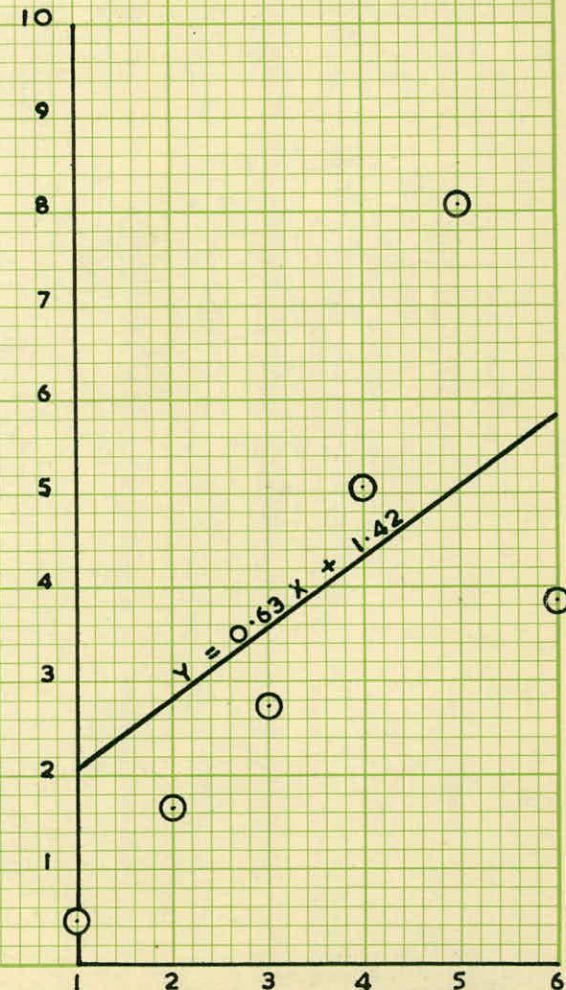
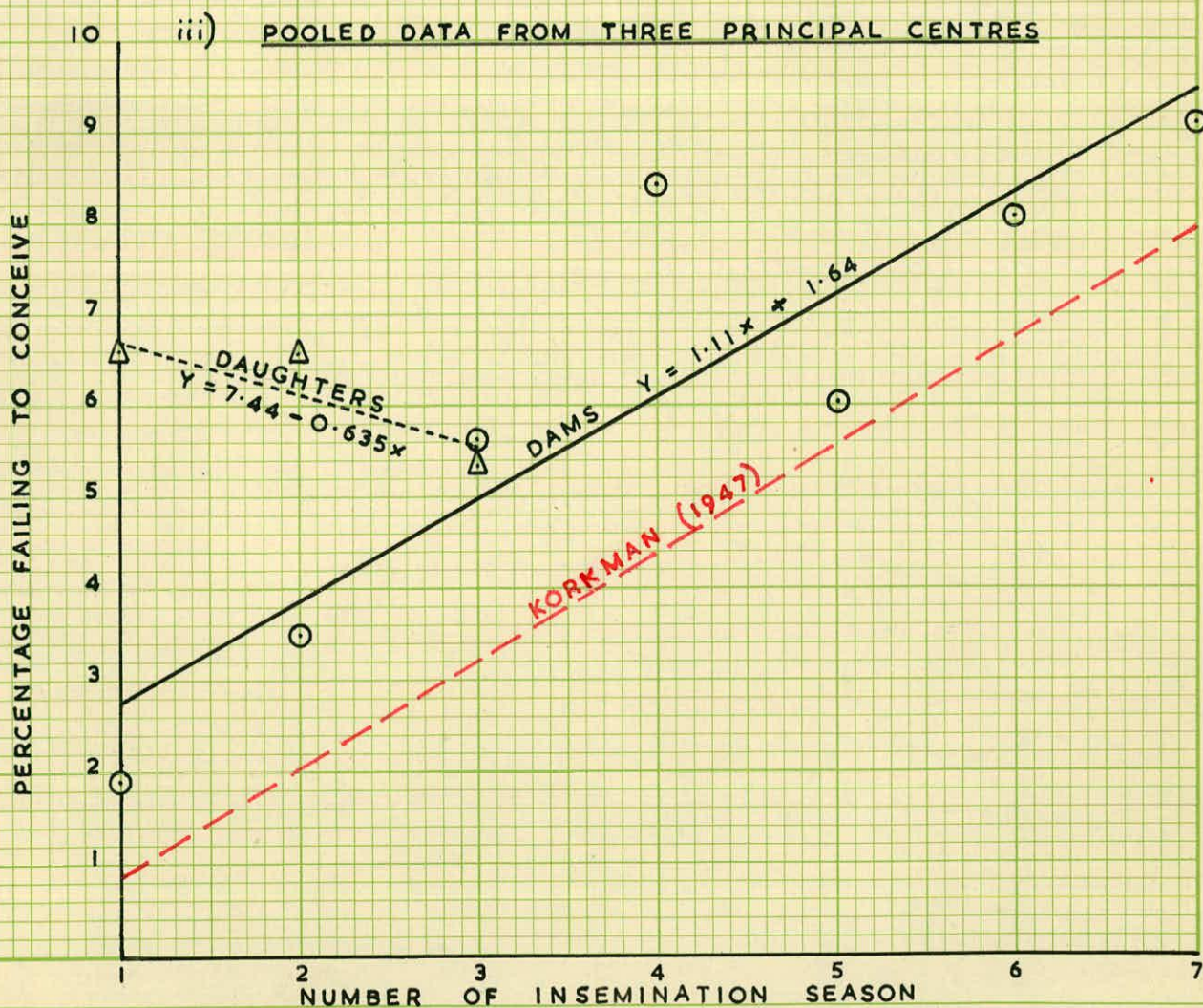
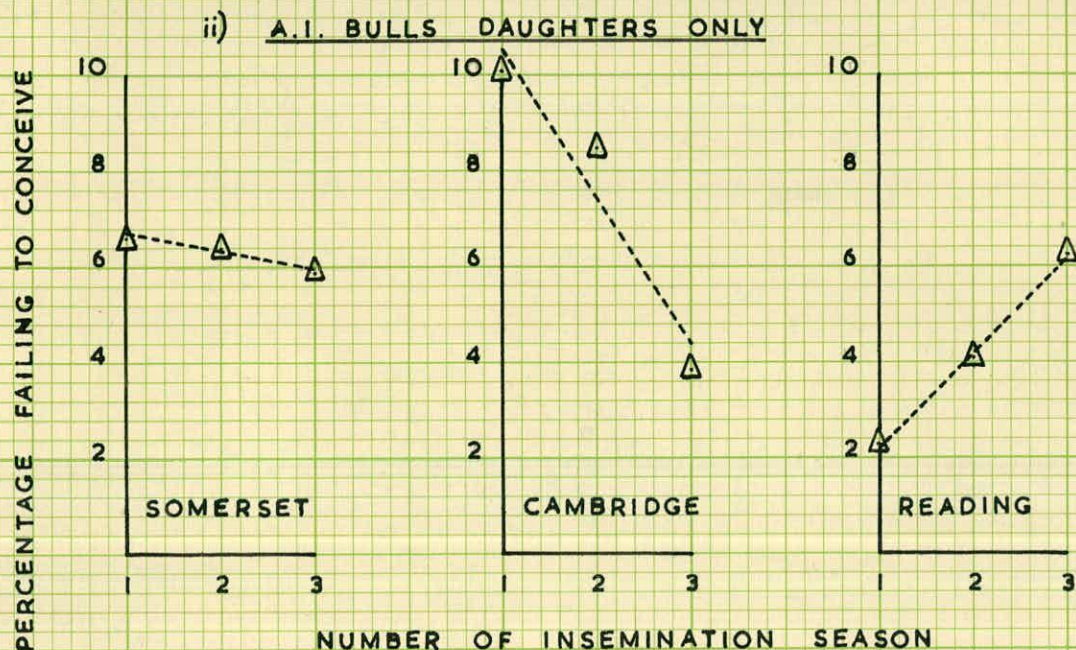


FIGURE NO.8

PERCENTAGE OF COWS PRESENTED FOR INSEMINATION IN SUCCESSIVE SEASONS

WHICH WERE CLASSIFIED AS BARREN OR APPARENTLY FAILED TO CONCEIVE



inseminations are considered together, only the Reading centre reveals a progressive increase in contra-distinction to a very sharp progressive decrease at Cambridge, and a moderate progressive decrease in Somerset.

The different application of the term "barren" at the different centres undoubtedly contributes something to the conflict between results as the Reading "dam-group" is peculiar in being almost entirely free from "barren" cows, although the proportion of total insemination failures is not very much lower than that estimated from the other centres' data. Since the same absence of "barren" cows does not appear among the Reading "daughter group" the apparent freedom from barreners among the "dam group" may reflect a modification of reporting procedure at this centre.

Results from all centres are consistent among the "dam groups" in indicating a progressive increase in the incidence of apparent infertility or sterility with age, and, although Clarke's investigation (1949) suggests the probability of this trend being accentuated by a progressive tendency to cull or dispose of cows on the basis of

criteria other than fertility, it is reasonable to suppose that such influences would not entirely discount the present evidence.

No directly comparable data derived from naturally served cows in Britain was found, but Korkman (1947b) offers statistics on the incidence of culling in respect of sterility or breeding troubles with advancing age among a large population from many herds of Ayrshire cattle of Finland. Using Korkman's figures for groups of cows aged from 2 years to 12 years to compute a regression of infertility-culling percentage on age

$$b = + 1.408 \pm 0.095\% \text{ per year}$$

which is of very similar order to that computed from the records used in this study.

A progressive selection bias, such as that envisaged above, can be avoided in a comparatively fertility study between dams and daughters, by assessing the regression of daughters' fertilities on dams which have all been subject to the same intensity of selection. In the absence of complete information on the age of the dams, the best compromise would be to sort the dams into groups in

which each has been inseminated for the same number of seasons and to compute the regressions of daughter's fertility on the dam's mean fertility within such groups.

When comparing fertilities of half-sister groups, restriction of the comparison to an equal number of seasons would remove the bias due to age and selection, provided they were all recorded for the same seasons.

As this requirement does not hold in the present data, because of the practice on some farms to bull their heifers and to inseminate their cows, it will be more satisfactory to adjust the single heifer records made at less than thirty months to selected adult equivalent records by the addition of 0.14 inseminations, and then to compare all other half-sisters on the basis of their second breeding season, or on the basis of the breeding season which falls within the age limits of 33 to 44 months, in order to avoid difficulties where pre-insemination histories are not available.

3. (1) Age. (b) Bulls.

The literature on the effect of age on the fertility of bulls is reasonably consistent in

reporting very little effect except for an eventual decline in the fertility of bulls from about eight or nine years of age (Morgan & Davis, 1938; Dawson, 1938; Hilder et al, 1944; McCullough et al, 1951; Gembrowicz, 1952).

Bowling et al (1940) reported a steady decline in fertility of bulls from two years (1.50 services per conception) to seven years (just over 2 services per conception) and thereafter a 'plateau' of steady fertility, under natural service conditions. The slight tendency to decreased fertility after three years of age was also shewn in the statistics of the bulls at the Milk Marketing Board (1949) insemination centres.

Morgan & Davis (1938) and Bowling et al (1940) both report on the interaction of age effect whereby heifers conceive more readily to service by young bulls when served naturally.

Tanabe & Salisbury (1946) reported very steady fertility levels for bulls of all ages up to ten years at an insemination centre in the State of New York, except for a marked drop among bulls of five to seven years of age, which they attributed to the return to service of bulls which had been

progeny-tested. Such progeny-tested bulls returned to the centre at five or six years of age and were then reselected on the basis of their fertility level which brought the average level of all bulls at the centre back to 'normal' in the eight year old group.

In order to ascertain whether the data of the present study followed the pattern of other studies, in respect of age effects on conception rates, sample analyses were made.

A preliminary analysis was made of the mean annual conception rates of those bulls at the Cambridge, Somerset, and Dumfries centres which had been in regular use.

Few very young bulls had been consistently used at these centres, although Dumfries had used six Ayrshire bulls under two years of age. The conception rates were calculated on a calendar-year basis, and calendar-year means were then sorted according to the age (in completed years) which individual bulls attained during the calendar year.

The mean conception rates for bulls at different ages, on this basis, are tabulated in Table No.15, together with the 5 percent fiducial

Table No.15.

The mean conception rates of bulls standing at insemination centres grouped according to the age of bull.

Age of bull in years	Data derived from					
	Own study			M. M. B (1949)		Cembrowicz (1952)
	No. of bulls	Annual mean conception rate & fid. limits. (5%)	No. of bulls	Annual mean concep. rate	No. of bulls	Annual mean concep. rate.
Less than 1	-	-	13	58.5	-	-
1 to 2	10	63.95 $\pm$ 3.18	70	60.8	16	65.3
2 to 3	32	66.62 $\pm$ 1.91	48	64.4	20	68.0
3 to 4	27	65.78 $\pm$ 3.09	37	65.0	20	67.7
4 to 5	19	64.18 $\pm$ 2.64	32	64.7	12	65.3
5 to 6	10	64.42 $\pm$ 4.65	26	62.5	9	65.8
6 to 7	8	64.86 $\pm$ 4.24	20	61.6	5	67.9
7 to 8	12	63.65 $\pm$ 4.48	15	61.7	8	66.4
8 to 9	8	62.06 $\pm$ 5.43	12	56.9	6	66.3
9 to 10	6	61.48 $\pm$ 10.47			3	72.1
10 to 11	2	61.90			1	68.9

limits for each mean, and in comparison with the results quoted by the Milk Marketing Board (1948), and by Cembrowicz (1952), much of whose data is included in the present study but in respect of differing periods of the bulls' lives. The present study included only those bulls which had served consistently at a centre for a minimum of seven months, and had provided semen for a minimum of one hundred first inseminations during the year concerned, and which were believed to be free from infection and reproductive disorders. The small numbers of older bulls would cause the fiducial limits to widen in these data, but it is quite probable that they would widen naturally as a result of differential rates of loss of fertility with age among individual bulls.

Such an approach to the examination of age effects is not satisfactory unless the same individual bulls are used from year-to-year. At insemination centres this requirement is fulfilled by only a few bulls, and, in view of the wide range of conception rates between bulls, an extreme individual standing for only one year could introduce considerable bias into data derived from relatively small numbers.

As an approach to adjusting this possible bias the above data were resorted, and only bulls offering reliable conception rate data in two or more consecutive years (for at least 7 months in each calendar year) were accepted. The differences between consecutive mean annual conception rates were then calculated for each bull, and these differences were grouped according to the years involved in the changing age of the bull. The results of this examination are presented in Table No.16 together with the standard errors of the estimations.

A significant change in conception rates, handled in this way, was recorded only for the improvement from 6 to 7 years of age, but this significance is probably only a reaction to an atypical drop in the conception rates of the bulls sampled between 5 and 6 years of age. Otherwise no significant change was found from year to year although the overall trend tended to confirm the initial examination.

Table No. 16. Age of bull effect

The change of mean conception rate between consecutive years with advancing age of bulls.

Age of bulls in years changing from	No. of Bulls sampled	Mean change of conception rate between consecutive years of age	
		Mean	standard error
1 to 2	8	- 0.91 "% units "	1.83 NS
2 to 3	27	+ 1.16 do.	1.03 NS
3 to 4	16	+ 1.89 do.	0.93 NS
4 to 5	11	+ 0.58 do.	2.46 NS
5 to 6	6	- 0.65 do.	3.65 NS
6 to 7	10	+ 2.79 do.	1.23 X
7 to 8	9	- 1.93 do.	2.83 NS
8 to 9	6	- 4.20 do.	5.26 NS
9 to 10	3	- 1.80 do.	2.01 NS
10 to 11	1	- 7.60 do.	-

The conception rate data derived from Reading was assessed at 16 weeks, instead of the more usual 3 months criterion adopted at the other centres, and a supplementary examination of age effect was made of the Reading bulls by comparing monthly mean conception rates for the same calendar months in consecutive years for all bulls whose semen was used for at least 20 inseminations in each of the paired months.

The result of this examination is presented in Table No. 17.

Table No. 17.

Age of bull effect

The effect of age of bulls on their conception rates as measured by changes in the monthly mean conception rate for identical calendar months in consecutive years at the Reading centre.

Age of bulls in years changing from	No. of bulls	No. of pairs of months	Mean change of conception between rate consecutive years of age	
			Mean	Standard error
2 to 3	8	52	+ 0.19 "% units"	2.15 NS
3 to 4	6	53	+ 6.38 do.	1.39 XX
4 to 5	8	55	- 5.99 do.	2.32 NS
5 to 6	6	45	+ 4.95 do.	2.40 X
6 to 7	5	32	- 2.58 do.	2.26 NS
7 to 8	5	29	+ 1.63 do.	2.22 NS
8 to 9	5	30	- 5.91 do.	5.39 NS
9 to 10	2	21	+ 0.05 do.	- NS

Table No. 18.

Year to year changes in annual mean conception rates measured by changes in the monthly-mean conception rates of individual bulls which served during the same calendar month during consecutive years at the Reading centre.

Years	No. of bulls	No. of pairs of months	Mean change of conception rate between consecutive years	
			Mean	Standard error
1945 to 1946	8	51	- 4.64 "% units"	1.89 ^x
1946 to 1947	8	69	+ 4.63 do.	1.25 ^{xx}
1947 to 1948	8	62	- 9.81 do.	2.02 ^{xx}
1948 to 1949	8	62	+ 4.40 do.	1.84 ^x
1949 to 1950	8	56	+ 5.93 do.	2.24 ^{xx}

There was a very significant improvement in conception rate from 3 to 4 years of age, on this basis of comparison, and a significant improvement from 5 to 6 years of age, but this latter improvement would not have been significant had there not been such a pronounced, but non-significant, drop in

conception rate from 4 to 5 years of age, which was probably accentuated by rather unusually high conception rates among the bulls sampled at 4 years of age. These results may also be misleading in view of the fact that, with the small number of acceptable bulls, there was considerable confounding between bull-age effects and calendar-year effects (which would include technical and other effects). In this connection it is pertinent to record that the very significant improvement in conception rates from 3 to 4 years of age was largely confounded with a very significant improvement of 4.63 "percentage units" between conception rates for calendar years 1946 and 1947 at this centre; and the depression from 4 to 5 years of age was partially confounded with a very significant depression of - 9.81 "percentage units" of conception rate at this centre between the calendar years 1947 and 1948. The calendar year analysis of these same data is shown in Table No. 18.

It is therefore doubtful whether the significance of the changes recorded in Table No. 17 is attributable to age trends or to some other cause, or to both.

From this examination of bull fertility there appears no adequate reason to adjust data for variations in the probable fertility of semen attributable to age of the bulls used.

3. (ii) Disease.

Any study of environmental conditions associated with differential fertility of cattle populations must take cognizance of pathological conditions. Pathological influence on fertility may be direct, or indirect in so far as any pathological condition which seriously impairs the well-being of an individual animal will tend to prejudice the fertility of that animal, albeit only temporarily.

The direct causative agents associated with loss of reproductive efficiency in cattle in Britain include Brucella abortus, Trichomonas foetus, Vibrio foetus, Mycrobacterium tuberculosis, and pleuro-pneumonia-like organisms; while bacteria such as Corynebacterium pyogenes are associated with inflammatory and pyogenic conditions of the genital tract which probably arise from infection during insemination, service, or parturition, and can lead

to temporary or permanent loss of reproductive function.

It is not within the scope of this study to examine the effect of disease organisms on fertility, but it is necessary to recognise that the data collected for this study will be affected by such influences, and to estimate the probable direction in which such influences may bias the results of the investigation.

Essentially disease will tend to affect the individual rather than populations, although instances will occur when small sub-populations, such as herds, will have a high incidence of infection.

Where individuals are affected, and where there is no hereditary predisposition to infection, heritability studies on fertility should not be seriously biased by low incidence of disease over large populations, as the influence would tend to fall at random. On the other hand, where the investigation depends on relatively small samples of sibs a chance distribution of disease could seriously affect comparisons of sib-groups.

Under the conditions of this study of records from insemination centres, it is probable

that disease effects tend to fall at random over all groups of sibs under consideration, but they may contribute a large proportion of the variance between different farms, and thereby bias any data which is gathered from a limited number of farms.

The simplest method of reducing excessive bias attributable to disease would be to seek identification of such "problem herds" from the veterinary staff of the insemination centres and to discard all data derived from such herds.

It is recognised that in so doing any hereditary predisposition to reproductive diseases will have been largely discounted, and it is possible that some of the extreme pairs of dams and daughters whose low fertility has contributed to the designation of a "problem herd" may in fact have owed their low fertility to hereditary factors unassociated with disease.

Owing to the lack of adequate facilities for combining a close clinical study with this investigation it seemed probable that less error would be introduced into the heritability estimates by discarding "problem herds", but this was only done in the few cases where a veterinarian was aware

of a positively diagnosed history of reproductive disease in the herd, and not in cases where the low fertility could not be attributed to any known infection.

Suspected cases of pathological significance among individual bulls standing at centres which have contributed to this study have been reported (Rowson, 1950; Ballinger & Rowson, 1951; Cembrowicz, 1952), and it has seemed advisable to discount completely all inseminations by such bulls during the period when their conception rate was persistently below the normal expected spread of individual conception rates. It is possible that other bulls were also rendered sub-normal in fertility level by pathological influences, but in the absence of any professional opinion no other bulls were withheld from consideration in these heritability studies.

Following the line of enquiry suggested by the work of Christian & Casida (1951), and Flerchinger & Erb (1953), an examination of the Somerset and Dumfries datum cards used in this study was made to determine whether there were any bulls which appeared to have a depressing effect on the conception rates of other bulls whose semen was used

for insemination of their "repeat" inseminated cows. As a result of this examination it was noted that, out of fifty-two bulls examined, which were standing at the Somerset centre, eight bulls - RWA, LMK, SCB, HWP, BV, TL, WMA, and HPG⁴ - appeared to cause cows inseminated by them to have a much lower than average chance of conceiving to the subsequent insemination (about 50% conception rate), but the amount of suitable data available in the sample extracted onto datum cards was too small for satisfactory analysis.

Of the eight bulls examined at the Dumfries centre none had significantly depressed the conception rate of bulls whose semen was used to inseminate cows which had failed to conceive to a preceding insemination with their semen.

3. (iii) Lactation.

There is widespread opinion that the really high-yielding cow is more predisposed to reproductive failure than the average dairy cow. This opinion is given credence by the fact that anoestrus is often associated with the flush of lactation, although Asdell (1931) has stated that oestrus "is rarely

entirely suppressed", and it seems probable that the level of production of milk which predisposes the hormone balance of the cow to high probability of disturbance, of a degree likely to reduce breeding efficiency, is well above that of good commercial herds, provided management is adequate. The question of management is probably the crux of any correlation which may be apparent, as it is well established that the milk "urge" is very powerful indeed in the freshly calved cow, and such a cow will produce milk "if it kills her" as Eckles & Palmer (1916) almost demonstrated by maintaining a freshly calved cow on water only until she could hardly stand, although she continued to secrete milk.

When a herd is maintained under marginal nutritional conditions there may well be an apparent inverse correlation between milk yield and reproductive efficiency, particularly where factors such as phosphorus, calcium or vitamin D are ⁱⁿ limited supply.

From the point of view of a comparative fertility study the only factor with which the investigator would be directly concerned is the possible effect of the level of milk production of

the two cows under comparison at the time when they were required to conceive.

Since this information is not available in respect of all the animals concerned in this study, any interaction between fertility and milk yield becomes a point of academic interest only. As some data were available concerning milk yields of cows concerned in this study advantage was taken of these records to carry out a supplementary investigation which has been reported in Section Three of this thesis, as it has no bearing on the immediate problem.

4. CONSIDERATIONS APPLYING PARTICULARLY TO ARTIFICIAL INSEMINATION.

4. (i) Technical Operations at the Insemination Centre.

The research which has been done on various aspects of bull management, semen collection, dilution, storage and transportation, is so extensive that it would be out of place to review it in this thesis.

It is in the interests of commercial insemination centres to keep in touch with developments, and to apply promising techniques as

they become available. At experimental centres new techniques are tested and developed. These variations are therefore likely to contribute to a time trend in the overall fertility levels achieved with inseminations from each centre.

In order to assess the possible impact of such changes on the probability of cows conceiving to inseminations given at different times, a detailed questionnaire was completed at each centre to draw attention to all major changes of technique, and to enable comparisons to be drawn between centres.

In practice it appeared that all the centres concerned in this study followed very similar proven technical practices in nearly every respect. Only at Reading had any planned experimentation on techniques been carried out, but at some centres there was indecision on this point and some centres had modified procedure for testing a new idea over short periods, but exact dates of trials were not always available.

In this respect the records at Reading were exceptionally informative and it was possible to examine the effects of some specific variations in technique as they applied to the actual sample data

extracted for this study.

At Reading the split semen sample technique had been used for testing alternative treatments. Treatments tested during the period covered by this investigation included comparison of effects of dilutions of 1:20 and 1:50, and later of dilutions of 1:20 and 1:50 with dilution of 1:100; and also examination of the effect of addition of sulphanilamide over a period of two months.

These split samples of data were analysed statistically to ascertain whether any correction need be applied to the extracted information used in this investigation, but the data so treated were limited to those which applied specifically to this investigation.

The results of these sample tests are given below:-

- A. Comparison of dilution rates of 1:20 and 1:50 during period from December 1947 to December 1948, measured in terms of "non-returns" to oestrus within 16 weeks of insemination.

1:20 mean "non-return" rate 59.894%

1:50 mean "non-return" rate 62.329%

Standard error of difference among
52 pairs of split samples 1.858

$$t = \frac{2.435}{1.858} = 1.310 \text{ NS}$$

B. Comparison of diluted semen with and without
sulphanilamide added during February and
March 1949, measured in terms of non-returns
to oestrus within 16 weeks of insemination.

With sulphanilamide mean "non-return"
rate 65.600%

Without sulphanilamide mean "non-return"
rate 66.550%

Standard error of differences among 12
pairs of split samples 2.6642

$$t = \frac{0.950}{2.6642} = 0.3566 \text{ NS}$$

With sulphanilamide difference between
"non-return" rates at 4 weeks and 16 weeks
16.685 % units

Without sulphanilamide difference between
"non-return" rates at 4 weeks and 16 weeks
16.650 % units

Standard error of difference among

12 pairs of split samples 2.1578

$$t = \frac{0.033}{2.1578} = 0.01529 \text{ NS}$$

C. Comparison of dilution rates of 1:20 and 1:50 with dilution of 1:100 during period from April 1949 to April 1950, measured in terms of "non-returns" to oestrus within 16 weeks of insemination.

1:20-50 mean non-return rate 61.174%

1:100 mean non-return rate 63.890%

Standard error of differences among 86 pairs of split samples 2.739

$$t = \frac{2.716}{2.739} = 0.9916 \text{ NS}$$

From these analyses it was concluded that no significant effect resulted from any of the variations in technique tested.

The results of a test on the use of streptomycin in the diluent at Reading were, however, not available at the time of my visit to the centre, and Stewart et al (1951) have subsequently reported on the significant improvement in conception rates

achieved by this modification. Streptomycin was introduced into the diluent as a routine practice at Reading from the 13th July 1950, on-wards, but as very few inseminations relevant to this investigation were involved the effect on the outcome would be negligible.

Another modification of technique which appeared to have significant results occurred towards the end of the investigational period at Dumfries centre, when they changed the source of their sodium citrate and added 0.5% sulphanilamide during September, 1950. A very significant increase in conception rate occurred in the six months following this change, relative to the results during the preceding eight months (see facing page 254, Table No. 49/ under "Stage of Oestrus" in Part III), but this may have been partly the result of a temporary seasonal effect in that particular year, as the trend at Dumfries centre was towards improved winter conception rates, and there were no "control" inseminations made during the period against which to measure the effect of the new diluent. This change also affected a negligible number of inseminations with which this study is concerned.

The occasional use of semen more than two days old may have introduced a bias into the early data of this investigation. Inseminations made with such semen have a lower probability of achieving conception (Swanson, 1951) than those made with semen only one or two days old, such as has been used almost exclusively in the latter years of this investigational period.

The extent of this possible bias cannot be accurately assessed as the collection reference, or age of semen, has not been consistently recorded in these data. The effect will be to make some of the dams appear less fertile than they really were. It will not affect the half-sib comparisons as these cows were all inseminated in the later years.

Apart from the variations mentioned above the technique at each centre has involved careful veterinary attention to the bulls, which have usually been used only once or twice weekly and have been rested periodically. Semen has seldom been diluted with more than twenty parts of diluent, although exceptionally one part of semen in one

hundred parts of diluted semen has been used. Generally accepted diluents have been used, with the exception of short trial periods at some centres. Semen has been examined microscopically at all centres before it has been accepted for use. Cold shock has been avoided. Semen has been stored in ordinary household refrigerators operating at about 5°C., and latterly it has been the practice at most centres to split the diluted semen into separate containers for each day's use to avoid disturbance of the second day's semen, and surplus semen from the first day's inseminations has been discarded at the end of that day.

Some trouble was reported at two centres concerning the inseminators' thermos storage jars failing to hold an adequately cold temperature throughout a long day during the summer months, but refreshing the ice-charge during the day usually corrected this variable within a short period of time.

No sub-centre semen has been used in this study except that used at the Bromyard centre. This sub-centre was able to provide more suitable

data for this heritability study than was available at its parent centre. To determine whether fertility levels were different at the main centre and at Bromyard, the conception rates achieved with semen of six popular bulls during the same months were examined at both centres for every month during a period of three years, from January 1948 to December 1950, when twenty or more inseminations had been made in each area with the same semen. The results achieved at the two centres for the same month, for each bull, were paired and the difference (Bromsgrove conception rate minus Bromyard conception rate) was calculated. This difference was then analysed for significance in this sample of data and was found to be very highly significant in favour of the main centre at Bromsgrove. The relevant figures are given below.

Total number of bull-months compared = 92

Sum of differences + 643. Mean difference
= 6.989 % units

Sum of squares of deviations from the mean of
differences = 15247

Standard error of differences = 1.2578

$$t = \frac{6.989}{1.258} = 5.56 \text{ xxx}$$

In view of this difference and the disproportionate amount of data available from the sub-centre it was decided to rely entirely on the sub-centre for data.

In Tables Nos.4 to 6 very significant differences were revealed in the annual mean results at the three principal centres. At Somerset the differences appear as an improvement trend which might be expected, but at the Reading and Cambridge centres the differences between years have fluctuated irregularly.

To examine further these fluctuations, annual mean conception rates were computed for individual bulls used extensively at these two centres, and are listed in Appendices 10 and 11. The changes between annual mean conception rates of bulls used in consecutive years was computed for comparison with the annual trend of the centre.

The consistency with which nearly all bulls at the Reading centre tend to vary in the same direction from year-to-year suggests that the cause of the annual fluctuations at this centre lies in some environmental factor, or technique, which is

common to the whole centre or area, rather than to the introduction of new bulls.

To a lesser extent the same may be said of the Cambridge centre, but fewer bulls have been retained from year-to-year at Cambridge so that few year-to-year comparisons are available.

Three pairs of extensively used Reading bulls were then chosen, solely on the basis of consistent use, and correlations were determined to ascertain whether their fertility reacted similarly to shorter term changes which would be revealed in monthly mean conception rates. As no significant correlations between any pair of bulls was found within the single year, the monthly mean conception rates of the two bulls which had been in longest service at the centre were correlated over a period of fifty-eight months in which each bull's semen had been used for at least ten first inseminations. This correlation was also insignificant (Table No.19).

Table No. 19.

Correlations between monthly-mean conception rates of contemporary bulls standing at Reading.

Bulls	Breed	Years	No. of months	Correlation coefficient
BA SCJ	Friesian Jersey	1947	12	- 0.1953 NS
LMP KGM	Guernsey Guernsey	1948	12	- 0.0808 NS
MLD 15 HBC	Shorthorn Friesian	1949	12	- 0.2886 NS
WR LMP	Shorthorn Guernsey	1945 to 1950	58	+ 0.1007 NS

The conclusion is reached therefore that a series of temporary fluctuations occur in the conception rates achieved by each bull each month which are independant of the changes affecting other bulls.

Such fluctuations may reflect temporary maladies, or some accident in the handling of a semen sample. But at the same time an overall trend

is operating which is affecting all the bulls simultaneously, if perhaps imperceptibly, from month-to-month.

Thus the fluctuations can be regarded as responses to micro-variables operating within a macro-variable.

Comparative fertility studies dependant on results of inseminations must therefore be subject to a degree of uncontrolled variation until such time as advances in knowledge of reproductive physiology, and in technique, expose the causes or remove them. The magnitude of this uncontrolled variation is indicated by the curves presented in Figure No. 3.

In the absence of any understanding of these trends it does not seem rational to attempt to smooth out their effects on comparative fertility data to accord with an hypothesis of ignorance.

4. (ii) Recognition of oestrus.

Correct recognition of oestrus is a fundamental requirement for successful insemination practice, the failure of which can remove nearly all

possibility of an insemination succeeding, or can create a false classification of a previous insemination.

This factor must add to the sum of other uncontrolled variables in a comparative fertility study, as there appears to be no means of adequately avoiding its effects.

To some extent the effects might be reduced by accepting the inseminator's report that the cow was "not on heat" when he inseminated it, but this might lead to rejection of more late, but potentially fertile, inseminations than others.

In extreme cases of persistent inefficiency of recognition of oestrus at a specific farm, the herd might appear in the records of the centre as a "problem" herd, in which case it would be better to exclude its records from investigational work. It is most likely to occur in those herds in which a combination of inexperience, marginal nutritional plane, and over-worked staff tends to create a "problem" herd in respect of other aspects of infertility.

4. (iii) Occurrence of oestrus during pregnancy.

Under artificial insemination conditions there is the additional possibility of loss of reproductive efficiency arising from the insemination of cows which appear to manifest the external symptoms of "heat" whilst they are in fact in early pregnancy. If such cows are on "heat" in the sense that they would stand for a bull, there is little probability of natural service interrupting the existing pregnancy, whereas if such cows are inseminated, and particularly if the intra-uterine technique of insemination is used, there is a definite possibility of interrupting the existing pregnancy and very little possibility of achieving another conception to the insemination being given at the time.

The fact that cows do sometimes exhibit signs of oestrus when pregnant has been recognised for a considerable time. Henderson (1933), reporting a study of reproductive histories of a large dairy herd of mixed breeds in New York State, stated "many cows, of course, showed estrum while safely pregnant". Knapp et al (1940) quoted six cases out of 133 calving cows in the Beltsville

herds which had accepted service when pregnant. Donald (1943), and Branton (1949), estimated that the expectancy of this phenomenon was about 3.5 percent in average populations of dairy cattle.

In an experiment conducted by the author in Tanganyika (not yet published) 8 zebu cows out of a herd of 240, which was under permanent observation by observers and running with heavily raddled bulls, were thoroughly mounted and served whilst quite definitely about forty to fifty days pregnant (pregnancy being confirmed by two independent examiners, per rectum). This frequency is equivalent to 3.35 percent, which is in very close agreement with the frequencies estimated by Donald (1943) and Branton (1949).

Since confirmation of pregnancy in a cow at the time of insemination is seldom obtainable from inseminators reports, the possibility of deducing such occurrences from the insemination records of the cows was examined.

It was found that thirty-four inseminations out of 8,166 repeat inseminations (0.42 percent) were given to cows which subsequently calved on a date which was approximately a normal gestation period

from the date of penultimate insemination, and more than 20 days less than the recognised normal gestation from the last recorded insemination.

In view of the doubtful parentage of the calf and of the correct assessment of fertility of the cow in such cases these data were discarded from this examination.

4. (iv) Stage of oestrus at which the cow is inseminated.

Comparative fertility studies will be influenced by any differential probability of conception which may apply to inseminations made at different stages of oestrus.

Trimberger & Davis (1943) shewed that inseminations at the beginning of oestrus achieved only 44.0 percent conception compared with 82.5 percent during mid-oestrus and 75.0 percent at the end of oestrus. Inseminations made after the end of oestrus were less likely to achieve conception, but 8.0 percent conception was still possible thirty-six hours after the end of oestrus.

The time prior to ovulation at which insemination is made is a more critical variant than

the time relative to oestrus, but the latter is the only practical criterion on which to assess the variability of conception rates in connection with commercial insemination records.

The time of insemination relative to the time at which oestrus was observed in the cow was recorded at some co-operating centres, but not at all and at some centres it was discontinued after a trial period.

This inconsistency makes it impracticable to apply any consistent "corrections" to the data used in this study, but an indication of the extent of probable errors from this cause has been estimated from the data which were available and the results are presented in Part III of this thesis.

4. (v) Insemination technique.

Several studies have been made of the differential conception rates achieved by inseminating either into the cervix, or through the cervix into the uterus.

Lasley & Bogart (1943) observed that intra-uterine insemination achieved a higher conception rate than intra-cervical insemination. Holt (1946) reported very much better conception to intra-uterine

insemination, but the intra-cervical inseminations were carried out by a different inseminator. Raps (1948) also recorded better conception by deep cervical or intra-uterine insemination than by intra-cervical insemination using a speculum. Weeth & Herman (1951) obtained similar results and noted that the intra-uterine method was particularly to be preferred when the semen used was over 24 hours old. Salisbury & Van Demark (1951) however recorded no significant difference between deep-intra-uterine, mid-intra-uterine, and intra-cervical insemination during three separate studies, but it is relevant to observe that in their studies "intra-cervical" technique involved passing a catheter through the cervix, by manipulation per rectum, and then the catheter was withdrawn to the middle of the cervix before the semen was intentionally deposited. Thus their technique was by no means similar to that which was described as intra-cervical in the other studies which involved the simple insertion of the tip of a catheter into the os of the cervix, as seen through a speculum, and immediate discharge of the semen. As the advantages claimed for intra-cervical insemination include less risk of infecting the uterus

and of aborting a pregnant cow, and simplicity of instructing inseminators, the technique described by Salisbury & Van Demark cannot be accepted as "intra-cervical" in the recognised sense.

The results of Knight et al (1951) tend to support those of Salisbury & Van Demark in shewing no significant difference between the two principal methods of insemination although their intra-cervical results are not quite as good as their intra-uterine results, and, moreover, they omit to describe the exact method of their intra-cervical technique.

At the centres which contributed data to the current study intra-uterine or deep intra-cervical insemination have been the intended standard techniques throughout the period under consideration, with the exception of a few inseminations carried out from the Reading centre during 1945, which were intra-cervical and done with the aid of a speculum.

The amount and concentration of semen used for each insemination could also influence the expectation of achieving conception, but in this particular study all centres were using more concentrated semen than that which might be considered marginal.

One millilitre of diluted semen was the approximate amount used by inseminators of all centres for each insemination. At the dilutions usually employed, and bearing in mind the high level of bull management and infrequent collection, it would be reasonable to estimate that the concentration of motile spermatozoa in semen used for insemination at all centres has been over six million per millilitre, which has been shewn to be adequate for a conception rate of seventy percent (Branton et al. 1952).

Cembrowicz (1952) has examined the effect of individual inseminators at the Somerset centre by comparing the first twelve months' results of 12 inseminators. The first two months operation by inseminators appeared decidedly sub-normal. Holt (1952) has maintained that the rate at which a new inseminator becomes proficient is related more to the number of inseminations he does than to the length of time he has been working. Holt also produces figures representing the mean conception rates achieved, during each of their first twelve months of official operation, by a group of 12 new inseminators.

No indication is given by either Cembrowicz or Holt of the time spread of the data contributed by

their twelve new inseminators, and in view of the very wide variations which can occur in conception rates at a centre from month-to-month, for reasons other than the skill of the inseminator, the validity of their findings in respect of such small samples might be challenged, unless some precaution was taken to remove the effects of other variables.

To seek further evidence on this point the conception rates achieved by the inseminators at the Dumfries centre were critically examined.

To reduce the effects of uncontrolled variables the conception rate achieved each month by each inseminator was expressed as a percentage of the mean conception rate for the month - in respect of first inseminations only. The percentage achieved by a new inseminator in progressive months of his experience then gives an approximate measure of his value relative to his more experienced colleagues, because the mean conception rate for the month is naturally weighted towards the standard of the experienced inseminators. A month of "experience" was counted as any calendar month in which an inseminator completed more than ten commercial first inseminations.

The assessments of Dumfries inseminators on this basis are tabulated in Table No. 20, and the mean

Table No.20.

Analysis of monthly relative conception rates achieved by new inseminators during their first 18 months at Dumfries centre, expressed as a percentage of the mean conception rate for the month. (Only 1st. inseminations used).

Months experience	New inseminators and month commenced							Total	Mean
	MB. 1/48	RM. 3/48	RJ. 5/48	BB. 2/49	CG. 2/49	JM. 11/49	HL. 11/49		
1	101.7	99.3	126.8	100.8	84.9	86.2	84.3	684.0	97.7
2	102.1	106.4	103.2	103.2	102.5	100.2	95.9	713.5	101.9
3	83.0	93.6	103.0	116.4	98.7	100.8	104.2	699.7	100.0
1-3 MEAN	95.6	99.8	111.0	106.8	95.4	95.7	94.8	2097.2	99.9
4	111.0	76.6	94.2	105.4	93.8	95.2	97.8	674.0	96.3
5	79.6	61.6	100.9	101.8	97.9	118.9	104.7	665.4	95.1
6	100.3	96.6	98.0	94.3	85.4	107.0	85.1	666.7	95.2
4 - 6 MEAN	97.0	78.3	97.7	100.5	92.4	107.0	95.9	2006.1	95.5
7	118.9	92.4	95.9	83.6	110.5	90.6	100.0	691.9	98.8
8	106.5	112.3	107.4	95.8	100.7	110.9	89.6	723.2	103.3
9	102.0	96.2	104.2	99.0	95.7	110.3	86.3	693.7	99.1
7-9 MEAN	109.1	100.3	102.5	92.8	102.3	103.9	92.0	2108.8	100.4
10	100.9	97.7	103.6	114.4	98.2	77.7	93.2	685.7	98.0
11	94.4	110.3	98.6	94.8	94.2	102.6	100.7	695.6	99.4
12	106.9	116.5	94.4	102.1	94.7	73.7	100.1	688.4	98.3
10-12 MEAN	100.7	108.2	98.9	103.8	95.7	84.7	98.0	2069.7	98.6
13		95.6	93.8	112.8	99.8			402.0	100.5
14		112.3	94.1	111.4	102.1			419.9	105.0
15		86.8	101.3	88.0	104.1			380.2	95.1
16		108.7	94.8	97.8	116.6			417.9	104.5
17		121.5	100.0	89.3	96.3			407.1	101.8
18		87.8	101.6	101.1	101.0			391.5	97.9
13-18 MEAN		102.1	97.6	100.1	103.3			2418.6	100.8

ANALYSIS OF VARIANCE.				
	d.f.	s.s.	m.s.	F
Total	107	11425.97		
Months 1-12 & 13-18	1	88.88	88.88	NS
Error	106	11337.09	106.95	
FIRST 12 - MONTHS ONLY				
Total 1st 12 months	83	9345.44		
Quarters	3	301.32	100.44	NS
Months	11	465.44	42.31	NS
Inseminators	6	551.88	91.98	NS.
Error	63	8026.80	127.41	

FIGURE NO.9

THE MEAN RELATIVE EFFICIENCIES OF NEW INSEMINATORS DURING THEIR FIRST 18 MONTHS
OF DUTY, EXPRESSED AS A PERCENTAGE OF MONTHLY MEAN NON-RETURN RATES ACHIEVED
BY ALL INSEMINATORS AT DUMFRIES CENTRE DURING THE SAME OPERATIONAL MONTHS



changes in their merit during progressive months of experience are illustrated in Figure No.9, on which the findings of Holt and Cembrowicz are superimposed.

The analysis of variance of the results of seven new inseminators at the Dumfries centre reveals that individuals produced such inconsistent results from month-to-month that there was no significant change in mean efficiency during the first twelve months of operations when assessed on either a monthly or a quarterly basis.

Furthermore there was no significant difference in efficiency between any of the seven inseminators during their first twelve months, and there was no significant difference between the conception rate achieved by the seven inseminators during their first twelve months and the mean conception rate of four of them for a six month period after they had already had twelve months of experience.

Despite these negative findings the trend revealed in Figure No.9 supports Holt's contention that beginners tend to relapse towards lower efficiency for a few months after they have acquired sound technique.

Similar tendencies were reported, in the

discussion on Holt's paper, by Campbell - whose inseminating staff for the Southbar centre are trained on a common course with the new inseminators for the Dumfries centre.

The inconsistencies of results of individual inseminators, although reputed to be using identical techniques, are such that no basis for establishing a suitable "correction" for this variable with regard to comparative fertility studies is yet apparent.

4. (vi) Administrative Considerations.

It is common practice at inseminating centres to assess their success on the basis of assumed conceptions. Any factor affecting the accuracy of this assumption, or causing the method of arriving at the assumption to alter, will be a source of additional variation in comparative fertility studies which depend on these assumptions as criteria of fertility.

It would be more satisfactory to use pregnancy diagnoses as evidence of conception, but this criterion is beyond the scope of commercial insemination units at present, although most centres make a determined effort to obtain calving records, which meets with very variable response.

It is now universal practice for insemination centres in Britain to assess the fertility of their bulls as a "non-return" rate.

It is usual to reassess the fertility of each bull every month on this basis in respect of the total number of cows whose first insemination during her current breeding season has been made with the bull's semen during the month concerned.

The definition of the period of time considered as a basis of estimation of "non-returns" varies between centres. The usual practice being to count the "non-returns" to first inseminations at the end of the third calendar-month after that in which the inseminations were given.

This is loosely described as the "3-month non-return rate", but it will be based upon results in respect of cows inseminated within a period of 90-122 days previously. The Reading and Dumfries centres adopted precise periods of sixteen weeks and ninety days respectively at which they assessed conceptions on a "non-return" basis.

When bulking data from all centres for the purposes of this study a "standard" was adopted whereby cows were credited with a conception if they

reached the ninetieth day after insemination without further insemination or report of failure. This process of standardisation involved reclassification of "breeding seasons" of some cows. Under standardisation a cow inseminated on the ninetieth day, or after, was deemed to have commenced a new "breeding season" and the insemination was classified as a "first" insemination, whereas in the records of the centre the cow might still be shewn as being in the same season as before and as receiving a "repeat" insemination. In some cases a single "breeding season" on the centre's records was sub-divided into three standardised breeding seasons.

This "standard" season has been used throughout this study wherever records of individual cows are concerned, but the centres' statistics have been accepted when discussing overall bull "conception" rates in supplementary investigations.

For the purpose of computing relative conception rates achieved by different bulls, or inseminators, only "first" inseminations (on centres' ⁽²⁾

(2) The term "first" insemination is used in this thesis to refer to the first insemination given to a cow during each breeding season.

The term "repeat" insemination is used to refer to any insemination other than "first" inseminations.

classification) have been taken into consideration.

This is established procedure at all insemination centres in Britain, and is founded in the belief that the population of cows receiving "repeat" inseminations includes progressively disproportionate numbers of either temporarily or permanently sterile cows for whose failure to conceive neither the semen nor the inseminator is necessarily to blame. There is some evidence to support this belief and the question is discussed in Part Three in relation to the data derived from this study.

The scale of charges operative at different centres could exercise a bias on apparent fertility of inseminated cows by creating an economic threshold at the point where further inseminations will involve a further fee.

The normal practice is to allow up to three inseminations for one fee, and thereafter an additional fee is chargeable for every multiple of three inseminations until the cow is assumed to have conceived. At Dumfries up to six inseminations were allowed for the one fee, and at Reading and Cambridge there was considerable laxity in applying the additional charge when the infertile cow was of

investigational interest to the centre.

The official scale of charges at the co-operating centres were as follows:-

Somerset 25/- for every multiple of 3
inseminations until conceived.

Cambridge 25/- ditto.

Reading 27/6 ditto.

Dumfries 35/- for first 6 inseminations, and
20/- for each additional multiple
of 3 until conceived.

Hampshire 30/- for first 5 inseminations
and 20/- for every additional
multiple of 3 until conceived.

Worcester 25/- for the first 3 inseminations,
and 10/- for every additional multiple
of 3 until conceived.

The cost of additional inseminations is so small relative to the value of most dairy cows that it seems unlikely that any farmer would withhold a cow from additional inseminations on the grounds of expense alone, but the fact that a cow has failed to conceive to three successive inseminations is enough to suggest to many farmers that something other than chance is responsible for the failure, and to

persuade him to try natural service, or, if the cow is not particularly valued for her contribution to the economy of the herd, to tip the scales against her and to confirm an unpromulgated decision to cull her on some other grounds.

Whatever the cause, at most centres there is certainly a demonstrable inflation of apparent conception rate to third inseminations attributable to lack of reports of results to the centres, which is not reflected in the calving rate. That the cause may be largely economic pressure encouraging review of culling is suggested by the absence of this inflationary tendency at the Dumfries centre. The patterns of relationship of "non-returns" to calving rates for progressive inseminations at the Somerset and Dumfries centres are compared in Figure No.10, which demonstrates the high degree of repeatability of pattern at these two centres, as well as the contrast between centres.

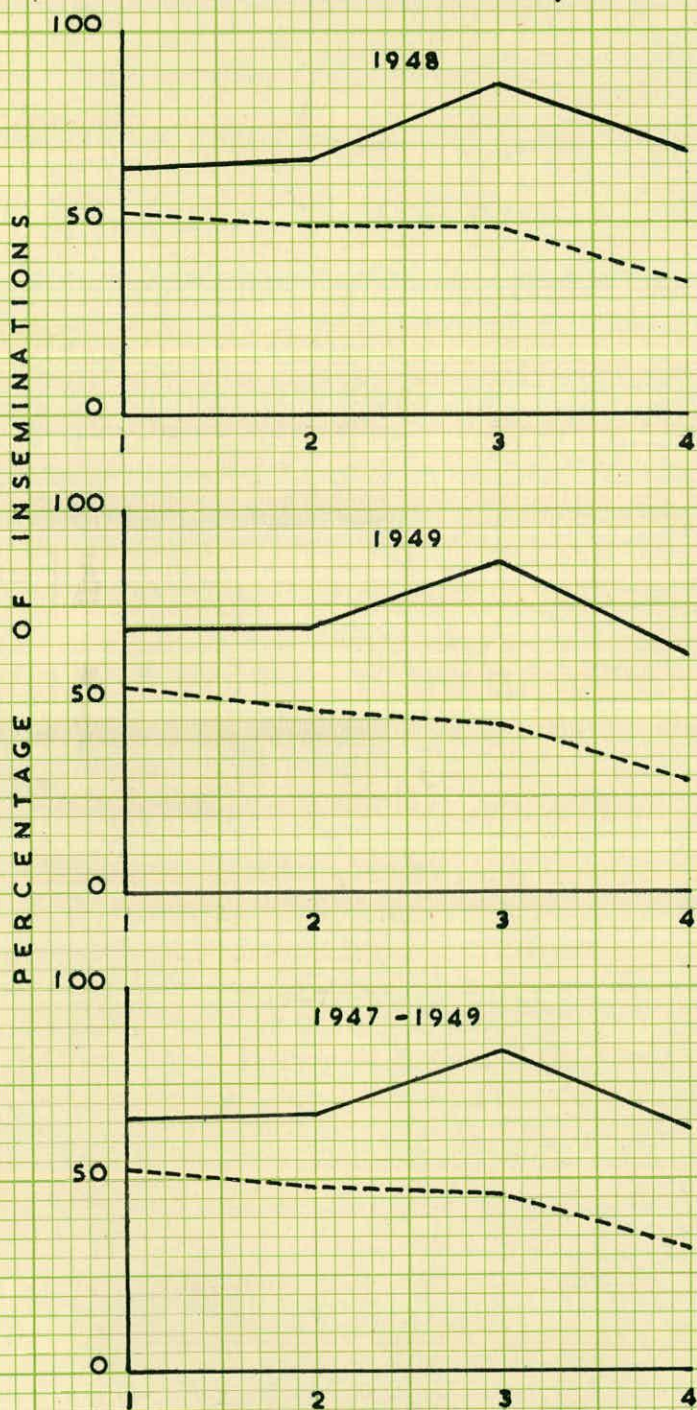
One must conclude therefore that apparent conceptions to third inseminations are unreliable at centres which charge an extra fee for fourth inseminations, but that they can be regarded as satisfactory in the case of records from the Dumfries

FIGURE NO.10

COMPARISON OF NON-RETURNS RATES AT THREE MONTHS WITH CALVING
RATES IN RESPECT OF 1 ST., 2 ND., 3 RD., AND 4 TH.. INSEMINATIONS
AT TWO CENTRES

SOMERSET

(THREE INSEMINATIONS PER FEE,
LARGE CENTRE)



DUMFRIES

(SIX INSEMINATIONS PER FEE,
SMALL CENTRE)



NUMBER OF INSEMINATION

NON-RETURN RATE AT 3 MONTHS

CALVING RATE

centre.

To reduce the unreliability of third insemination records every endeavour was made to obtain confirmation of results of these through calving returns, disposal reports, and in some cases, where many data were concerned, by enquiry at the farms. Where no information could be obtained conception was presumed where the cow was inseminated again within ten to fourteen months afterwards, provided no interim insemination had been given. If the cow was inseminated again after more than fourteen months from the last recorded insemination of the previous season, failure of insemination was presumed. Where the cow was not presented again during the following year then her final breeding-season record was discarded.

The administration at each farm, or type of farming practice, can influence the apparent conception rates recorded at insemination centres. In particular the practice of having heifers inseminated and then turning them out onto a remote area of the farm, possibly with a bull to serve those which return to oestrus, and out of range of frequent observation, tends to inflate apparent conception

rates at the centre and can lead to considerable doubt as to the correct parentage of calves born. The records from one large farm which were contributing much to this study were queried when it was observed that the frequency of gestations exceeding 300 days was high. Enquiry then revealed that heifers were running with bulls after insemination, and, as a precaution, all daughters of sires concerned in this study born on that farm and born after gestations of 290 days, or more, were excluded from this study.

The practice of having nurse cows inseminated and then used for natural rearing under conditions which restrict observation will have a similar inflationary effect on apparent conception rate, and when comparing the apparent fertility levels of bulls this possibility should be kept in mind, particularly with bulls of beef or dual purpose type, as such bulls will be used more frequently on the nurse cows or potential cull cows from the dairy herds.

A possible illustration of this effect is given in Table No.21, wherein the breakdown of the full-term results of those inseminations which were classified as "90-day non-returns" for each bull at the Dumfries centre is given, in so far as it was possible to obtain results by enquiries from

the farmers.

The interesting column is that shewing "no record" available. The two bulls having the highest "wastage" of results (HSK and WSP), and therefore the greatest inflation of non-return conception rates, are both white Dairy Shorthorn bulls standing in an Ayrshire stud. It is reasonable to assume that the wastage will largely reflect inseminations of "marginal" dairy cows from which replacements were not being bred and which would later be culled or turned over to the farm beef unit. Differential wastage among inseminations with semen of dairy bulls may reflect a market value for a fashionable herd name which farmers who trade in-calf cows and heifers would wish to realise.

Table No. 21. Results of first inseminations at Dumfries.

Bull	Period	No. of first inseminations	Percentage 90-day non-returns	Percentage of 90-day non returns			
				Preg-nant	Non-preg-nant	No record	Aborted
RBI	1/48-7/48	436	60.6	86.2	8.2	5.3	2.4
UTD	1/48-1950	2902	62.3	81.5	5.8	12.7	2.0
HR	1/48-8/48	343	61.2	86.6	7.9	5.5	3.8
LK	6/48-10/49	597	64.3	87.1	2.3	10.6	0.5
BWF	8/48-1950	2705	60.3	85.3	2.3	11.9	0.3
BV	6/48-1950	1049	69.1	85.3	4.1	10.6	2.1
WSP	6/48-1950	601	61.9	79.0	6.7	14.3	0.9
HSK	5/48-1950	365	55.1	70.2	1.8	28.1	3.5

5. SUMMARY OF THE EFFECTS OF ENVIRONMENTAL
INFLUENCES ON FERTILITY STUDIES with
particular reference to the present investigation.

In Table No.22 the conclusions reached under the headings and sub-headings under which environmental effects on fertility have been classified in this Section are summarised before proceeding to the treatment of data in Part Two of this thesis.

Table No. 22.

Classification of environmental effects on fertility data, and estimates of their particular effects and control in the current investigation.

Classification of environmental factor	Nature of influence	Probable effect in this study	Proposed method of handling the effect
1. Habitat	i) Geographical	No means of assessing, data confounded. Probably very small within Britain.	Ignore.
	ii) Meteorological	Not significant in Britain.	Ignore.
	iii) Nutritional	Not at present significant, but might become so - reflected in seasonal variations - if other uncontrolled variables come under closer control.	Ignore.
2. Managerial	i) Age at first service.		
	(a) Heifers	No significant effect in this study.	Ignore
	(b) Bulls	Not significant in this study, but might become so if progeny testing bulls is standard policy.	Ignore.
	ii) Service period	Very significant depressing effect on inseminations within 50 days of parturition	Omit all records of inseminations given at less than 50 days previous from calving.

Table No. 22 continued

Classification of environmental factor	Nature of influence	Probable effect in this study	Proposed method of handling the effect
2. Managerial (continued)	iii) Mating Practice iv) Supplementary feeding	Standard procedure in these data. No information obtained in these data, but presumed that it will contribute to difference between herds and therefore to the correlation between dams and daughters, but should have little effect on correlation between half-sisters if these fall at random over different farms.	Ignore. Analyse farm effects statistically among selected group of farms having five or more cows' records among these data, and then consider desirability of analysing reduced amount of dam-daughter data on intra-farm basis.
3. Biological	1) Age and selection (a) cows	Heifers, and cows under 30 months of age, significantly more fertile than older cows.	Add 0.14 inseminations to number required to achieve conception in cows under 30 months of age at time of fertile insemination and analyse on basis of expected adult-equivalent fertility. Regressions of daughters on dams to be computed within groups of dams having the same number of insemination seasons.

Table No.22 continued

Classification of environmental factor	Nature of influence	Probable effect in this study	Proposed method of handling the effect
3. Biological (continued)	(b) Bulls	Not significant in this study	Ignore.
	ii) Disease	Inadequate factual data. Will probably contribute to the difference between herds	Clinically identified cases omitted from data - both individual cows and "problem" herds. Unidentified cases will have reduced effect if data analysed on intra-farm basis (see 2 (iv)), and age correction probably is partially a reflection of cumulative disease factors among older cows.
	iii) Lactation	Daily yields of milk at time of insemination were not available, and the effect of total lactation yield was not sufficiently defined in this study	Ignore. Only few cows contributing to the data were milk-recorded.

Table No.22 continued

Classification of environmental factor	Nature of influence	Probable effect in this study	Proposed method of handling the effect
4. Artificial Insemination Practice	i) Technical operations at centres	Unexplained month-to-month variations are very largely and do not appear to follow any defined pattern.	Analyse results within centres. Analysis within years and centres is desirable when single seasons are being compared. Inseminations with semen more than two days old omitted. No sub-centre records used except Bromyard, whose main-centre records are not used.
	ii) Recognition of oestrus	Unable to estimate effect in these data. May create a "problem" farm effect.	Ignore, except in so far as omission of data from "problem" farms may reduce this variable.

Table No. 22 continued

Classification of environmental factor	Nature of influence	Probable effect in this study	Proposed method of handling the effect
4. Artificial insemination practice (continued)	iii) Occurrence of oestrus during pregnancy	Of low incidence, but can confuse relationships between animals as well as influence apparent conception rates.	Discard all daughters born after an abnormally short gestation which would have been a "normal" gestation to a penultimate insemination. Discard both inseminations in such cases from records used in this study.
	iv) Stage of oestrus at which cow is inseminated.	Inseminations within 4 hours of first observation of oestrus, and after 20 hours from first observation have significantly lower fertility.	Unable to adjust as time of insemination is not recorded consistently throughout the data.
	v) Inseminating technique	Very large inconsistent variations between inseminators although presumed to be using same technique, but no significant consistent differences.	Ignore.

Table No. 22 continued

Classification of environmental factor	Nature of influence	Probable effect in this study	Proposed method of handling the effect
4. Artificial Insemination Practice (continued)	vi) Administrative considerations	Possible inflationary effect on apparent conception rates of bulls based on "non-returns" due to lack of information from farms, particularly where extra fee necessary for next insemination, and among bulls used preferentially for marginal dairy cows. Different systems at centres confuse the sequence classification of inseminations.	Only "first" inseminations used for assessing bull and inseminator data. Cows' final season records discarded if no report of result of last insemination. Arbitrary standard period of 89 days "non-return" imposed as measure of conception for all inseminations except the final one in the cow's final season where no result reported.

PART TWO.THE ESTIMATION OF THE HERITABILITY OF FERTILITY.

The theory underlying the estimation of heritability has been discussed by Lush (1948) and by Lerner (1950), and there have been very many heritability studies of various characteristics of all farm livestock reported in the literature during the last fifteen years. Further discussion of the principles involved would therefore be out of place in this thesis.

The data available for this study are those of 1,231 unselected heifers, or young cows, whose immediate parentage is known, together with 56 further heifers whose sire is known but whose dam has not been identified.

These heifers are the daughters of 57 bulls, representing four of the principal dairy breeds in Britain, and included among them are 26 pairs of full-sisters, and 31 pairs of maternal half-sisters.

The full sisters are sired by fourteen of the more popular bulls and are not adequate to provide as reliable an estimate of heritability as could be obtained from the number of half-sisters available

but their inclusion in the groups of daughters of any sire will tend to increase the average genetic relationship within the groups.

The sires of all the heifers concerned in this study probably represent a partially selected population in so far as fertility is concerned, and any estimate of correlation or regression in relation to the sires would be minimised owing to the reduced variability among them. The dams of the heifers are a partially selected population with regard to fertility in that they must necessarily have been sufficiently fertile to produce a heifer calf in order to qualify for inclusion in these data. In addition it is to be supposed that a certain amount of selection pressure may have been directed against infertility among the dams by the farmers, but where the reason for culling is based on the insemination history of the cow the measure of her infertility will be recorded in these data except that complete failure to fertilise the cow during her last "standard" season will be excluded.

The daughters involved in these data must also be regarded as a partially fertility-selected population, because 17.06 percent were presented for insemination for the first time at an age exceeding

thirty months, which suggests that they may have already calved previously, although some may have been heifers which had failed to conceive to natural services and were inseminated late for this reason. There were 766 daughters for whom no definite information concerning the result of inseminations could be obtained, or implied from subsequent insemination history, and these were excluded from the data. Of these excluded daughters 63.84 percent had received only one insemination, and 86.16 percent had received less than the three inseminations to which they were entitled without further fee. These heifers cannot be regarded as having been culled on account of infertility, but the balance of 13.84% which had received three or more inseminations (9.92% received three inseminations only, and 3.92% received more than three) will include a proportion which were culled, phenotypically, on the basis of their low fertility, or on an interaction of characteristics which probably included some measure of their infertility.

The degree of selection applied to the daughter populations concerned in this study will certainly be less than that applied to their dams, and in view of

the probability of temporary infertility having contributed to the phenotypic infertility on which many were excluded it will probably not involve a large error to regard the daughter population as unselected in respect of their genotypes for fertility (excluding the cases of absolute sterility with which this study is not primarily concerned).

To the extent suggested by the above discussion the mating system which resulted in the birth of the daughters used in this study may be regarded as mildly phenotypically assortive. It is very improbable that conscious effort was made to mate the most fertile bulls to the most fertile cows, although it is possible that, occasionally, semen from the most fertile bulls may have been chosen for use on "repeat-breeder" cows.

The extent of the phenotypic assortive mating involved cannot be assessed in this study, but it is improbable that the mating system departed from random genotypic matings to an extent greater than that of average matings among the whole population of dairy cattle in Britain, and the findings of a heritability study based on these data are therefore not likely to be unduly biased by the mating system,

and no modification of treatment of the data on this account is proposed.

1. Repeatability.

As a preliminary approach to estimating heritability an examination of all the available data was made to determine the repeatability of the characteristics as arbitrarily defined for the purposes of this study.

To this end the number of services required to achieve a defined pregnancy (90 days non-return) in each season of cows having two or more completed season insemination histories were tabulated in a correlation table in respect of each centre, using every consecutive pair of insemination seasons as a separate observation.

The overall correlation between the number of services required to achieve conception in consecutive seasons of the same cow was computed as

$$b = + 0.1063^{xx}$$

from 5,521 pairs of consecutive seasons.

Although this is very highly significant in respect of the pooled data from all centres, the

Table No.23.

Correlations between the number of services required per assumed conception (90 day "non-return") in consecutive breeding seasons of the same cow

Centre	No. of pairs of seasons correlated	No. of services per conception		Correlation co-efficients	
		Mean of 1st season of pair	Mean of 2nd season of pair	All services	Up to 3 inseminations only
Somerset	1664	1.45	1.44	+ 0.2143 XXX	+ 0.1308 XXX
Cambridge	870	1.67	1.77	+ 0.0777 X	- 0.0227 NS
Reading	718	1.51	1.55	- 0.0511 NS	- 0.0508 NS
Dumfries	1777	1.47	1.61	+ 0.1082 XXX	
Hampshire	212	1.58	1.61	+ 0.0178 NS	+ 0.0763 NS
Worcester	280	1.41	1.46	+ 0.0142 NS	- 0.0541 NS
Overall	5521	1.50	1.57	+ 0.1063 XXX	
* Overall plus "barren-ers"	5587	1.50	1.59	+ 0.0954 XXX	

* Cows reported as "barren" were included in this correlation as requiring an arbitrary number of inseminations estimated at two more than the last insemination actually given in the "barren" season.

correlations determined in respect of individual centres were not significant for Reading, Hampshire and Worcester centres, as may be seen from Table No. 25.

The two centres which provided most data for this examination, Dumfries and Somerset, both provided very highly significant positive correlations.

In view of the necessity of removing cows classified as "barren" from these data, and the possibility of reducing the true correlation by removal of the presumably more infertile cows, a recomputation of the pooled data was made in which all "barren" cows were arbitrarily assumed to have required two further services after the one on which they were classified as "barren". In this computation the correlation was in fact slightly reduced to

$$b = + 0.0954^{xxx}$$

from which it may be deduced that the classification of "barren" was more commonly applied to cows which failed to conceive during one particular season than to cows which had a previous history of difficult conception.

Because of the possibility of an economic or selective bias operating among cows requiring more

Table No. 24

Effect of number of inseminations required for conception in one season upon the mean number of services required per conception in the following season.

No. of services required for conception in 1st season	No. of services required for conception in the following season, and no. of observations at													
	Somerset		Cambridge		Reading		Dumfries		Hampshire		Worcester		Overall	
	No.	Serv-ices	No.	Serv-ices	No.	Serv-ices	No.	Serv-ices	No.	serv-ices	No.	Serv-ices	No.	Serv-ices
1	1154	1.36	532	1.69	480	1.57	1194	1.55	131	1.59	197	1.46	3688	1.511
2	341	1.50	195	1.86	156	1.49	426	1.71	53	2.12	60	1.43	1231	1.626
3	127	1.70	87	1.77	51	1.51	104	1.75	20	1.90	18	1.44	407	1.703
4	27	1.93	31	2.00	18	1.56	31	1.77	5	1.60	2	2.50	114	1.842
5	6	2.00	13	2.15	11	1.64	12	2.33	1	2.00	2	1.50	45	2.022
6	8	3.50	8	3.13	1	2.00	8	2.38	1	1.00	1	1.00	27	2.810
7	1	1.00	1	1.00			1	1.00					3	1.000
8			2	1.00	1	1.00			1	1.00			4	1.000
9			1	1.00									1	1.000
10							1	4.00					1	4.000
Regression of services in season 2 on services in preceding season	+ 0.2026		+ 0.0900		- 0.0179		+ 0.1339		+ 0.0182		+ 0.0152		+ 0.1190	

than three inseminations, at centres other than Dumfries, recomputations were made in respect of cows which conceived in both seasons within the first three inseminations. The reduction of variation imposed on this computation reduced the level of the Cambridge correlation to insignificance, and only the Somerset centre retained a very highly significant, but reduced, correlation co-efficient.

In Table No.24 these data are re-tabulated to show the mean number of services required per conception in the season following a conception to a specific number of services. The regression co-efficients of services per conception in the following season on services required in the preceding season were also computed and are shown in this table.

The repeatability of the Cambridge data was recomputed after exclusion of all inseminations given within fifty days of calving, and this correction increased the correlation to

$$b = + 0.1041^{XX}$$

for 760 pairs of seasons.

On the assumption that fertile cows will normally conceive to the first or second insemination, and

that the "infertile" cows will require more than two inseminations, the pooled data from all centres were used to compute a repeatability correlation in respect of "infertile" cows only - excluding those which conceived to first and second inseminations during the first season considered.

The correlation among this population of cows increased to

$$b = + 0.1309^{xx}$$

for 586 pairs of seasons.

It is concluded that repeatability between seasons is measurable, but is of a low order and a large bulk of data is necessary to obtain a reliable estimate. Reference to the last four lines of Table No. 24 does, however, emphasize that the fact that a cow requires many services to conceive in any one specific season is no definite indication that her inherent fertility is below average. The influence of selection operating against cows which require many inseminations will almost certainly reduce the apparent repeatability computed from data of this nature below that which would occur naturally if all cows which were capable of conceiving were allowed as many inseminations as necessary to ensure

conception.

The repeatability estimates obtained from these data are in reasonable agreement with those estimated by Olds & Seath (1950) and by Pou et al (1953), in respect of the same criterion, but lower than the estimate of Berge (1942) whose data covered a long period of time, and would probably have included considerable time trend effects.

A further estimate of repeatability within more restricted populations is derived from analyses of variance during the course of estimating heritabilities.

2. Predictability.

Predictability of future performance from the basis of an initial performance is an aspect of repeatability for the estimation of which data covering several seasons of the same cow are required. Such data were extracted in order to seek an answer to the misgivings postulated by Cochrane (see pages 95, 96 and Table No.12 (page 97)) concerning a possible adverse affect of repeated artificial insemination on the fertility of cattle.

The 254 cows in these data which had had five or more completed seasons of insemination were classified according to the number of services required to achieve conception during their first insemination season and the number of inseminations required to achieve conceptions during the next four breeding seasons.

The correlation between the first season figure and the number of inseminations during the next four seasons was only

$$r = + 0.0882^{xx}$$

but this was highly significant over the 1,016 pairs of seasons correlated. Thus the first season results of insemination only account for about 0.78 percent of the variance in the ^{"remaining"} /lifetime" fertility performance of the animal.

The regression of the mean number of inseminations required in subsequent seasons on the number required during the first season was

$$b = + 0.0804 \pm 0.0735$$

$$(P=0.01),$$

and the prediction equation for the estimated mean number of inseminations per conception which a cow will require during her following four breeding seasons is

$$Y = 0.0804x + 1.404,$$

where Y is the predicted value, and x is the number of inseminations necessary during the cow's first season.

The agreement of this "prediction" value with the computed values from the data is shown below in Table No.25.

Table No.25.

No. of inseminations during first season	No. of observations	Mean No. of services during next 4 seasons	
		Actual	Predicted
1	660	1.492	1.484
2	226	1.540	1.565
3	88	1.636	1.645
4	24	1.750	1.726
5	12	1.833	1.806
6	8	2.000	1.886

3. Heritability.

With the type of data available two approaches can be made to determination of heritability. An estimation can be made of the similarity between daughters of a common sire, or the similarity between dam and daughter can be estimated.

Each of these approaches will be made in turn.

A. Correlation between daughters of a common sire.

i) Number of services required to achieve conception

The 1,287 daughters available for this study were distributed as shown in Table No.2 (page 52).

All inseminations given within fifty days of a previous calving were excluded, and the data were then analysed in respect of the number of inseminations required to achieve an assumed conception (ninety days without further reported observation of oestrus). In the first instance no correction was applied for age, as 82.94 percent of these daughters were first inseminated at an age of less than thirty-one months; and no attempt was made to remove the variance between farms, as the daughters were widely distributed over 380 farms, of which 57.89 percent provided only one or two cows and offered no satisfactory means of assessing variance.

The analysis of variance of these data is presented in Table No.26 below.

Table No. 26.

Source of variation	d.f.	s.s.	m.s.	F
Total	2040	1522.6860		
Centres	5	26.9849	5.3970	7.404 ^{XX}
Breeds	3	6.3911	2.1304	2.923 ^X
Bulls	56	90.9711	1.6245	2.229 ^{XX}
Between cows	1286	937.3660	0.7289	1.091 ^X
Within cows	690	460.9729	0.6681	

Variance was then partitioned into estimates of components of each mean square in the above table, using the formula

$$k_0 = \frac{1}{n-1} (Sk - \frac{Sk^2}{Sk})$$

(Snedecor, 1946, p.234)

to obtain the following corrected "average" number of observations under each variable :-

Average k for centres 521.5902 seasons

Average k for breeds 471.4529 seasons

Average k for bulls 35.4780 seasons

Average k for cows 1.5855 seasons

The mean squares of the variables were assumed to be estimates of the following composite parameters.

Centres $\sigma^2 + 1.5855 \sigma^2$ cows + 35.4780 σ^2 bulls + 321.5902 σ^2 centres

Breeds $\sigma^2 + 1.5855 \sigma^2$ cows + 35.4780 σ^2 bulls + 471.4529 σ^2 breeds

Bulls $\sigma^2 + 1.5855 \sigma^2$ cows + 35.4780 σ^2 bulls

Cows $\sigma^2 + 1.5855 \sigma^2$ cows

Within
cows σ^2

On this basis the variance attributable to each variable was estimated as set out in Table No. 27 below.

Table No. 27.

Source of variation	Variance	Percentage of variation	
		Within breeds & centres.	In General
(i) Centres	0.0117	1.572	-
(ii) Breeds	0.0011	0.148	-
(iii) Bulls	0.0252	3.335	3.445
(iv) Cows	0.0383	5.145	5.235
(v) Within cows	0.6681	89.750	91.320
Total	0.7444	100.000	100.000

From Table No. 27 it is apparent that, although the four variables were shewn (in Table No. 26) to vary significantly, the amount of the total variance for which any one of these variables accounts is small, and 89.75 percent of the total variance

remains due to undefined variations between seasons of the same cow.

An estimate of the repeatability of the number of services required to achieve conception in any cow inseminated at a given centre and among cows which are inseminated with semen of a specific breed, is given by the intra-cow correlation within centres and breeds,

$$r_1 = \frac{(iii) + (iv)}{(iii) + (iv) + (v)} = 0.0868$$

The repeatability of this criterion of fertility among cows which are part of a population of half-sisters would be estimated by the correlation

$$r_1 = \frac{(iv)}{(iv) + (v)} = 0.0542$$

Thus within an average herd, which will usually consist of a number of half-sisters and other non-related cows, the repeatability of the number of services required to achieve conception among the fertile cows in the herd is estimated to lie between 0.054 and 0.087.

The repeatability estimate corresponding to that derived from bulked data used in the preceding sections of this thesis is given by the correlation

$$r_1 = \frac{(i) + (ii) + (iii) + (iv)}{(i) + (ii) + (iii) + (iv) + (v)} = 0.1025,$$

which is in close agreement with the estimate derived from the correlation tables using less restricted data.

The proportion of variance contributed by differences between bulls constitutes an estimate of the correlation between paternal half-sisters as a result of the sample half of their common sire's genotype which each daughter, within a group of paternal half-sisters, has received.

The genetic correlation between non-inbred, random mated, half-sisters is expected to be 0.25 in respect of genes acting additively, plus a small additional amount in respect of any epistatic interactions, the amount of which would depend upon the number of genes interacting. There would be no expectation of correlation between half-sibs due to genes acting dominantly, as dominant and recessive alleles would be distributed at random through a group of half-sisters; and as the correlation which would be expected for epistatic interactions has been estimated as $1/16$ for two-gene interactions, and $1/64$ for three-gene interactions (Lush, 1948), the contribution to the overall genetic correlation from such interactions, if they apply, can be disregarded

without introducing any serious error.

Of the total variance 3.385 percent is attributed to the differences between groups of daughters of different bulls. This provides an estimate of heritability of

$$h^2 = \frac{3.385}{0.25} = 13.54 \text{ percent,}$$

which is greater than the estimated repeatability of conception rate among cows.

Since the population considered includes twenty-six pairs of full-sisters, the genetic correlation between daughters of a common sire will in fact be slightly greater than 0.25, and the contribution of both epistatic interactions and dominance deviations to the correlation will be slightly increased by the presence of full-sisters, but the difference among such a large population of half-sisters will be very small.

The corrected estimate of heritability, taking into account the full-sisters in the population, is

$$h^2 = \frac{3.385}{0.255} = 13.26 \text{ percent.}$$

Before discussing these results further analyses of the data will be considered.

A. (ii) Conception to first two inseminations.

The same data were reconsidered on the basis of an all-or-none criterion of fertility defined as whether or not the cow conceived to either the first or second insemination in each season.

In view of the very many chance variables over which there is no control in these data it was considered that an adequately fertile cow might easily fail to conceive to any one insemination due to reasons for which she ought not to be penalised, whereas the chance of similar misfortunes attending two consecutive inseminations of the same cow in different oestrous periods seemed unlikely. The broader criterion than the more commonly used conception to first service could, at the worst, include the least undesirable of the inherently subfertile cows in the fertile group, whereas the more stringent criterion would probably exclude a larger proportion of inherently fertile cows which failed to conceive owing to some mismanagement of technique.

As this criterion of fertility is distributed as a binomial, and not as a continuous variable, the data were transformed to angles prior to analysis of variance, in accordance with the transformation

$$\text{angle} = \text{arc sin } \sqrt{\text{percentage}}$$

(Snedecor, 1946, p.447)

Thus conception represented 100 percent fertility, or an angle of 90.00 degrees, and failure represented zero percent fertility, or an angle of 00.00 degrees.

Using the transformed data the analysis of variance is presented in Table.No.28.

Table No.28.

Source of variation	d.f.	s.s.	m.s.	F
Total	2040	1627897.5992		
Centres	5	28094.7868	5618.9574	6.658 XX
Breeds	5	6864.1152	2288.0384	2.711 X
Bulls	56	80685.4284	1440.8112	1.707 XX
Between cows	1286	929966.8849	743.1469	N.S.
Within cows	690	582286.8839	843.8933	

The estimates of variance corresponding to those given in Table No.27 in the previous analysis are set out in Table No.29 for this analysis.

Table No.29.

Source of variation	Variance	Percentage of variation	
		Within breeds and centres	In General
(i) Centres	12.9921	1.484	-
(ii) Breeds	1.7971	0.205	-
(iii) Bulls	16.8250	1.922	1.955
(iv) Cows	-76.1567 ^(a) (NIL)	0.000	0.0000
(v) Within COWS	845.8953	96.589	98.045
Total	875.5075 ^(a)	100.000	100.000

On the basis of this criterion there are still highly significant differences between centres and between bulls, and significant differences between breeds of sire, but the difference between cows has become insignificant.

A contributory factor to the apparent lack of repeatability among cows is that only 11.42 percent of cows fail to conceive to two inseminations, and of those which do fail to conceive to two inseminations their failure occurred during the last recorded breeding season in 58.37 percent of cases, which limited the opportunity of demonstrating any inherent repeatability of failure to conceive.

(a) The negative variance has been taken as indicating an estimate of zero for the purpose of partitioning the proportion of total variance contributed by variables.

Since there is no detectable difference in fertility between cows in these data there can be no estimate of repeatability of fertility assessed by this criterion.

The estimate of heritability provided by the variance between groups of paternal half-sisters is

$$= \frac{1.922}{0.255} = 7.53 \text{ percent.}$$

Young (1953) has emphasised the difficulty of obtaining a satisfactory measure of fertility in cattle when sub-fertility is under consideration owing to the impracticability of extending continuous measurements, such as conception rates or calving intervals, to infinity. Even absolute sterility is more often assumed than physiologically confirmed.

Because the all-or-none criterion of conception to a specific service, as used by Korkman (1947a), Koort (1948), and Dunbar & Henderson (1953), does take into account sterile animals it may seem more desirable than a limited continuous criterion, but it has the practical disadvantage of failing to differentiate between infertile and sub-fertile animals.

The choice of the type of criterion used should take into consideration the nature of the

practical problem of principal concern to the breeder.

Thus in Scandinavian herds, where a high incidence of hereditary gonadal hypoplasia has resulted in a major problem of sterility or marked infertility, it seems reasonable to adopt an "all-or-none" measurement of fertility, but in other countries where available evidence suggests that the infertility problem is primarily one of sub-fertility it would seem more rational to adopt a continuous measure of fertility, but at the same time to remain aware of the possibility of sterility factors which might at any time assume a local importance necessitating a temporary modification of emphasis in the study of the problem.

The further analyses of this investigation have been restricted to fertility assessed as the number of inseminations required to achieve assumed conception on the grounds that this is the rational criterion to use for a sub-fertility investigation, although the limitations and probable bias of the data in respect of this criterion are recognised.

B. Intra-sire regression of daughters on dams.

The 1,231 daughter-dam pairs on which

complete information concerning at least one breeding season is available are distributed among centres, and breeds of sire of daughters, as set out in Table No.1 (page 51).

The phenotypic correlation between a daughter and her dam in respect of any characteristic will result from the sample half of the dam's genotype which the daughter has in common with her dam, and a contribution resulting from the similarity of environment which dams and daughters have in common.

The sample half of the dam's genotype received by the daughter in a random-mating community would be expected to include about half of the expression of that genotype resulting from additive gene effects, and a proportion of the expression of that genotype resulting from epistatic gene interactions, the extent of which would depend on the complexity of the interactions but would normally be less than one half of the epistatic fraction of variance among the dams.

Dominance effects would affect individual resemblances between dam and daughter, but would not be expected to contribute to the mean resemblance of adequately large groups of dams and daughters in a random mating population, although the effect of any

selection on the dams which differentiated between dominant and recessive genes affecting the character would tend to reduce the correlation between the dams and their daughters by reducing the similarity between the genotype and phenotype of the dams.

The fact that the dams will probably be a more selected population than their daughters in respect of fertility will tend to reduce the correlation between dams and daughters by removing the extreme individuals at the low-fertility end of the dams' range. It is reasonable to assume that any selection in favour of fertility among the dams will have been done on individual phenotypic assessment only and that family estimates will not have influenced selection to any significant extent. In this case the regression of the daughters on their dams will not be biased by the effect of selection although the reduction of range of the parents may restrict the applicability of the regression.

The accuracy of estimation of heritability from the regression of daughters on dams will depend very largely on the removal of common environmental influences which increase the resemblance of daughters and dams.

These influences in respect of fertility have been considered in detail in Part One of this thesis, and the most important identifiable influences appeared to be those of time of service relative to previous calving (service period) and age of cow.

The influence of service period will have been very largely removed from these data by omitting all records from inseminations given within fifty days of previous calving, and a coarse adjustment of age of cow effects can be made by adding 0.14 services to number required to achieve conception among animals in these data which were inseminated at under thirty months of age.

The composite influence of variations in techniques of insemination and of the gross environmental influences between areas which may influence dams and daughters similarly can be removed by the analysis of the data on an intra-centre basis.

Time trends ought not to influence the relationship to any great extent as the rate of turnover of cows in herds is such that few of the total inseminations given to dams and their daughters fall in the same year for both, and the general trend is not consistent so that time effects will tend to

operate as a random short-term variable, rather than a consistent bias.

The small amount of the overlap in time between records of dams and their daughters will also reduce the influence of the local environment of the farm in so far as this changes from season to season, but there may be a farm influence remaining which could tend to induce extremes of fertility among all cows on the farm.

Since most of the records used in respect of either the dams or the daughters in these data are grouped over a period of four years, or less, there is little likelihood of any major time trend affecting the similarity of groups of dams and their daughters differentially.

The tendency for matings to be assortive in respect of phenotypic fertility could result in an inflated estimate of heritability from doubling of the general regression of daughters on dams, the extent of which would depend on the genotypic correlation between the parents, but if the regression is computed on an intra-sire basis the need for any estimated adjustment on this account is avoided.

In view of the relatively low repeatability of criteria of fertility during single seasons among

the cows in these data it is desirable to consider the relative values of the phenotypic assessments of their fertility, as estimates of their genotype, when different numbers of observations contribute to their phenotypic assessments.

These values are given by the solution of the formula

$$\sqrt{\frac{n}{1 + (n-1)t}},$$

(Lush, 1948)

where n is the number of seasons for which records are available and t is the repeatability of single observations.

On the basis of an approximate repeatability of 0.10 this formula indicates the following relative values of the phenotype as an estimate of genotype:-

1 observation,	value	1.00
2 observations,	"	1.82
3	"	2.50
4	"	3.08
5	"	3.57
6	"	4.00

The regressions of daughters' fertility on dams' fertility will therefore be influenced by the number of observations on which the dams' fertilities

Table No. 30.

Analyses of Variance and Covariance among daughters (not age-corrected) and their dams, of the number of inseminations required to achieve conception during their first season of insemination.

Source of variation	d.f.	Dams' s.s.	Dams x daughters s.p.	Daughters'			Dams'	
				s.s.	m.s.	F	m.s.	F
Total	1230	941.740	+ 22.106	881.678				
Centres	5	4.605	+ 0.023	17.298	3.460	5.122 xx	0.921	1.215 NS
Breeds	5	1.135	+ 1.208	3.855	1.285	1.902 NS	0.378	NS
Bulls	56	51.716	+ 6.376	73.345	1.310	1.939 xx	0.924	1.219 NS
Cows within subgroups	1166	884.284	+14.499	787.180	0.675		0.758	
Regression	1			0.238	0.238	NS		
Daughters within subgroups adjusted for regression	1165			786.942	0.6755			

Regression of daughters on dams within subgroups $b = + 0.0164 \pm 0.0542$ (5% fiducial limits)
 $S_b = 0.0276$

have been classified, and to remove bias from this cause the dams should be grouped according to the number of observations on which their mean fertility is assessed and regressions should be calculated within groups of dams assessed on equal numbers of observations.

B. (1) Intra-sire regression. First season of daughters on first season of dams.

The whole available data were utilised to determine the intra-sire regression of the number of inseminations required to achieve conception during the first season of daughters (not age-corrected as 82.94 percent were under thirty months of age at the time of their inseminations) on the number of inseminations required to achieve conception during the first season of their dams. The analyses of variance and covariance are set out in Table No. 30.

The estimate of regression obtained would provide an estimate of heritability of 0.0328, or 3.28 percent, but as the standard error of the regression is greater than the regression coefficient there is no indication that the regression coefficient, and thus the estimate of heritability, differs

significantly from zero.

The regression accounts for no significant portion of the variance among the daughters, and the analysis of the variance among the daughters in this more restricted population confirms the indications of the analysis of variance given in Table No. 26.

The partitioning of the variance among the daughters in this population is given in Table No. 31.

Table No. 31.

Source of Variation	Variance	Percentage	
		Within centres and breeds	In General
Centres	0.0119	1.659	-
Breeds	-0.0001(Nil)	Nil	-
Bulls	0.0297	4.142	4.212
Cows	0.6755	94.199	95.788
Total	0.7171	100.000	100.000

The estimate of heritability derived from groups of paternal half-sibs in respect of conception rate during the first insemination season only is, therefore,

$$h^2 = \frac{4.142}{0.255} = 16.24 \text{ percent.}$$

The analysis of variance among the dams is of interest in that of no significant difference in

conception rate to first service was detectable between groups of dams submitted for insemination with semen of any particular bull, nor was there any significant difference between the mean of first season fertility of dams inseminated at the different centres. This is in marked contrast to the highly significant differences occurring between the mean first-season fertility of the daughters of different bulls and between means of all daughters inseminated from different centres.

The lack of significance in the differences between groups of dams is a composite result of greater variation within the dam groups than within the corresponding daughter groups, and less variation between means of the various dam groups than between means of the corresponding daughter groups. If selection for fertility had been effectively operative among the dams decreased variability within groups relative to unselected daughter groups would have been expected, and the reverse tendency presumably indicates an overriding effect of a variable influence affecting individual cows such as infection.

That significance is not apparent between means of daughters sired by bulls of different breeds

suggests that the variations in fertility are associated with individual bulls rather than with breed groups of bulls.

The mean fertility of various groups and principal sub-groups of cows considered in these analyses are presented in Appendices 25 to 27.

B. (ii) Intra-farm, intra-sire regression.
First season of age-corrected daughters
on first season of dams.

In order to estimate the variance contributed by different farms to the environmental variance the total available data were sorted into groups of cows maintained on separate farms.

In these data 330 farms were represented. The distribution of dam-daughter pairs among these farms, according to the number of pairs available from each farm, is shewn in Table No. 32.

Table No. 52.

No. of A.I. daughters "n"	No. of farms	Cumulative percentage of farms having "n" or more A.I. daughters
1	145	100.00
2	77	62.37
3	49	42.11
4	28	29.21
5	17	21.84
6	15	17.37
7	15	13.42
8	8	9.47
9	2	7.37
10	2	6.84
11 to 14	15	6.32
15 to 19	3	2.37
20 or more	6	1.58
	580	

From the total data those relating to farms having four or more dam-daughter pairs were extracted, and these extracted data were further modified so that no bull was represented by fewer than three daughters.

These data were then analysed in respect of the number of services required to achieve conception during the first insemination season of both dams and daughters, but in this analysis the fertility of

daughters was age-corrected in order to reduce variation between farms resulting from the practice at certain farms of serving all heifers naturally, whereas heifers at most farms were submitted for insemination.

A preliminary analysis of variance was made on the bulked data derived from both daughters and dams. This is presented in Table No. 33.

Table No. 33.

Source of variation	d.f.	s.s.	m.s.	F
Total	1637	1373.9832		
Centres	5	7.5280	1.5056	1.827 NS
Farms	103	106.1146	1.0302	1.250 *
Other causes	1529	1260.3406	0.8243	

The variance is partitioned between centres, farms and other causes as follows :-

	<u>Variance</u>	<u>Percentage of Total variance.</u>
Centres	0.0020	0.238
Farms	0.0131	1.561
Other causes	0.8241	98.201

In order to determine whether farms exercised a more important influence on fertility in

certain areas the data of the four principal centres were analysed independantly, and the mean squares and partitioning of variance is summarised in respect of each centre in Table No.54.

Table No.54

Source of variation	d.f.	m.s.	F.	Variance	% of total variance
Somerset					
Farms	45	0.9314	1.29 ^{NS}	0.0140	1.909
Other	628	0.7195		0.7195	98.091
Cambridge					
Farms	19	0.4091	1.26 ^{NS}	0.0166	1.467
Other	344	1.1152		1.1152	98.533
Reading					
Farms	16	1.2411	1.35 ^{NS}	0.0210	2.251
Other	255	0.9202		0.9202	97.769
Dumfries					
Farms	15	0.2895	0.61 ^{NS}	Nil	Nil
Other	142	0.4730			100.000

As no significant difference was recorded between farms at any of the main centres and the difference between farms was barely significant in the overall data it is evident that the local environment caused by different methods of management does not in fact affect the mean fertility level of

Table No. 35.

Analyses of Variance and Covariance among daughters (age corrected) and their dams; of the number of inseminations required to achieve conception during their first season of insemination, analysed within farms and within sires.

Source of variation	d.f.	Dams'	Dams x Daughters	Daughters'		Dams		
		S.S.	S.P.	S.S.	M.S.	F	M.S.	F
Total	818	708.2222	- 3.2444	664.6809				
Centres	5	5.9552	- 3.7174	16.5352	3.3070	4.556 ^{XX}	1.1910	1.385 ^{NS}
Farms	103	72.9869	- 20.4748	104.7230	1.0167	1.401 ^X	0.7086	NS
Breeds	3	1.8602	+ 0.2671	3.2937	1.0979	1.512 ^{NS}	0.6201	NS
Bulls	60	70.9931	- 6.6218	70.4966	1.1749	1.619	1.1832	1.376 ^X
Cows within sub-groups	647	556.4268	+ 27.3025	469.6324	0.7259		0.8600	
Regression	1			1.3786	1.3786	1.902 ^{NS}		
Daughters within sub-groups adjusted for regression	646			468.2538	0.7249			
Regression of daughters on dams within sub-groups $b = + 0.0491 \pm 0.0716$ (5% fiducial limits)								
$S_b = 0.0365$								

the dairy cow on the farm very much, and differences between farms over the data as a whole appear to be responsible for only 1.56 percent of the total variance of first-season fertility between cows.

Using these same data more detailed analyses of variance and covariance among dams and daughters were made and results are presented in Table No.35.

Estimates for k for numbers of observations in sub-groups were :-

k for centres	121,215
k for farms	7,842
k for breeds	178,366
k for bulls	13,256

Variance is partitioned among the variables in Table No.36.

Table No. 36.

Source of variation	Variance	Percentage	
		Within centres farms & breeds	In general
Centres	0.0189	2,319	-
Farms	0.0372	4,565	-
Breeds	-0.0004 (nil)	Nil	-
Bulls	0.0339	4,160	4,468
Cows	0.7249	88,953	95,532
Total	0.8149	100,000	100,000

In view of the results of the preliminary analysis of farm effects it is surprising to find a highly significant effect of farms among the daughter group in these data. Computation was rechecked to verify this finding, and then the farm effect was re-examined within the four principal centres in respect of variance among daughters only.

The results of these examinations are presented in Table No. 37 and reveal that there is no significant difference between farm groups of daughters at Somerset, Cambridge or Dumfries, but that farms associated with the Reading centre are responsible for a very large contribution to the total variance among the fertility of groups of daughters. Detailed scrutiny of the Reading area farms revealed only two farms whose daughters required a mean of more than two inseminations per conception during their first season, but in one of these farms the mean for daughters was 3.64 inseminations per conception whereas their dams all conceived to their first insemination. It seems very probable that this herd should have been omitted from the data on clinical grounds if these facts had been noticed in time to raise a specific enquiry,

Table No. 37.

Source of variation	d.f.	m. s.	F	Variance	% of total variance
Somerset					
Farms	43	0.6851	1.182 ^{NS}	0.0139	2.342
Other	292	0.5795		0.5795	97.658
Cambridge					
Farms	18	1.0945	0.802 ^{NS}	Nil	Nil
Other	163	1.3648			100.000
Reading					
Farms	15	1.6342	3.221 ^{XX}	0.1385	21.446
Other	120	0.5073		0.5073	78.554
Dumfries					
Farms	13	0.1200	0.347	Nil	Nil
Other	64	0.3456			100.000

but the overall herd conception rate was not outstanding and the clinical problem, if any, would probably have arisen latterly and have concerned the daughter groups, but not their dams. If this one herd had had a daughter mean reduced only to two inseminations per conception the total mean square in the entire data for daughter groups associated with farms would have been reduced to less than the mean square for dam groups associated with farms, and the farm effect would have been insignificant.

In the absence of any evidence supporting the deduction of a clinical problem in this herd there is no justification for removing the herd from these data just because it appears to fall outside the expected pattern of behaviour.

The other point of particular interest about the results presented in Table No.35 is that the local farm environment does not appear to exert any common influence on dams and daughters inseminated in the same herd. On the contrary there is a substantial negative covariance between groups of dams and their daughters inseminated on the same farm, which is reflected in an increased estimate of regression of daughters on dams when computed on an intra-farm intra-sire basis instead of a reduced regression as would have been expected if farm environments affected the fertility of dams and their daughters in the same way.

If the negative correlation between fertility of groups of dams and daughters inseminated at different farms is not the result of sampling variation, the only reasonable explanation which suggests itself is that the effect of disease on reproductive efficiency of herds tends to be cyclical

with a modal interval of a few years. Thus a herd with a contagious abortion problem might adopt an inoculation policy which could result in contrasting fertilities of dams and their daughters. Similarly an infection-free herd could acquire a general infection before the cause was suspected, and in such case the fertility of a daughter group might be prejudiced in contrast with the fertility of their dams.

Apart from specific clinical causes of contrasting fertility at farms over periods of a few years the available evidence suggests that, in general, the local farm environment does not contribute significantly to the variation of fertility among inseminated cows, and the further analyses of this study will be computed on an intra-centre, intra-sire basis only.

The heritability estimate derived from the analysis of covariance presented in Table No. 35 would be

$$h^2 = 0.0982, \text{ or } 9.82 \text{ percent,}$$

but there is no evidence that the regression of daughters' fertility on dams' fertility differs significantly from zero.

The estimate of heritability derived from the paternal half-sib variance is

$$h^2 = 17.87 \text{ percent.}$$

B. (iii) Intra-sire regression of daughters' fertility on the fertility of their dams assessed on the records of more than one season.

Further analyses of variance and covariance among daughters and their dams were made of groups of dams and daughters sorted according to the number of seasons which could be used as a basis of estimate of the dams' fertilities.

All dams for which two or more seasons' records were available were included in the "two seasons" group, but only the records of the first two seasons were used in estimating fertility in this group. Similarly the records of the first three seasons of dams with three or more records contributed to the "three seasons" group, and the mean of all available records of dams inseminated for more than three seasons was used to define the fertility of the dams in the "four-or-more seasons" group. In each group, except the "one season"

Table No. 38.

Summary of heritability estimates derived from data analysed on criteria of dams' fertility derived from progressively increasing numbers of insemination.

AGE-CORRECTED DAUGHTERS							
No. of seasons of dams used	No. of pairs	Daughter - Dams			Paternal Half-sisters		Reference
		Daughter-dam regression	5% fiducial limits	Heritability estimate (percentage)	Percentage of variance among daughters due to sires	Heritability estimate (percentage)	
1	1231	+ 0.0089	± 0.0551	1.78	2.998	11.76	Appendix 16
2	944	- 0.0261	± 0.0672	Nil	6.044	23.52	Appendix 17
3	578	+ 0.0155	± 0.1122	3.10	2.621	10.04	Appendix 18
4	290	+ 0.1314	± 0.1993	26.28	0.105	0.39	Appendix 19
Mean		+ 0.0026		0.52	3.26	12.64	
DAUGHTERS NOT ADJUSTED FOR AGE							
1	1231	+ 0.0164	± 0.0542	3.28	4.142	16.24	Table Nos. 30 and 31
2	944	- 0.0248	± 0.0664	Nil	8.656	33.68	Appendix 13
3	578	+ 0.0553	± 0.1107	11.06	2.822	10.81	Appendix 14
4	290	+ 0.1422	± 0.1918	28.44	- 0.229	Nil	Appendix 15
Mean		+ 0.0124		2.48	4.56	17.67	

groups, the fertility of the daughters was defined as the mean of all available records, but two series of analyses were computed, in one of which the daughters' records were adjusted for age during first season, and in the other series the daughters' records were not adjusted as the application of an age-correction factor to the daughters which could not be applied to their dams is not very satisfactory and could lead to more bias than it removes.

The detailed analyses of variance and covariance are tabulated in Appendices 13 to 19 and the results are summarised in Table No. 58.

The mean estimates of the intra-class correlations among paternal half-sibs derived in each group of analyses were computed by transformation of the correlation coefficient to z , where

$$z = \frac{1}{2} (\log_e (1 + r_1) - \log_e (1 - r_1)),$$

(Snedecor, 1946, p.151)

and the z values were weighted by the reciprocal of their variance before the average was taken. From the estimated average z a correction factor was computed to reduce each determined individual z value by

$$\frac{\text{mean } z}{2(n-1)},$$

(Snedecor, 1946, p.154)

and a mean of corrected weighted z values was then recomputed, from which the mean values of the intra-class correlations were determined.

The mean values of the daughter-dam regressions in each group of analyses represent the mean of each regression coefficient weighted by the reciprocal of its own variance.

The process of taking an average of estimates derived from the data handled in the way described has included data from each dam-daughter pair a number of times represented by the number of recorded seasons available for the dam, up to four. The mean therefore does not carry the value which would be associated with one derived from a series of independent estimates, but the process used seemed the most convenient way in which to summarise the findings, and the actual values used as indications of the dams' fertility have been modified by the addition of an extra observation for each season progressively included.

Analyses were also made of the data grouped according to the actual number of insemination seasons during which records of the dams were available, so that dams for whom two records were available were

Table No. 39.

Summary of heritability estimates derived from data grouped according to the actual number of insemination seasons recorded for each dam, and from age-corrected estimates of daughters' fertility (each record used once only).

No. of seasons of dam recorded	No. of pairs	Daughter - Dams -			Paternal Half-sisters		Reference
		Daughter-dam regression	5% fiducial limits	Heritability estimate (percentage)	Percentage of variance among daughters due to sires	Heritability estimate (percentage)	
1	242	+ 0.0542	$\pm$ 0.1483	10.84	- 0.023	Nil	Appendix 20
2	304	+ 0.0272	$\pm$ 0.1065	5.44	3.004	12.02	Appendix 21
3	216	- 0.0568	$\pm$ 0.1710	Nil	10.780	42.14	Appendix 22
4	290	+ 0.1314	$\pm$ 0.1993	26.28	0.105	0.39	Appendix 19
MEAN	1052	+ 0.0322		6.44	2.64	10.31	

analysed as a group, and those having three records were analysed as a separate group but contributed nothing to the "two-season" group, and so on.

From the various groups of data records of daughters of bulls which contributed fewer than four daughters to the group were discarded, and each group was then analysed on an intra-centre, intra-breed, and intra-sire basis as in the preceding analyses.

The detailed analyses of variance and covariance of this series are shewn in Appendices 20 to 22 and the heritability estimates derived from them are summarised in Table No. 59. Appendix 19 is common to this and the previous series.

In this series the means of estimates were computed in the same way as previously described for the data on progressive seasons of dams, but in this series the mean is derived from four estimates based on independent data.

Grouping the data in this way not only takes into consideration the differential reliability of estimates of the dams' fertilities, but also reduces any effect of selection of the dams by comparing only dams which have survived a similar number of seasons of insemination without being culled. This does not

necessarily imply that they have survived a similar number of breeding seasons as their pre-insemination history is not known.

Discussion.

From the foregoing analyses repeatability of the number of inseminations required to achieve conception in a cow has been estimated at approximately ten percent in general populations, and rather less in limited populations.

Significant differences have been shown to occur between the mean fertility levels of groups of daughters sired by different bulls and heritability has been estimated to lie between 7 to 12 percent when computed from similarities between daughters of a common sire, and between $\frac{1}{2}$ to 6 percent, or less, when computed from the regression of daughters' fertility on dams' fertility.

None of the daughter-dam regression coefficients differed significantly from zero, but there was a trend towards a low positive value.

Theoretically it would be expected that uncontrolled environmental influences common to

daughter and dam, particularly permanent farm effects, would cause the daughter-dam regression to support a higher estimate of heritability than an intra-sire correlation among half-sibs when the latter are scattered over sufficient farms to remove most of any common environmental effect.

On the other hand, the estimate of heritability from half-sib correlations is subject to greater exaggeration than estimates based on resemblance of parent and offspring owing to the necessity of multiplying any uncorrected errors of estimate in the correlation by four, or rather less when the average relationship of the populations is closer than half-sibs. It is possible that this may account for part of the value of relatively high heritability estimates derived from half-sib correlations.

An uncontrolled source of variance which might cause groups of paternal half-sisters to appear more alike than genetically expected is the possibility of temporary influences among the unidentified causes of variations at the insemination centres affecting groups of daughters of particular sires differentially if many daughters of one sire are presented for insemination within a short period

of time. Managerial practice attempting to concentrate calvings of heifers to increase the winter milk production of the herd might cause groups of daughters of individual bulls to be differentially subjected to such short-term temporary influences.

Such effects might be reduced by analysis of data within time intervals, but, to be effective, the intervals would need to be short and computation would be very much extended.

Whether this source of variance would differentially affect daughters of different sires to an extent which would justify the computation is doubtful. The outstanding feature of all these analyses has been the magnitude of the uncontrolled variance within cows, and the very small amount of variance attributable to such factors as different centres (or areas), different breeds of bull, and even different farms. Furthermore, the variance attributable to quarter-seasons of the year was computed by Dunbar & Henderson (1953) among inseminated Friesian cows, and it was found to account for only 0.1 percent of the total variance between cows in respect of an all-or-none criterion of fertility.

As expected in the case of a characteristic of low heritability there is a trend towards higher estimates of heritability as the independent variable of the regression on which it is estimated is more adequately defined. This trend is, however, subject to modification by the very large influence of a few unusual records when the segmentation of the data results in relatively small sub-samples being used as a basis of estimate. One cow, for example, required two inseminations one year and sixteen during the following season, but finally conceived and calved after a series of reasonably normal "returns" on an 18 to 20 days cycle. There are several less extreme cases of cows conceiving to one insemination, then requiring six or eight inseminations during the next season, and only one or two inseminations again during the third season. Such records heavily weight estimates derived from relatively small samples of which they form a part.

The partitioning of variance is informative concerning possible genetic effects on fertility in so far as it suggests very strongly that any genes affecting extremes of fertility are distributed in such a way that individual bulls are far more

important than breeds. This point cannot be deemed conclusive from evidence in this study as the breeds of the cows are not known, and the daughters of any sire may be a mixture of grades, from half-bred to purebred, of the sire's breed. It is also interesting to observe that in the undivided data there was no significant difference between the mean fertility of groups of the dams, when estimated on records of one or two insemination seasons, either between centres or between groups mated to different breeds of bull, although significance between dams at different centres became manifest as the precision of estimation of dams' fertility increased by use of records of three or more seasons. On the other hand the daughters' mean fertilities differed very significantly between centres both on first season and total available records.

This significance was attributable to the relatively lower fertility of the daughters inseminated by the Cambridge and Hampshire centres, which was a reflection of low fertility among daughters of a few individual bulls.

Although the great majority of bulls examined sired daughters whose fertility approximated to

population mean a few bulls produced daughters which differed from the mean enough to attract attention.

The following "high" and "low" fertility daughter-groups extracted from Appendix 25 illustrates this point:-

High-fertility daughter groups

LH	Cambridge Friesian	7 daughters	1.00	insems/concept.
LK	Dumfries Ayrshire	9	"	1.09 " "
BWE	Hampshire Shorthorn	7	"	1.12 " "
HR	Dumfries Ayrshire	15	"	1.13 " "
BB	Worcester Friesian	8	"	1.13 " "
WPP	Worcester Shorthorn	10	"	1.14 " "
EMF	Somerset Shorthorn	20	"	1.15 " "
BV	Dumfries Ayrshire	13	"	1.17 " "
KD	Somerset Friesian	46	"	1.22 " "

Low-fertility daughter groups

OSB	Cambridge Shorthorn	18 daughters	1.72	insems/concept.
HDK	Cambridge Shorthorn	9	"	1.78 " "
KH	Cambridge Friesian	41	"	2.07 " "
LC	Reading Guernsey	9	"	2.18 " "
WBD	Hampshire Shorthorn	4	"	2.42 " "
DS	Worcester Ayrshire	4	"	3.00 " "

Population mean 1.45 ± 0.35 inseminations per conception.

Where a disproportionate number of daughters

of these "extreme" bulls feature in the smaller data groups they have a pronounced effect on the estimate of heritability derived from the half-sib correlation, as exemplified by the estimate of 42.14 percent from the group whose dams had precisely three seasons of insemination records (Table No. 40).

A managerial factor which affects groups of daughters differentially in these data is the practice of bulling heifers. Nearly all the Hampshire Shorthorn daughters were presented for their first insemination at three to four years of age, and other daughter groups were affected to a lesser extent. Age-correction has therefore tended to reduce variation between bull-groups relative to variation within bull groups, and for this reason has tended to reduce the estimates of heritability from age-corrected half-sib correlations, and to make them more reliable.

The effect of age-correction is also to reduce the extreme values of daughters, in that no heifer can conceive to fewer than 1.14 inseminations, and this reduced variation is reflected in lower values for regression coefficients of daughters' fertilities on the fertility ratings of their dams,

and thus in lower estimates of heritability derived from age-corrected daughters' data.

One other possible explanation for the large estimate of heritability derived from paternal half-sib correlations can be considered.

If a proportion of the genes principally associated with female fertility are located on the X sex chromosome then the theoretical relationship between paternal half-sibs in respect of those genes is 0.50, instead of 0.25 in respect of genes distributed among the autosomes. Such sex-linkage would not affect the relationship of dam and daughter, and would therefore tend to cause a larger estimate of heritability derived from half-sib correlations than that derived from daughter-dam regressions. If sex-linkage does play an important part in the inheritance of female fertility it should have become apparent from comparison of estimates reported in the literature derived by these two methods. Unfortunately no directly comparative estimates have been reported in respect of the criterion "number of services per conception", but there is slender

corroboration in the fact that both Inchiosa & Pfau (1954) and Brown et al (1954) recorded slightly higher estimates of heritability of calving interval derived from paternal half-sib correlations than they obtained with the same data from daughter-dam regressions.

In order approximately to reconcile the estimates derived from this study by the two methods it would be necessary to postulate complete sex-linkage of all genes governing female fertility, which is very improbable, but it is not unreasonable to suppose that some important genes may in fact be located on the X chromosome of dairy cattle.

The estimate of heritability of the "all-or-none" criterion of conception to first two inseminations in each season was assessed from the paternal half-sib correlation as 7.53 percent. Any criterion involving coarse groupings will tend to produce a lower estimate of heritability than that derived from a continuously variable criterion of the same character, but in the case of these data the coarseness of grouping of an all-or-none criterion is not much greater than the grouping of number of inseminations per conception, especially when the

latter are subject to an economic or other threshold at the value of three.

This estimate is therefore in reasonable agreement with the lower range of estimates of sire-to-daughter heritability of fertility derived from the remainder of this study.

C. Male Fertility.

Pedigrees of 224 bulls which had been used at the six co-operating centres up to 1951 were examined to identify close relationships with a view to obtaining material for a study of heritability of fertility among males.

Thirty-three pairs of sons and sires, and twenty-two pairs, or groups, of half-brothers were identified, but unfortunately it was found that very many of the related bulls in the population had been used for only a few inseminations - presumably as a test, or because they had only recently arrived at centres.

Owing to inadequate conception rate data the number of close relationships available for study was reduced to seventeen pairs of sires and sons, and nine pairs and one quartet of half-brothers. For each

of the bulls in these groups records of conception rate resulting from ten or more first inseminations given in each of two or more calendar months were available.

This small sample was not considered adequate material for a thorough investigation of heritability of male fertility among dairy cattle, but a cursory examination was made to determine the indications, if any.

The monthly conception rates of the forty-six bulls involved in one or more of these relationships were transformed to angles (Snedecor, 1946, p.447), and variance was analysed in respect of centres, breeds, and bulls. The result is presented in Table No.40.

Table No.40.

Source of variation	d.f.	S.S.	M.S.	F
Total	1033	53212.1931		
Centres	4	4039.6902	1009.9225	5.514 ^x
Breeds	4	1821.7157	455.4289	1.585 ^{NS}
Between bulls	45	12953.6262	287.4139	8.266 ^{xx}
Within bulls	985	34417.1610	34.9415	

The partitioning of variance is shown below in Table No. 41.

Table No. 41.

Source of variation	Estimated K	Variance	Percentage of total variance
Centre	197.2969	2.8105	5.528
Breeds	132.7002	1.2661	2.490
Between bulls	21.3533	11.8208	23.252
Within bulls		34.9413	68.730
Total		50.8387	100.000

This analysis provides an estimate of repeatability of conception rate of these bulls of

$$r_1 = \frac{11.8208}{11.8208 + 34.9413} = 0.2528$$

Although the population was composed of pairs of closely related animals the mean relationship between animals picked at random from the population was only 0.023. The highly significant difference between bulls and reasonably high repeatability suggests that the "non-return" rate from first inseminations is a satisfactory criterion for differentiating between bulls of high and low fertility, provided it is based on ten or more first inseminations given in each of about twenty months, and fewer months may be adequate.

The sires and sons were then re-analysed as a separate group in which the variance attributable to differences between bulls was divided into that between sire and son pairs and that within sire and son pairs.

This analysis is shown in Table No.42.

Table No.42.

Source of variation	d.f.	S.S.	m. s.	F
Total	804	40727.7900		
Centres	4	5460.9033	1365.2258	4.444 ^{XX}
Breeds	5	517.9257	172.6419	0.562 ^{NS}
Bulls	33	10137.4027	307.1940	9.528 ^{XX}
Within bulls	763	24611.5583	32.2563	
Bulls total	33	10137.4027		
Between pairs of sires and sons	16	6160.4722	385.0291	1.646 ^{NS}
Within pairs of sires and sons	17	5976.9305	253.9371	

The mean squares derived in Table No.40 can be used to compute an intra-class correlation between sires and sons of

$$r_1 = \frac{385.0291 - 253.9371}{385.0291 + 253.9371} = 0.2441$$

but this correlation is not significant on the basis of this limited amount of data.

As the expected genetic correlation between

sires and sons is 0.50, this intra-class correlation would yield an estimate of heritability of

$$h^2 = \frac{0.2441}{0.50} = 0.4882, \text{ or } 48.82\%.$$

The data derived from half-brothers was not satisfactory for estimation of heritability because in addition to being very limited in amount the breed distribution was exceedingly uneven and three bulls of the two least represented breeds had unusually low conception rates. The variance between monthly conception rates was analysed in this group of data and results are presented in Table No. 43.

Table No. 43.

Source of variation	d.f.	S.S.	M.S.	F
Total	21	349.1398		
Breeds	2	119.3653	59.6826	21.8658 XX
Half-brother groups	9	202.4796	22.4977	8.2424 XX
Within groups	10	27.2949	2.7295	

The intra-group correlation from this analysis is

$$r_1 = 0.7836,$$

and if the breed differences are left in the groups the intra-group correlation is reduced to

$$r_1 = 0.2960.$$

In either case the sampling error is so large that heritability estimates exceeding one hundred percent would be obtained.

There is not adequate material presented under this heading to deserve discussion, but the indications are that the heritability of bull fertility may be considerably higher than the heritability of female fertility, and this point deserves study with the more extensive data which must have accumulated by this time.

D. Male fertility and female fertility interaction.

In order to examine whether the recorded fertility of bulls, assessed by the non-return rate of cows inseminated with their semen, was related to the mean fertility of the daughters of those bulls, assessed by the number of inseminations required to achieve conception, the overall mean fertility ratings of all groups of daughters used in this study, and those of their sires, were determined and the paired mean figures subjected to analyses of variance and covariance.

Two small groups of daughters (those of bulls MWP and TML) were omitted from these data as their sires were not in regular use at co-operating insemination centres and a reliable assessment of their sires' fertilities could not be made.

Mean conception rates for fifty-five groups of daughters were paired with fertility ratings for their sires.

Sires' fertilities were determined from the mean of all their monthly "conception rates" which had been derived from results of ten or more first inseminations during the month. The average number of monthly records used to determine fertility ratings was 29.05 months per sire. Only two sires were rated on less than seven monthly records and semen of each of these sires was used for many inseminations during the time they were in use.

The ratings of the sires are therefore considered to be dependable assessments of their characteristic level of fertility.

As progressively higher figures of the criteria used represent increasing fertility among sires and decreasing fertility among the daughters, any common relationship between the two sexes in

Table No. 44.

Analyses of variance and covariance of mean fertility ratings of groups of paternal half-sisters (inseminations per conception) and of their sires (percentage non-returns to first inseminations with their semen).

Source of variation	d.f.	Sires'	Sires x	Daughters'			Sires'	
		s.s.	Daughters s.p.	s.s.	m.s.	F.	m.s.	F.
Total	54	1290.1416	+ 1.1287	3.6229				
Centres	3	323.8300	+ 9.7521	0.5300	0.1060	1.824 NS	64.7661	3.511 XX
Breeds	3	117.7416	- 3.6081	0.4217	0.1406	2.420 NS	39.2471	2.128 NS
Individuals	46	848.5704	- 5.0153	2.6712	0.0581		18.4472	
Regression Drs.on Sires	1			0.0296	0.0296	0.504 NS		
Drs.adjusted for sires	45			2.6416	0.0587			
Correlation between daughters and sires $r = -0.1053$ NS								
5% fiducial limits of $r = +0.191$ to -0.385								

respect of these criteria would be represented by a negative correlation.

The analyses of variance and covariance are presented in Table No.44, from which it may be seen that a negative correlation of

$$r = - 0.1055.$$

was demonstrated between fertility ratings of sires and daughters, but that this estimate did not differ significantly from zero, and the fiducial limits (set by z transformation) are so wide as to preclude any useful inferences.

If further data substantiated a zero, or low negative, correlation between fertilities of sires and their daughters one might enlarge on the postulation that principal genes controlling female fertility are located on the x chromosome to the effect that principal genes controlling male fertility may be located on the Y chromosome.

In such an event the expected genetic correlations between related animals for fertility factors would approach :-

sire and son	1.00
dam and son	nil
sire and daughter	0.50

dam and daughter	0.50
among paternal half-sisters	0.50
among maternal half-sisters	0.25
among paternal half-brothers	0.50
among maternal half-brothers	nil,

although intermediate values would seem more probable as it is unlikely that no genes on the autosomes have any influence over fertility.

The evidence available from this study is not incompatible with such a postulation.

PART THREESUPPLEMENTARY INVESTIGATIONS.Introduction.

During the preparation of the data for this heritability study it was necessary to consider the reliability of the available records, and the possible effect of certain variables which seemed likely to affect the apparent fertility of the animals.

Thus variations in gestation period were liable to affect the reliability of the basic information of parentage records on which heritability studies relating to the sire are dependant.

The effects of variations in time of insemination relative to time of observation of oestrus, and of milk yield, are pertinent to considerations when preparing data for a heritability study on fertility, although it was found in this particular study that the information necessary to establish the effect of these variables on the chance of conception to each insemination was not always available. In the interests of completeness, investigations into the magnitude of these effects were made using those records which were suitable for

the purpose.

The very pronounced effect of service period on the chance of conception to a given insemination raised the question of the repeatability of this variable, and the extent to which it might be an hereditary characteristic.

Basically the interesting aspect of a study of infertility is the cause, or causes, of the infertility within the material studied. Detailed physiological information about the cows which failed to conceive to an insemination was not available, but it was possible to determine whether any characteristic patterns of reproductive performance or failure could be identified with individual animals.

In order to develop a satisfactory method of segregating available records according to probable causes of failure of conception it is desirable to know the extent of repeatability of "normal" cycles among unfertilised cows, and an attempt was made to arrive at an estimate of repeatability derived from an arbitrarily defined range of "return" cycles which were assumed to be cycles during which fertilisation had failed.

In the absence of information on cycles of

"unbred" cows this method offers a means of arriving at a conservative estimate of true repeatability, in that those cycles which are in fact influenced by fertilisation and have been included in the arbitrarily defined sample will tend to be unlike cycles of the same cow in which fertilisation has not occurred.

This Part therefore comprises six exploratory examinations which are supplementary to the main problem.

- 1) Variations in the length of gestation periods.
- 2) The effect on fertility of time of insemination relative to time of observation of oestrus.
- 3) The effect of milk yield on fertility of dairy cattle.
- 4) The repeatability of the length of service period after calving.
- 5) An examination of data relating to cows which fail to conceive to an insemination.
- 6) Repeatability and heritability of the length of post-insemination "oestrous-cycles".

The first four investigations have a bearing on the preparation of data for the type of heritability study which has been undertaken, and the last two

arise from the opinion expressed in Part IV, that a more analytical approach to the study of infertility among dairy cows would be more rewarding than the general approach used in this study.

1. VARIATIONS IN THE LENGTH OF GESTATION PERIODS.

Attention was drawn to the variation in gestation periods in this study because of the necessity of establishing satisfactory evidence of paternal parentage of the daughters whose fertility records were the subject of the principal investigation.

The apparent conception of certain cows to penultimate inseminations, and their subsequent manifestation of oestrus when presumably they were already pregnant has been mentioned in Part One of this thesis. Where the gestation period is abnormally short when calculated from the last recorded insemination, but normal when calculated from the penultimate insemination, there is little doubt as to the true parentage of the calf.

Apart from those gestation periods which were abnormally short for this reason, others were observed to vary considerably from expected periods, and it seemed possible that some of these abnormal gestations might have resulted from pregnancies to unrecorded natural services instead of to the last recorded insemination.

There are several recorded reports of abnormal bovine gestation periods (Schroter, 1901; Williams, 1927; Andres, 1931; Olafson, 1947; Jasper, 1950; Williams, 1956), and most studies record a wide range of gestation period (Schwarz, 1925, reported by Snyder, 1938; Knapp et al, 1940; Henderson, 1938).

In the records of this study, however, there appeared to be a tendency for "abnormal" gestation periods to recur in records of individual cows, and in related cows. One cow carried three successive calves for gestation periods of 258 days, 249 days, and 267 days.

An analysis of variance among all cows having one or more recorded calvings to inseminations was made with the results shewn in the Table No. 45 below.

Table No. 45.

Analysis of variance of gestation length among all cows having one or more recorded calvings.

Source of variation	d.f.	s.s.	m.s.	F.
Total	3933	213179		
Individuals	1979	166625	84.20	3.53 XXX
Within individuals	1954	46554	23.82	
Between individuals of different breeds	4	12513	3128.25	40.09 XXX
Between individuals of the same breed	1975	154112	78.03	
	Estimated k	Variance	Percent of total variance	
Breeds	632.32	4.81	8.16	
Individuals	1.99	30.34	51.54	
Within individuals		23.82	40.39	
Total		58.97	100.00	

These results provide an estimate of repeatability, among the total population of cows studied of 0.5602. within breeds.

Using only the records of the daughters of bulls standing at the centres a further analysis of variance was made to estimate the heritability of

gestation period. This analysis is shown in Table No. 46 below, and the results provide an estimate of repeatability of 0.3064 within breeds, and an estimate of heritability of

$$h^2 = \frac{11.30}{0.253} = 44.66 \text{ percent.}$$

Table No. 46

Analysis of variance of gestation length among a population of groups of paternal half-sibs.

Source of variation	d.f.	s.s.	m.s.	F
Total	985	41563		
Individuals	711	32516	45.73	1.38 ^{xx}
Within individuals	274	9047	33.02	
Between individuals of different breeds	4	3566	89.15	2.18 ^{NS}
Between individuals of the same breed	707	28950	40.96	
Between individuals of same breed having different sires.	54	7603	140.80	4.31 ^{xxx}
Between paternal half-sisters	653	21347	32.69	
	Estimated k	Variance	Percent of total variance.	
Breeds	148.86	- 0.35(Nil)	Nil	
Bulls	17.67	5.33	11.30	
Cows	1.38	9.21	19.34	
Within cows		33.02	69.36	
Total		47.61	100.00	

An examination of the relationships between daughters and dams in respect of gestation lengths was made by computing the intra-sire regressions of daughters' mean gestation periods on dams' mean gestation periods within each of the three principal "breeds". For the purpose of this classification "breed" was determined solely by the sire of daughters and mate of dams. The regressions were computed among a population in which all the dams had three or more recorded calvings.

The results, shewn in Table No. 47, revealed significant positive regressions among the Shorthorns and Guernseys, and a positive regression, which just failed to reach the level of significance, among the Friesians.

On the basis of the weighted mean of these three regressions (weighted by the reciprocals of their own variance) heritability of gestation periods between daughters and dams was estimated as

$$h^2 = 62.02 \text{ percent.}$$

Table No. 47. Regressions of daughters' mean gestation periods on mean of three or more gestation periods of their dams in three "breeds" classified according to the breed of the daughters' sires.

Source of variation	d.f.	Dams' s.s.	Dams x Daughters s.p.	Daughters' s.s.
SHORTHORN SIRES				
Total	190	1719.74	755.90	4493.09
Bulls	26	547.45	339.49	1229.34
Cows within bull groups	164	1372.31	416.41	3263.75
$b = + 0.5034 \pm 0.2358$				
FRIESIAN SIRES				
Total	108	1482.46	354.44	2517.70
Bulls	11	111.26	55.28	270.61
Cows within bull groups	97	1371.17	319.16	2247.09
$b = + 0.2328 \pm 0.2550$				
GUERNSEY SIRES				
Total	36	435.05	277.15	983.90
Bulls	5	31.33	23.32	77.37
Cows within bull groups	31	403.72	253.83	906.53
$b = + 0.6287 \pm 0.5071$				
Mean regression of daughters' gestation period on dams' gestation period (weighted by reciprocal of variance of regressions)				
$b = + 0.3101$				
Estimated heritability = $h^2 = 62.02$ percent.				

The mean gestation periods for all cows whose calvings were recorded, classified by breed of mate or sire, are tabulated in Table No. 48 below.

Table No. 48.

Breed of sire or mate	Gestation periods of							
	Daughters				Dams			
	No. drs.	No. GPs	Mean	Std. dev.	No. dams	No. GPs	Mean	Std. dev.
Shorthorn	384	532	284.25	6.35	586	1464	284.20	5.22
Friesian	216	301	280.54	6.26	333	809	280.51	11.39
Guernsey	76	100	285.70	5.54	156	344	285.23	5.37
Ayrshire	22	32	283.53	4.02	181	300	283.08	5.00
Jersey	14	21	279.86	7.99	13	31	280.48	4.67

These means include all apparently abnormal gestations on which animals were excluded from the main study on the grounds of doubtful parentage. The cows inseminated with Friesian semen, for example, included those having gestation periods of 319, 314, 266, 260, 256, 244 and 241 days. There is quite a high probability that some of these records are in error, either as a result of unrecorded service or clerical entries, and since they exert most influence on the standard deviation it is reasonable to assume that the actual standard deviations of authentic gestation periods are lower than those shown in

Table No. 48.

A number of published reports have drawn attention to breed differences in mean gestation periods (Knoop & Hayden, 1934; Henderson, 1938; Rife et al, 1943; Livesay & Bee, 1945; Alexander, 1950; Brakel et al, 1952), and while this study confirms the relative breed periodicities reported from American sources it is interesting to note that all breeds examined in these data provide estimates of gestation periods in excess of those reported from America by one-and-a-half to three days.

Knapp et al (1940) reported very significant differences between mean gestation periods for different cows, and Jafer et al (1950) found that the genotype of the calf accounted for forty-eight per-cent of the total variance among gestation periods in a Friesian herd.

In this study the heritability of gestation has been considered in respect of the cow carrying the calf rather than from the point of view of the genotype of the calf, but the combined evidence all indicates that gestation period is a highly heritable and repeatable characteristic.

It follows that selection pressure applied

to gestation period should result in fairly rapid modification if this is desired. To what extent modification would be possible or desirable is not known, but it seems unlikely that any effort in this direction would be worth while as it would be necessary to reduce the period by nearly twenty-percent to save enough time for an expectation of obtaining one extra calf in the lifetime of a reasonable proportion of dairy cows, and such a modification would probably involve concomitant problems arising from the birth of weaker calves.

The more practical application of these findings, however, relates to the repeatability of gestation period and the value of the gestation period as supporting evidence of correct identification of parentage of calves.

It has been shown that the sex of calf (Brakel et al, 1952; Jafer et al, 1950), the age of cow (Knoop & Hayden, 1934), twinning (Brakel et al, 1952), and size of cow (Jafer et al, 1950), all influence the length of gestation, but only over a range of a few days, and where records of gestations of a particular cow are consistent within a few days, except for one or two conspicuously abnormal

gestations, the high repeatability of this character would strongly suggest the possibility that the abnormal gestations were incorrectly recorded unless there was sound circumstantial evidence to corroborate the records. Unrecorded mating would be the most likely cause of error.

The particular application to this study arises from the doubt which is thrown on the assumed parentage of calves born after abnormal gestation periods, and also on the fertility of inseminations which were assumed to have resulted in these abnormal gestations.

In view of this doubt records associated with extreme variations of gestation were discarded from the data for the heritability study.

2. THE EFFECT ON FERTILITY OF TIME OF INSEMINATION
RELATIVE TO TIME OF ONSET OF OESTRUS.

Trimberger & Davis (1943) and Trimberger (1948) have demonstrated a depression of fertility resulting from inseminations made before, or very early in, oestrus, and after oestrus, or more than twenty-four hours preceding ovulation, and less than seven hours preceding ovulation.

These effects are presumed to result from interactions between the viability of spermatozoa in the female tract, the possibility of a final phase of maturity being necessary for spermatozoa in the female tract, the time of ovulation relative to oestrus, and possibly the time necessary for movement of the spermatozoa from the vagina to the ovum in cases where the post-oestrus sensitivity of uterine muscle is decreased to an extent which might interfere with aspiratory-assisted transportation.

Records maintained at commercial insemination centres sometimes include the time which elapses between first observation of oestrus and time of insemination, or, more commonly, an assessment is made by the inseminator of whether the cow is "coming on", "on", "going off", or is "off" heat at the time of insemination.

Detailed time records had been maintained at the Dumfries centre during the period from February 1950 to March 1951, and advantage was taken of these to estimate the effect of these intervals, between the time at which farmers first observed oestrus and the time of insemination, on fertility under practical conditions of commercial insemination.

First inseminations only were grouped at four-hour intervals from time of observation of oestrus to time of insemination, and the percentage of conceptions achieved by these inseminations was determined for each time interval in respect of each month. Since some of these conception rates were computed on relatively small numbers of inseminations (a minimum of nine inseminations and a mean of 69.5 inseminations per four-hour-month "cell") the percentages were transformed to angles (Snedecor, 1946, p.447), and analyses of variance computed in respect of the angle values are presented in Table No.49 which also summarises the detailed data tabulated in Appendix 12.

The data were analysed in two parts, before and after the first of October 1950, owing to the pronounced increase in overall fertility at that time.

Table No. 49.

Analysis of effect of interval between time of first observation of oestrus and insemination on the 90 day "non-return" rate for first inseminations at the Dumfries centre.

		1-4 hrs.		5-8 hrs.		9-12 hrs.		13-16 hrs.		17-20 hrs.		21-24 hrs.		Over 24hrs		Total
		Ins.	%C.R.	Ins.	%C.R.	Ins.	%C.R.	Ins.	%C.R.	Ins.	%C.R.	Ins.	%C.R.	Ins.	%C.R.	
Feb. '50 to	sum	226		759		1025		409		474		281		117		3291
Sep. '50	mean C.R.		54.3		65.0		62.0		64.4		64.5		59.4		44.4	62.0 %
Oct. '50 to	sum	170		846		724		326		371		233		47		2717
Mar. '51	mean C.R.		69.9		75.1		69.1		70.1		69.5		65.9		42.6	70.5 %
Overall	sum	396		1605		1749		735		845		514		164		6008
	mean C.R.		61.6		69.6		65.7		65.7		66.9		63.0		43.9	65.8 %
% Distribution		6.6		26.7		29.1		12.2		14.1		8.6		2.7		100.0

Analyses of Variance of periods from 1-24 hours after observation of oestrus

Source of variance	Analysis of variance over whole period				Analysis of Variance of first 8 months				Analysis of Variance of last 6 months					
	d.f.	s.s.	m.s.	F.	d.f.	s.s.	m.s.	F.	d.f.	s.s.	m.s.	F.		
Total	83	1989.206			Total	47	916.118			Total	36	391.717		
1st pt.v.	1	681.371	681.371	48.896 ^{xxx}	Mths.	7	37.465	5.352	0.290 ^{NS}	Mths.	5	57.228	11.446	1.277 ^{NS}
2nd pt.														
Between times	5	234.824	46.963	3.370 ^{xx}	Times	5	233.358	46.672	2.531 ^x	Times	5	101.432	20.286	2.263 ^{NS}
Error	77	1073.011	13.935		Error	35	645.295	18.437		Error	26	233.057	8.964	

This may have been attributable to use of a new diluent, containing 0.5 percent of sulphanilamide, which was introduced during the month of September 1950, but, in the absence of any "controls", it was not possible to demonstrate cause and effect.

It is apparent from Table No.49 that the interval from five to eight hours after observation of oestrus was the most successful interval for inseminations in both periods.

Significantly lower conception rate was achieved during the first period in the first interval of one to four hours than in the intervals from five to twenty hours, and there was a drop in fertility in the last interval of twenty-one to twenty-four hours. During the period from October 1950 onwards the conception rate from both early and late inseminations improved relative to those made in intermediate intervals and no significant differences in conception rate were recorded.

The conception rate for inseminations made later than twenty-four hours after observation of oestrus was very low during both periods, but the number of such late inseminations each month was too small to include in the analysis of monthly

conception rates.

As 82.1 percent of all inseminations were made during the more fertile intervals from five to twenty hours after observation of oestrus the loss to the insemination centre resulting from 6.6 percent early and 11.3 percent late inseminations is not likely to cause concern.

Prior to introduction of detailed recording of the time interval from observation of oestrus to insemination at the Dumfries centre the inseminators recorded their opinion of stage of oestrus at the time of insemination, as also did inseminators at the Cambridge centre.

A comparison of the distribution of inseminations on this classification, and the conception rates achieved at these two centres is shown below in Table No. 50.

Table No. 50

Centre and number of inseminations	Stage of oestrus			
	Coming on	On	Going off	Off
Dumfries % Distribution	6.1	58.3	28.6	7.1
3047 % Conception rate	67.0	66.8	69.1	66.2
Cambridge % Distribution	0.7	90.7	2.9	5.7
1092 % Conception rate	88.9	56.3	53.1	48.4

The distribution of inseminations at Dumfries is in close agreement with the distribution of inseminations recorded in Table No.49, but the distribution of the Cambridge inseminations reveals an extreme mode of cows "on" heat. Unless there is a particularly efficient administrative organisation at the Cambridge centre one might suspect a lack of discrimination in the Cambridge classifications.

Cembrowicz (1952) reported "no noticeable difference" between conception rates at the Somerset centre from inseminations made within five hours of receiving the report of the cow being "on heat", and those made on the morning following an afternoon report of a cow being seen "on heat"; and Stewart (1950) published figures derived from insemination results in the Reading area shewing a decreasing conception rate from 65.9 percent for cows inseminated during the same afternoon as they were seen "on heat", to 47.7 percent for cows inseminated at twenty-four hours, or more, after being observed "on heat".

The conclusion to be drawn is that, under practical dairy farming conditions in Britain, inseminations will seldom be given at a stage of

oestrus early enough to prejudice conception rate, but that centres should endeavour to organise a system of administration which ensures that all cows are inseminated within twenty-four hours of being observed "on heat".

Because the records of time of insemination relative to first observation of oestrus, or stage of oestrus at the time of insemination, were not consistently maintained at all the co-operating centres during the period covered by this study it was not possible to modify all the data in respect of very early and very late inseminations. The distribution of records which were classified suggests that no more than ten percent of all records would fall outside the limits of expectation of normal conception rate, and that very few of this ten percent of inseminations would incur a greatly reduced probability of conception. Where such occasions have occurred they can be expected to fall at random over the population studied, and will operate as a minor uncontrolled environmental error tending to reduce the estimate of heritability.

5. THE EFFECT OF MILK YIELD ON FERTILITY OF DAIRY CATTLE.

Reference was made in Part One of this thesis to the possibility of lactation competing physiologically with the requirements for optimum fertility of dairy cows.

An interaction might tend to occur between fertility and lactation either as a result of competition for specific nutrients, trace elements, or vitamins, required to maintain optimum tone in each of the systems involved, or possibly as a result of antagonistic requirements in respect of hormonal balance.

In either event the direct approach to the investigation of any relationship between lactation and fertility would be through a comparison of ease of conception and of milk yield at the time of service, or insemination.

An attempt was made to collect information on milk yield of cows at the dates of insemination, but only complete lactation yields were readily available.

Total lactation yields serve as a less sensitive criterion of level of milk production for

Table No. 51.

The effect of total lactation yield of milk on the percentage of cows which conceive to a single insemination.

Milk yield to nearest 100 gallons	SOMERSET CENTRE						READING CENTRE		BOTH CENTRES	
	Shorthorn semen		Friesian semen		Semen of all breeds		Various semen		Various semen	
	No. of Insems	% concvd to 1st Insems	No. of Insems	% concvd to 1st Insem.	No. of Insems	% concvd to 1st Insem.	No. of Insems	% concvd to 1st Insem	No. of Insems	% concvd to 1st Insem
1	6	16.7	1	0.0	9	22.2	-	-	9	22.2
2	10	70.0	1	0.0	11	63.6	9	100.0	20	80.0
3	15	60.0	4	50.0	20	60.0	15	60.0	35	60.0
4	34	55.9	20	50.0	57	56.1	20	75.0	77	61.0
5	93	59.1	56	62.5	155	60.0	52	73.1	207	63.3
6	182	58.8	143	60.8	334	58.7	83	62.7	417	59.5
7	87	65.5	132	62.9	220	64.1	135	63.0	355	63.6
8	136	57.4	144	63.9	284	60.9	85	69.4	369	62.8
9	37	62.2	62	62.9	101	63.4	62	58.1	163	61.4
10	42	61.9	20	30.0	64	51.6	48	64.6	112	57.2
11	7	57.1	11	54.5	21	52.4	29	58.6	50	56.0
12	5	60.0	5	40.0	10	50.0	10	40.0	20	45.0
13	1	100.0	-	-	1	100.0	6	66.7	7	71.4
14	-	-	-	-	-	-	8	62.5	8	62.5
Total	655	59.5	599	60.4	1287	59.8	562	64.8	1849	61.3
Mean Yield	666.26 galls		709.18 galls		685.55 galls		746.09 galls		703.95 galls.	
* Regression of percentage conception to 1st service on milk yield					-0.935 %per 100 g ± 0.902 ^x		-2.089 %per 100gs ± 2.023 ^x		-1.844 %per 100 galls ± 1.247 ^x	

* Regressions computed on means of groups in which a minimum of 10 cows were represented.

comparison with fertility.

In order to include in the examination as many recorded cows as possible, the criterion of fertility used was whether or not the cow conceived to her first insemination during the lactation concerned. As the lactation yields were only approximate relative estimates of production at the time of insemination, refinements of grouping were considered unnecessary and cows were grouped by lactation yield to the nearest one hundred gallons of recorded milk.

Within each group the percentage of cows which conceived to first insemination was calculated, and regressions were computed of "percentage units" of fertility on hundreds of gallons of milk yield.

From the Somerset data - 223 cow-seasons were discarded owing to the inseminations being made with semen from two bulls which were currently achieving only 11.6 and 22.4 percent conception rate respectively from first inseminations, and were believed to be in an abnormal condition, but all other recorded cows were included.

The data are summarised in Table No. 51.

From this rather coarse examination significant negative regressions were obtained in respect of the

milk recorded cows inseminated by both the Somerset and Reading centres.

These regressions are illustrated in Figure No.11, from which it is more readily apparent that the trend is not very definite, and it is only the groups of cows yielding one thousand gallons of milk, or more, that are responsible for the regression.

The conclusion is that, under average dairy farming conditions in the South of England, an interaction between fertility and lactation tends to operate over a threshold of production level in such a way that cows producing over one thousand gallons of milk per lactation are likely to conceive less readily than cows which are producing less milk.

This threshold is probably subject to modification by adjustment of management.

Korkman (1947b) found that, among Ayrshire herds in southern Finland, the herds whose average milk production was above population average tended to include a higher proportion of more fertile young cows, under five years old, but that the fertility of their older cows dropped more acutely than that of the older cows of the lower-producing dairy herds. This suggests that a higher "wear and tear" effect

may operate among the higher yielding cows to the prejudice of their fertility, but this is also an aspect which may be subject to modification by good management.

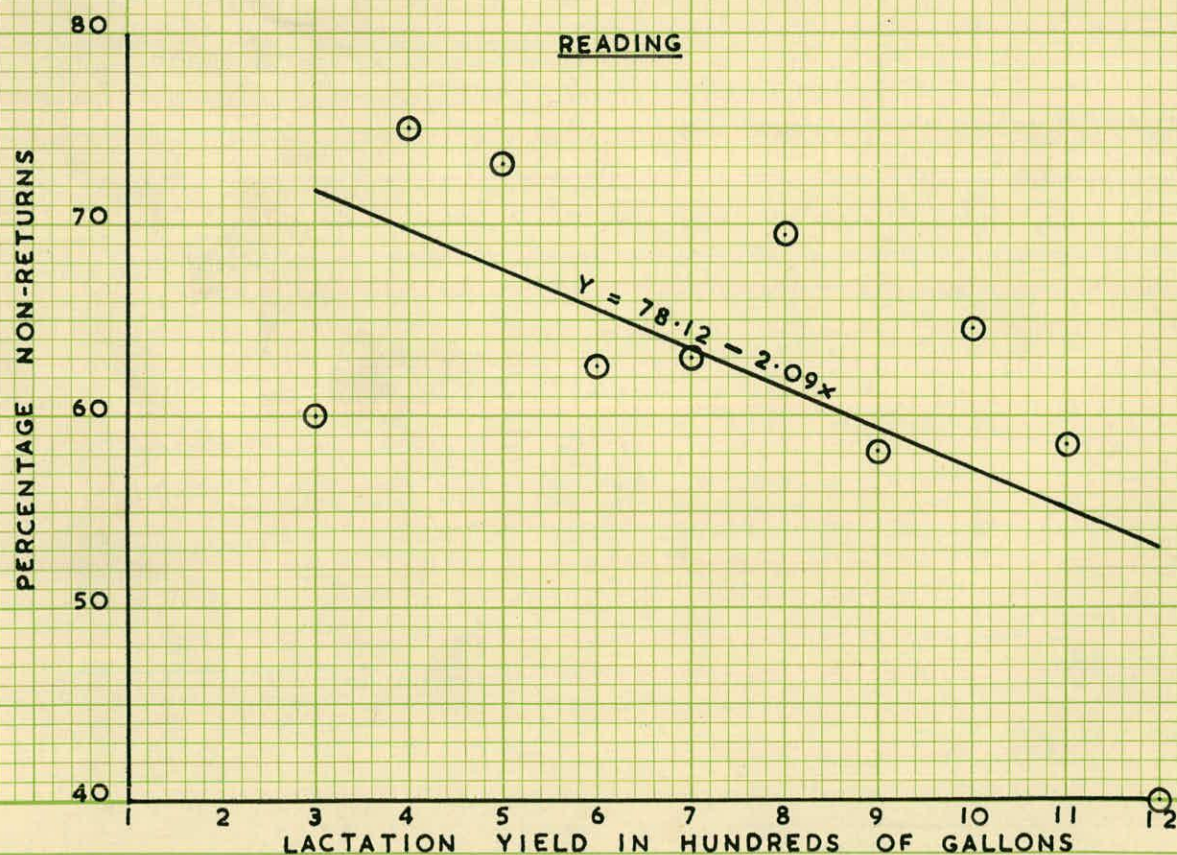
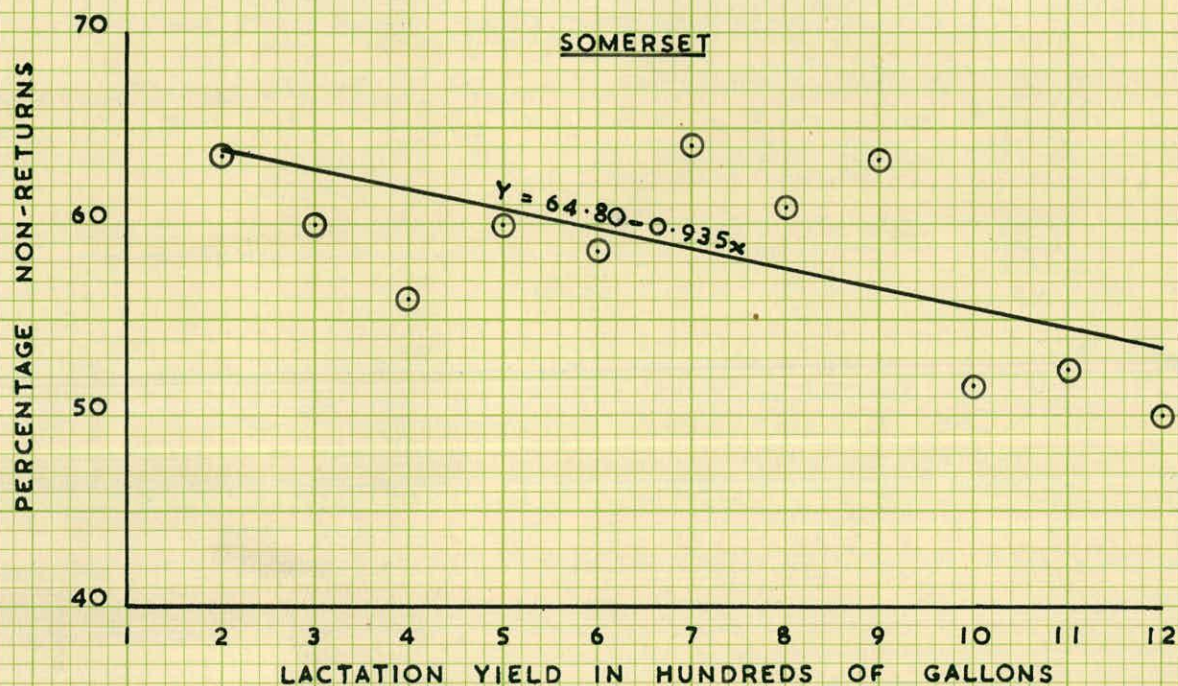
Owing to the fact that only a small proportion of all the cows contributing to the data of the main study were milk-recorded it was impracticable to modify the handling of the data in such a way as to remove any bias attributable to variations in lactation. Since the National average production of milk among milk-recorded herds was of the order of 700 gallons (Milk Marketing Board, 1955) it seems unlikely that many individual cows within the population used for this heritability study will have been subject to reduced chance of conception on account of their milk yield, and as level of milk yield is more a characteristic of a farm or herd than of a family (Rendel & Robertson, 1950; Robertson & Rendel (1950)) any variation in fertility attributable to lactation would tend to add to the inter-farm effect on fertility which, in these data, has been shewn to be very small.

Within populations of high-yielding dairy cows the question of heritability of fertility may assume

greater importance than in the general population if there exists a definite physiological antagonism between high yield of milk and fertility.

FIGURE NO. 11 -

REGRESSIONS OF PERCENTAGE OF COWS "CONCEIVING" TO FIRST
INSEMINATION ON TOTAL LACTATION YIELD OF MILK TO THE
NEAREST HUNDRED GALLONS



4. REPEATABILITY OF THE LENGTH OF SERVICE PERIOD AFTER CALVING.

Reference has been made in Part One of this thesis to the influence of service period on the fertility of the first insemination after calving.

The service period is an indication of the time taken for involution of the uterus and the re-adjustment of hormonal balance to normal cyclic functions of the non-pregnant state, but, in so far as some breeders may withhold service at first post-partum oestrus, it is subject to considerable managerial influence.

The information available in respect of all those daughters whose calving dates were known was used to examine the repeatability, and to estimate the heritability, of this characteristic.

Table No. 52 presents an analysis of variance of these daughters.

A high repeatability of service period is indicated, which is highly significant. The "permanent" characteristics of the cow, whether genetically or managerially imposed, account for 25.0 percent of the total variance of service period, and the variations from season to season of the

To face page 265.

Table No.52

Analysis of variance among recorded service periods classified by breed of sire of cow.

Source of variation	d.f.	s.s.	m.s.	F.
Total	895	766773		
Individuals	612	588475	961.56	1.53 ^{XX}
Within cows	283	178298	630.03	
Between cows of different breeds	4	14689	3672.25	3.89 ^{XX}
Between cows of the same breed	608	573786	943.73	
Between cows of same breed having different sires	53	78844	1487.62	1.67 ^{XX}
Between paternal half-sisters	555	494942	891.79	
	Estimated k	Variance	Percent of total variance	
Breeds	143.36	18.91	2.082	
Bulls	16.42	32.04	3.528	
Cows	1.46	227.08	25.007	
Within cows		630.03	69.382	
Total		908.06	99.999	

$$\begin{aligned} \text{Repeatability within breeds} = r_1 &= \frac{32.04 + 227.08}{32.04 + 227.08 + 630.03} \\ &= 0.2914 \end{aligned}$$

$$\text{Heritability} = h^2 = \frac{3.528}{0.252} = 14.00 \text{ percent}$$

service periods of individual cows account for 69.4 percent of the total variance. Managerial practice will probably account for a portion of the permanent characteristic of a cow, but it would not be usual for good managerial practice to attempt to control the service period at less than fifty days, because this would mean reducing the dry period between lactations to less than eleven days, if the cows are milked for lactations of about 315 days, and this would seriously reduce the subsequent lactation performance of the cow. It therefore seems probable that service periods of less than fifty days normally occur on farms where management is lax, and sometimes in a deliberate, but misguided, attempt to commence serving a cow soon after calving because she was difficult to "settle" during the previous season. Occasionally restricted service periods may be deliberately imposed, in combination with restricted lactations, in order to adjust the time calving to a different season for economic reasons.

By discarding all data concerned with inseminations given within fifty days of calving the tendency will probably have been to remove one of the principal causes of variance in fertility levels which

would normally be attributable to "between farm" effects, and this may account for the relatively small "farm" effect in the data of this study.

High repeatability of service period has also been reported by Chapman & Casida (1955) among dairy cows in Wisconsin, and Olds & Seath (1958) have reported a high repeatability of post-partum interval to first oestrus, which is subject to much less managerial influence than service period.

The correlation between paternal half-sibs in respect of service period is unlikely to be biased in the data of this study, and the heritability estimate of 14.00 percent derived from the analysis in Table. No. 52 should be a reliable estimate, provided this characteristic is controlled by autosomal genes.

The highly significant differences between cows of different breeds and between paternal half-sib groups suggests that a very definite genetic influence exists in respect of this characteristic, and by selection for short interval between calving and first oestrus - but withholding service at first oestrus - it might be possible to reduce the adverse effect of short service period on fertility by increasing the proportion of cows which have a second

post-partum oestrus in less than fifty days from calving, as Trimberger (1954) has shewn that conception at second oestrus is not prejudiced, as it is at first post-partum oestrus. Such selection would only be of practical use however if it was associated with a reduction of lactation period involving a more intensive programme of production and reproduction.

5. AN EXAMINATION OF THE DATA RELATING TO
COWS WHICH FAIL TO CONCEIVE TO AN
INSEMINATION.

Reference has been made in Part One of this thesis to the standard practice of using results from first inseminations only for assessing the fertility ratings of different bulls, and the relative efficiency of different inseminators.

In Figure No. 10 (page 166) the relationship of the "non-return" rates and calving rates in respect of cows which were given a specific number of inseminations was illustrated.

Further evidence of the different results achieved by first, second, third and higher order inseminations at the Somerset centre are tabulated in Table No. 53.

The third insemination non-return rates are quite evidently affected by the neglect of farmers to notify failures to the centre. This bias may also influence the slight upward trend of second insemination non-returns relative to first insemination non-returns, and may contribute to the increased discrepancy between the non-return rates and calving

Table No. 53.

Average of monthly means and 5 % fiducial limits of monthly means of results of progressive inseminations carried out at the Somerset centre during period from January 1947 to September 1949. ^(*)

Year	"Non-return" rates		Calving Rate ^(z)	"Barren" cows	Cows sold	"No information" ^(x)	Correlation between 3-mth. NR and calving rate.
	At 1 month	At 3 months					
1ST INSEMINATIONS							
1947	73.75 ± 2.84	63.83 ± 1.94	51.78 ± 2.02	4.96 ± 0.93	2.49 ± 0.36	4.06 ± 1.03	
1948	74.57 ± 7.38	64.81 ± 2.05	52.44 ± 2.84	4.61 ± 0.75	3.12 ± 0.55	5.58 ± 0.71	
1949	76.89 ± 2.04	68.63 ± 2.00	53.94 ± 3.68	3.21 ± 0.33	3.52 ± 0.31	7.36 ± 2.04	
1947/49	75.03 ± 1.62	65.52 ± 1.26	52.61 ± 1.45	4.35 ± 0.48	3.00 ± 0.27	4.82 ± 0.86	r=+0.7433
2ND INSEMINATIONS							
1947	76.37 ± 2.42	65.49 ± 2.86	46.91 ± 2.52	10.04 ± 1.89	2.64 ± 1.00	4.90 ± 1.82	
1948	78.07 ± 9.77	65.99 ± 3.77	49.31 ± 3.67	9.02 ± 1.59	3.06 ± 0.78	3.51 ± 0.81	
1949	78.77 ± 1.63	68.63 ± 1.93	47.80 ± 3.48	6.52 ± 1.83	3.50 ± 0.75	9.98 ± 3.69	
1947/49	77.48 ± 1.41	66.55 ± 1.71	47.98 ± 1.68	8.70 ± 1.05	3.03 ± 0.47	5.85 ± 1.47	r = + 0.5981
3RD INSEMINATIONS							
1947	88.09 ± 2.09	80.49 ± 3.12	43.58 ± 4.15	24.70 ± 2.99	3.44 ± 1.48	7.81 ± 2.69	
1948	91.53 ± 2.17	85.36 ± 3.76	48.55 ± 4.55	24.11 ± 4.08	4.49 ± 1.90	7.12 ± 3.08	
1949	90.89 ± 3.46	85.87 ± 3.57	44.70 ± 5.09	17.06 ± 3.73	4.90 ± 1.19	18.57 ± 4.75	
1947/49	89.57 ± 1.62	83.68 ± 2.00	45.61 ± 2.45	22.35 ± 2.20	4.21 ± 0.85	10.60 ± 2.52	r = + 0.3713
INSEMINATIONS AFTER THE 3RD.							
1947	71.96 ± 8.12	59.09 ± 5.80	32.00 ± 7.27	19.08 ± 2.98	3.19 ± 2.46	4.58 ± 2.38	
1948	81.27 ± 16.45	68.25 ± 7.49	34.30 ± 8.21	20.22 ± 3.51	6.05 ± 3.11	5.51 ± 2.98	
1949	77.34 ± 4.92	61.27 ± 7.35	28.43 ± 7.23	11.74 ± 6.06	5.73 ± 1.63	14.59 ± 7.50	
1947/49	75.15 ± 4.39	62.85 ± 3.78	31.79 ± 4.00	17.41 ± 2.44	4.89 ± 1.41	7.72 ± 2.68	r = + 0.6553

(*) Data for February 1948 is not included as complete records were not available for this month.

(z) 'Calving rate' includes abortions and stillbirths.

(x) "No information" cows include the total number of inseminations included as 3-month "non-returns" less all cows which were subsequently reported as having calved, aborted or died, or as having been sold, or culled.

rates of fourth and subsequent inseminations.

The general trend of lower calving rates from progressive inseminations supports the belief that the population of cows submitted for repeat inseminations becomes progressively weighted with cows which, for either permanent or temporary reasons, are less fertile than the population submitted for first inseminations.

The progressive increase in cows classified as "barren" also supports this view, although Clarke (1949) has shewn that many of the cows inseminated from the Somerset centre were misclassified as "barren" by the farmers. The inflation of the percentage of cows which received third inseminations and were classified as "barren" suggests a tendency for rather arbitrary use of that term by farmers who may regard three insemination failures as a threshold on which to review an animal's contribution to the herd economy.

The proportion of cows for which no information was obtainable by the centre follows the same trend as that of "barren" cows, and it is reasonable to suppose that a large proportion of them were culled as an interaction of sub-fertility and sub-average performance or appearance.

If the results of third inseminations are ignored, on the grounds of being misleading, the difference between one month non-returns and three month non-returns shows a slight upward trend from first insemination results to later insemination results, and the differences between three month non-returns and calving rates shows a steeper rise, as indicated in Table No. 53.

Table No. 53.

Inseminations	Difference in "% units" between	
	1 mth-3 mth. Non-returns	3 mth N.R to calving
Firsts	9.51	12.91
Seconds	10.93	18.57
Fourth and later	12.30	31.06

These figures probably reflect an increasing incidence of embryo mortality among repeat-inseminated cows, particularly in the later stages of pregnancy, which, in turn, may reflect an increased incidence of pathological infection among these cows, or of a physiological imbalance, of either genetic or environmental origin, which prejudices their chance of maintaining a pregnancy.

A comparative examination was made of the distribution of return intervals in respect of first, second, and third inseminations with the semen of each bull at the Dumfries centre. Records of six out of eight bulls revealed a trend towards an increase in proportion of returns within normal cycle interval after second and third inseminations, relative to the distribution of returns from first inseminations.

This suggests that fertilisation failure is a more important contributory cause in these cases than in the cases of the other two bulls whose results revealed an increasing proportion of returns in the interval from five to eight weeks after the later inseminations.

Following up this line of enquiry, very highly significant differences were found to exist between the means of monthly records of individual bulls in use at each of three other centres in respect of decline in non-return rate between four and eight weeks after insemination, also between eight and sixteen weeks after insemination, and between sixteen weeks and calving.

These intervals are those in use at the Reading centre, but similar results were obtained in respect

of analogous intervals used at the Somerset and Worcester centres (see Tables Nos. 54-57).

Table No. 54 . Analysis of variance of differences between "non-return" rates at 4 weeks and 8 weeks after first inseminations.
(Reading data 1945-1950.)

Source of variation	d.f.	s.s.	m.s.	F.
Total	530	21304.77		
Bulls	16	2229.21	139.326	3.86 XXX
Months	11	278.78	25.344	N.S.
Years	5	838.93	167.786	4.65 XXX
Error	498	17957.85	36.060	

Table No. 55. Analysis of variance of differences in "non-return" rates at 8 weeks and 16 weeks after first inseminations.
(Reading data 1945-1950.)

Source of variation	d.f.	s.s.	m.s.	F.
Total	530	14241.53		
Bulls	16	1060.04	66.252	2.63 XXX
Months	11	185.92	16.902	N.S.
Years	5	434.12	86.824	3.44 XX
Error	498	12561.45	25.223	

Table No. 56. Analysis of variance of calving results expressed as percentages of the "non-return" rate at 3 months after first inseminations, during 12 months period.
(Somerset data 1947-48)

Source of variation	d.f.	s.s.	m.s.	F.
Total	151	5111.02		
Breeds	2	328.25	164.125	6.90 XX
Bulls	12	949.87	79.156	3.33 XXX
Months	11	837.63	76.148	3.20 XXX
Error	126	2995.27	23.772	

Table No. 57. Analysis of variance of differences between "non-return" rates at 1 month and 3 months after first inseminations
(Worcester data - 1949).

Source of variation	d.f.	s.s.	m.s.	F.
Total	179	5567.75		
Bulls	9	602.38	66.931	2.51 X
Months	11	743.45	67.586	2.54 XX
Centres	1	9.51	9.510	N.S.
Error	158	4212.41	26.661	

(Worcester data - 1950)

Total	246	9940.90		
Bulls	10	1222.55	122.255	4.37 XX
Months	11	1226.14	111.467	3.98 XX
Centres	1	779.51	779.510	27.85 XX
Error	222	6212.72	27.985	

The point of principal interest in these results is that whereas some bulls were associated with a generally high incidence of returns and others with a generally low incidence of returns, some bulls were associated with high incidence of returns only within specific intervals after insemination.

Salisbury et al (1952a) have reported significant differences between bulls in the decline of non-return rate between one month and five months after inseminations made with their semen, and many investigations have been made into the various causes of returns (Casida, 1953; Tanabe & Almquist, 1953; Hawk, et al, 1955; Wiltbank et al, 1956, in the United States; and Laing, 1949, in Britain). As returns attributable to failures of different processes - fertilisation, implantation, and phases of embryo development - may result from independent causes it would seem more rational to attempt to study the factors affecting each separate process rather than to examine data relating to infertility within the gross classifications of whether or not a single criterion of fertility was achieved.

The exploratory examinations made in this study suggest that different causes of infertility are

operating in different bulls, and that it is possible to deduce, within very approximate limits, the probable processes involved in the failures from an examination of the pattern of returns associated with the use of semen of different bulls.

An analysis was made of 663 return intervals of 326 daughters of 23 bulls standing at the Somerset and Cambridge centres. This sample was composed of all daughters of bulls which had three or more daughters which had returned to oestrus within ninety days of any insemination, and returns at intervals later than ninety days were not included in the analysis. Much greater variance was found within individuals than between individuals and there was no indication of any repeatability of return intervals within individuals, nor was there any significant difference between mean return intervals of different groups of paternal half-sisters.

Examination of differences between months in decline of non-return rates between different post-insemination intervals revealed highly significant differences between individual months, but little consistency of pattern from year to year, so that no

significance was attached to differences between calendar months when results of several years were bulked together for analysis.

The "extreme" months for non-return decline between one month and three months after first inseminations made in three separate years at the Worcester centre are shown in Table No.58.

Table No.58.

Year	Months
Least difference between 1 mth. and 3 mth. non-return rate	
1948	July, June, December, March
1949	June, May, April
1950	May, August, April
Most difference between 1 mth. and 3 mth. non-return rate	
1948	January, February, May
1949	March, November, August
1950	March, December, November

The summer months occur more frequently in the top part of this table and winter months more frequently in the bottom half, which suggests a seasonal effect that causes a greater incidence of early embryo mortality during the early months of the year in the Worcester area.

An interesting differential trend was found in the results of the Reading centre over the six years from 1945 to 1950. The mean difference between non-return rates at four weeks and eight weeks increased progressively from 8.36 percentage-units in 1945 to 11.99 percentage-units in 1948, and thereafter declined slightly to 10.28 percentage-units in 1950, whereas the mean difference between non-return rates at eight and sixteen weeks after first inseminations remained constant between 6.61 and 7.51 percentage units from 1945 to 1949, and then shewed a highly significant drop to 4.64 units during 1950.

This drop is possibly the result of the introduction of streptomycin into the diluent used at this centre during 1950, and, if this is so, the results would confirm the finding of Foote & Bratton (1952) that the addition of antibiotics to semen diluents is associated with greater reduction of late returns than of early returns.

There is an implication in these results that undiagnosed pathological agents associated with the semen of bulls are probably responsible for some of the assumed embryo mortality, but there is room for much closer investigation of the causes of

infertility in respect of possible hereditary influences as part of "combined operations" against the problem of infertility.

6. REPEATABILITY AND HERITABILITY OF POST-
INSEMINATION "OESTROUS CYCLES"

When assessing the probable fertility or failure of a service or insemination more critically than is the custom of commercial insemination centres the interval at which a cow returns to oestrus after insemination must usually be the basis of discrimination in the absence of early pregnancy examination results. It is necessary to discriminate between normal "infertile" cycles, and cycles in which conception has occurred and has been interrupted for some reason. Knowledge of the degree of repeatability of normal cycle is desirable before attempting to discriminate between probable fertile and infertile cycles as a cycle which is only one standard deviation above the "infertile" mean of a long-cycle cow would appear as a highly probable "fertile" cycle in a short-cycle cow if repeatability is high.

Unfortunately no data were available on "unbred" cycles, and an arbitrary range of post-insemination cycles of 16 to 26 days was chosen as likely to include most cycles in which fertilisation had failed and few in which fertilisation had occurred

and the subsequent development of the zygote had failed.

All available records of "returns" which were within these prescribed limits were extracted in respect of dams or daughters mated or sired by bulls of the four principal breeds, and the analysis of variance, presented in Table No.59 was made to determine the repeatability of their prescribed post-insemination "oestrous cycles".

Table No.59. Analysis of variance among post-insemination "oestrous cycles" within the range of 21 ± 5 days.

Source of variation	d.f.	s.s.	m.s.	F.
Total	2079	10308.92		
Individuals	1138	7251.92	6.3725	1.962 XXX
Within individuals	941	3057.00	3.2487	
Between individuals of different breeds	5	356.10	118.7000	19.537 XXX
Between individuals of the same breed	1135	6895.82	6.0756	
	Estimated k	Variance	Percentage of total variance	
Breeds	432,1041	0.2336	4.642	
Individuals	1,8238	1.5496	30.798	
Within individuals		3.2487	64.560	
Total		5.0321	100.000	
Repeatability within breeds	$r_1 = \frac{1.5496}{3.2487 + 1.5496} = 0.3230$			

The means and standard deviations of the "oestrous cycles" included in this analysis are tabulated in Table No.60.

Table No.60. Means and standard deviations of post-insemination "oestrous cycles" within a range of 21 ± 5 days.

Breed of sire or mate	Post-insemination oestrous cycles (21 ± 5 days only) of							
	Daughters				Dams			
	No. drs.	No. cycs.	Mean	Std. dev.	No. dams	No. cycs.	Mean	Std. dev.
Shorthorn	203	329	20.05	2.94	275	567	20.50	2.03
Friesian	113	203	20.54	1.72	189	370	21.13	2.38
Guernsey	74	133	21.23	2.49	100	184	21.63	2.06
Ayrshire	94	137	21.12	1.82	91	157	20.97	1.82

Chapman & Casida (1937), reporting on an investigation of the variation in oestrous cycles in a large Friesian herd, found that differences between individual cows accounted for 41 percent of the observed variance, within cycles limited to a range of 17 to 27 days, when copulation had not occurred at the preceding oestrus, but that after copulation had occurred the individual cow only accounted for 19 percent of the variance within this prescribed range of post-service cycle.

Asdell (1946) reports the standard deviation

of oestrous cycles of unbred heifers as 2.33 days and that of cows as 3.68 days.

In view of the fairly high repeatability within individuals a margin of two standard deviations, or about eight days, from the mean "unbred" cycle length of the individual would serve as a reasonable criterion for separating return cycles associated with probable fertilisation failures from those associated with probable zygote mortalities, although it must be recognised that many "unbred" cycles do occur at abnormal intervals (Chapman & Casida, 1937; Asdell et al, 1949; Ellenberger & Lohmann, 1946; Roark & Herman, 1950), and Trimberger (1956) has made a classification of causes of abnormal cycles.

Such a segregation forms no part of the present heritability study, as the criterion of conception used by the insemination centres was thought to be a more practical criterion for this study in order that the results may be interpreted in relation to a commonly understood criterion, but the view is presented in Part IV of this thesis that the problem of infertility is likely to be resolved more readily if investigated more critically, and discriminately, than has been possible in the present study. To this

end it is desirable to attempt a segregation of probable causes of conception failures.

Opportunity was also taken of the available data to estimate the heritability of the prescribed post-insemination cycle. The analyses of variance and covariance among all available pairs of dams and daughters, in which both animals had one or more "returns" within the prescribed limits, are shewn in Table No. 57.

The regression of daughters' mean cycles on dams' mean cycles is

$$b = + 0.0511 \pm 0.1345,$$

which does not differ significantly from zero, and cannot therefore be regarded as a satisfactory basis for estimation of heritability. The intra-sire correlation among paternal half-sisters affords a slightly more reliable estimate, as the difference between mean's of groups of paternal half-sisters is almost significant ($P = 0.05$ requires a variance ratio of 1.42 whereas that derived in the computation is 1.417). Heritability is therefore estimated at 17.97 percent on the assumption that all the genes concerned are located on the autosomes.

Table No. 61.

Analyses of Variance and Covariance of post-insemination oestrous cycles within the range of 21 ± 5 days of daughters and their dams.

Source of variation	d.f.	Dams' S.S.	Dams x Daughters S.D.	Daughters' S.S. M.S. F			Dams' M.S. F	
Total	257	867.55	101.81	934.80				
Breeds	3	41.62	34.29	44.45	14.8167	4.567 ^{XX}	13.8733	4.072 ^{XX}
Bulls	49	127.51	31.81	225.30	4.5980	1.417	2.6022	0.764 ^{NS}
Cows	205	698.42	35.71	665.05	3.2441		3.4069	
Regression	1			1.82	1.82	0.560		
Daughters adjusted for dams	204			663.23	3.25			
Regression of daughters on dams $b = + 0.0511 \pm 0.1345$ $S_b = 0.0682$								
	Estimated k	Variance	Percentage of total variance	Estimates of heritability				
Breeds	60.638	0.2645	7.193	From daughter-dam regression $h^2 = 10.22$ percent From paternal half-sibs $h^2 = \frac{4.582}{0.255} = 17.97$ percent				
Bulls	5.118	0.1685	4.582					
Cows		3.2441	88.224					
Total		3.6771	99.999					

Highly significant breed differences were recorded in both analyses, but the proportion of total variance attributable to breed differences was rather larger owing to sampling variations in the reduced sample of material used in Table No.61.

PART FOURPRACTICAL APPLICATIONS OF RESULTS FROM THIS
STUDY

In the introduction it was stated that this study was intended to assist dairy cattle breeders in deciding to what extent they are justified in selecting for improved fertility among their animals.

It has been shewn that the repeatability of the number of inseminations necessary to achieve conception in a cow is low, and that such a record in respect of a cow during any one season is of very little value in predicting the number of inseminations she will require in future seasons.

This finding is in general agreement with the results from other studies tabulated at the end of Section One of Part One, and may be regarded as a confirmed finding at present applicable to most populations of dairy cows, other than those in which gene frequency for any specific condition leading to sterility, or very low fertility, is believed to be high - such as in the case of gonadal hypoplasia within defined populations of Scandinavian cattle (Lagerlof & Boyd, 1952).

Thus the probability is high that the cause of subfertility of an individual dairy cow in Britain is of a temporary nature.

It has also been shewn in this study that the chance of an individual dairy cow in Britain influencing the fertility of her daughters is very slight indeed, and therefore the breeder would be unjustified in prejudicing the selection of a heifer on the grounds of her dam's subfertility. It is desirable to note that the very low heritability of fertility among dairy cows is a reflection of the very large variations which occur from season to season in the record of the same cow for no apparent reason. If our understanding of such variations improves in the future and enables us to reduce them to a much lower level, then the heritability of fertility among dairy cows should be reassessed as it is probable that genetic variation will then become a significant factor in determining the relative fertility of daughters of different dams.

Very significant differences in mean fertility levels have been demonstrated between groups of daughters of different bulls in contradistinction

to the demonstrated homogeneity of mean fertility level of groups of cows inseminated with semen of different bulls. Furthermore this difference between the fertility of groups of daughters of different sires is a characteristic derived from the individual sire, and bears little or no relationship to the breed of the bull.

There is a tendency for daughters of Shorthorn bulls to be slightly more fertile than average, and for daughters of Guernsey bulls to be slightly less fertile than those of the other breeds studied but this is not a consistent difference, and the daughters of some Guernsey bulls exhibit above average fertility for all breeds.

Unfortunately the fertility level of the individual bull appears to be of little value for predicting the probable fertility level of his daughters, and therefore an individual bull's merit as a female-fertility improver cannot be assessed until his daughters are mature. At this stage, however, the fertility rating of the daughters of the bull could contribute to the value of a selection index derived from progeny test results.

Preliminary evidence suggests that the fertility rating of individual bulls may be of considerable value for predicting the probable fertility level of their sons. This finding requires confirmation on more extensive data before it is given full commercial application, but it seems probable that the sire's fertility level should contribute to the selection index of young bulls, particularly in the case of bulls being provisionally bred for artificial insemination centres where level of fertility would carry considerable economic weight.

The general indications from this study are therefore that breeders who wish to improve or maintain fertility among their dairy cattle might usefully consider the sire's fertility when selecting immature bulls, and should consider the daughters' fertilities when progeny-testing a mature bull, but the fertility of individual cows should be considered only in the light of removing possible temporary causes of infertility, or of culling the cow herself if there are indications of a permanent cause of infertility. The possibility that abnormal genitalia may result from genetic mutations, or from

relatively rare recessive genes existing in the population, should be borne in mind when such conditions are found, and further evidence can then be sought to determine the most suitable course of action in the particular case.

The low heritability combined with the relatively low economic importance of minor variations in fertility to the owner of average sized herds suggests that these results can contribute more readily to the improvement of the national economy through the medium of insemination centres than through application in individual herds.

Insemination centres have the facilities for adequate progeny testing, upon which effective selection for traits of low heritability is dependant, and the minor improvements in fertility levels which can be expected could contribute very significantly to the economy of insemination centres when spread over a large population of local cattle.

The nature of fertility is such that natural selection must exert constant pressure in its favour, and although the superimposition of man's direction may have restricted the relative advantages of

distribution attendant on high-fertility genes, it cannot have reduced significantly the natural exclusion of sterility genes.

Positive selection for improved fertility will therefore be a process of assisting natural selection to limit the distribution of mutant genes prejudicial to optimum fertility as they occur from time to time, and to reduce the frequency of such genes already present in the population.

In these circumstances it would be unrealistic to anticipate spectacular results from selection for fertility, but useful economic advantage should be attainable.

Arising from the study of factors influencing the fertility of dairy cattle in Britain, a few practical observations appear to be justified.

1. There would appear to be room for breeders in Britain to advance the age at which their heifers are first mated. In America, where similar economic considerations relating to cost of rearing and expected lifetime performance obtain, earlier mating is standard practice among dairy farmers, and there is no indication in the data derived from the present study that

fertility would be prejudiced by earlier mating in British dairy herds.

2. The high proportion (about thirty percent) of cows inseminated within fifty days of a previous calving appears to be a sad reflection on the standard of management of dairy cows in Britain.

This practice is prejudicial to the economic interests of both the farmer and the shareholders of the insemination centre, in that cows presented for insemination at first oestrus after calving are not only less likely to conceive at that oestrus than if submitted at second oestrus, but are likely to achieve a full term pregnancy later than cows which are allowed more time to adjust their reproductive system after calving (Trimberger, 1954).

Even in the event of conception occurring before fifty days after calving the cow must either be dried off before she has completed a standard lactation, or she must forego the six weeks dry period which is necessary if the succeeding lactation is not to be adversely affected.

In view of these considerations it is surprising to find such an authority as Wright (1955) advocating the mating of dairy cows as soon as possible after the thirtieth day after calving.

In the interests of both farmers and the shareholders it is suggested that insemination centres might consider the institution of a system of enquiry concerning calving dates of cows for whom insemination is requested, and should attempt to dissuade farmers from seeking insemination for recently calved cows until the cows are already in their second post-partum oestrus.

3. The introduction of a standard procedure at insemination centres for the evaluation of results achieved with the semen of each bull based on decreases of non-return assessments between specific intervals after insemination, might usefully be considered, in addition to the present conception-rate evaluation.

Not only would this provide information of value in further investigations into infertility problems, but also the early

recognition of bulls whose results indicate a characteristic pattern of returns may be of diagnostic value, and contribute to the commercial interests of the centre.

4. The attention directed to variations in gestation periods during the course of this study has revealed the high improbability of several cows being the true daughters of the sires indicated by the records at the insemination centres. Where these daughters are in pedigree herds it is probable that both the breeder's records and the official herd book records are inaccurate.

It is to be presumed that such inaccuracies have always occurred and have contributed to the general errors in all herd books. It is certainly not sufficient reason for discrimination against the entry in herd books of animals bred by artificial insemination, but it does suggest that the herd book authorities, and individual breeders, could improve the accuracy of their records by requiring that records of services, and inseminations, be registered at the time of occurrence, and by accepting for registration only those calves which are born within, say, two standard deviations interval of the breed

heifer mean gestation period, in the case of heifer dams, or within a similar interval of the dam's previous mean gestation period in the case of multiparous dams. Such a regulation might involve an occasional injustice, but it would certainly improve the accuracy of the pedigrees upon which the principal justification of the herd book societies is established.

RECOMMENDATIONS FOR FUTURE INVESTIGATION.

The results of nearly all investigations into the heritability of fertility among dairy cattle have concluded that it is low. This is to be expected in a characteristic which must have been subjected to generations of natural selection, but the problem of infertility still persists. It is even possible that we may be actively propagating deleterious genes whose effects would previously have restricted their distribution, but which, under the ameliorative influences of modern veterinary techniques and improved husbandry practice, now survive as contributors to subfertility.

Since infertility remains a problem it is

reasonable to postulate that there are gene combinations which contribute to the animal a higher expectation of fertility than others, but fertility is a resultant expression of the interaction of many physiological processes, so that one would expect more than a single gene, or complex of genes, to influence it, albeit the processes are so interdependant that one would also expect pleiotropic interaction between the genes or genic systems concerned.

If it is possible to identify genes, or gene complexes, with specific processes contributing to fertility, in the form of a series of thresholds, then an analytical approach to hereditary sub-fertility, is likely to be more informative than an approach to fertility as a single composite character.

On the other hand, if the various contributory processes of fertility are distributed as a series of progressive continuous variables then there would be no advantage in attempting to deal separately with each process, and treatment as a composite whole would be the rational approach unless the various processes involved had markedly different

heritabilities. In such a case an overall evaluation of fertility supplemented by an evaluation of processes more highly heritable than the composite character would offer scope for more rapid improvement than selection on the basis of the unweighted composite character alone.

The exploratory examinations reported in Sections 5 and 6 of Part III of this thesis, and the threshold nature of the processes involved in fertility, however, suggest that each might be independantly assessed with reasonable precision, and it is suggested that the next step of genetical contribution towards solving the infertility problem should be the development of suitable criteria to differentiate the recognised physiological processes involved, the estimation of the heritability of each process, and the formulation of recommendations as to whether attention to each process individually, or in the form of a suitably constructed selection index, or to the composite characteristic of fertility is the most efficient.

While statistical examination of records must form the basis of such an investigation the need for correlation of the records with physical

diagnosis of condition is emphasised, and the genetical-physiological approach commends itself for this reason.

In order to acquire adequate data of this nature to afford reliable estimates of characteristics subject to the influence of so many variables it is suggested that the problem could be handled more competently by a well co-ordinated team, than as a project, or series of projects, for independent investigation.

The suggestion, derived from Section C of Part II of this thesis, that male fertility might be a highly heritable characteristic, deserves further examination with the extensive data which must have accumulated by this time. Selection for male fertility might be of considerable value to the economy of the industry if heritability is found to be high, especially as the industry becomes increasingly dependant on artificial insemination.

Further evidence concerning the possibility of genes associated with the expression of fertility by each sex being located on the sex chromosomes is desirable in order to develop optional selection techniques.

In view of the very high milk yields which are obtained in many of the stud herds of dairy cattle it would seem desirable that a critical examination should be made of the relationship between fertility and lactation - particularly at the higher levels.

The very large short-term variations which occur in mean conception rates achieved by insemination centres are an obvious challenge to the investigator, and it is felt that the analytical physiological approach to the causes of infertility, over prolonged periods, may contribute valuable evidence to the resolution of the variables responsible for such fluctuations.

Arising from these points the following specific enquiries are suggested as likely to contribute to our understanding of subfertility among dairy cattle.

1. An examination of the relative importance of conception failure, implantation failure, and mortality of established embryo in the problem of subfertility, and estimates of the repeatabilities and heritabilities of each process.

2. An estimation of the heritability of male fertility among dairy cattle.
3. An estimation of the relationship of dam's fertility to son's fertility among dairy cattle.
4. An examination of the physiological antagonism or compatibility of high milk yields and the various processes of reproduction.
5. A detailed examination of the cause of short-term variations in apparent fertility achieved by insemination centres, based on a study of selected data concerning only those inseminations for which all the known main variables associated with fertility are disposed in a manner conducive to achieving an optimum conception rate.

Acknowledgements

It is with profound gratitude that I record my appreciation of the sponsorship of N.R. Reid Esq. M.B.E., B.V.Sc., M.R.C.V.S., lately Director of Veterinary Services, Tanganyika Territory, and of the generosity of the Government of Tanganyika Territory in providing the opportunity for me to undertake this study.

I wish to acknowledge the guidance of Professor C.H. Waddington, Sc.D., F.R.S., and Doctors Alan Robertson and J.M. Rendel, during my sojourn in Britain, and to express my regret that subsequent duties have restricted my opportunity of drawing on their valuable counsel.

I am indebted to the Agricultural Research Council of Great Britain for providing facilities for this research, and I have enjoyed most valuable co-operation from the Veterinary Officers and many members of the staff at each of the insemination centres visited.

I would like to thank the several assistants who, from time to time, have assisted with the sorting and tabulation of voluminous data, the

several librarians who have done so much to overcome the limitations of local reference facilities, Mrs. Jean Lake and Mr. Abel Mwakebunu for typing, J. Michell-Hedges Esq. for the photograph of an Interval Calculator, and A.B. Wylie Esq., O.B.E., Government Printer, for undertaking the binding of this thesis.

Finally I wish to acknowledge gratefully the constructive criticism and advice given by R.M. Arnold Esq., B.Sc., M.R.C.V.S., Chief Veterinary Research Officer, Tanganyika Territory, during the preparation of the final draft of this thesis, and to present apologies to my examiners for its excessive length which I submit to be correlated with the ramifications of the problem.

"Not that the story need be long,
but it will take a long time to
make it short".

Thoreau.

REFERENCES.

- Abrams, J.T. (1952) Vet. J. 108: 275-292
The relationship of sunlight to bovine reproductive efficiency and productivity.
- Alexander, M.H. (1950) J.Dairy Sci. 33: 377-378
Length of gestation in the five major breeds of dairy cattle.
- Andres, J. (1951) Dtsch. tierarztl. Wschr. 39: 567
reported by Jasper (1950).
- Asdell, S.A. (1931) Cornell Vet. 21: 147-152
Recent developments in the field of sex hormones.
- Asdell, S.A. (1946). Patterns of mammalian reproduction London: Constable & Co. Ltd.
pp.540-541.
- Asdell, S.A. (1952a). Report of the Second International Congress of Physiology and Pathology of Animal Reproduction and Artificial Insemination. Copenhagen. 2: 7.
- Asdell, S.A. (1952b). Vet.Rec. 64: 831-835.
Work on breeding troubles of dairy cattle at Cornell University.
- Asdell, S.A., De Alba, J., Roberts, S.J., (1949).
Cornell Vet. 39: 389. Studies on the estrous cycle of dairy cattle: cycle length, size of corpus luteum, and endometrial changes.
- Ballinger, H.J., Rowson, L.E.A., (1951). Vet.Rec. 63: 622-623. Infertility in a bull at an artificial insemination centre.
- Bane, A. (1952). K. LantbrAkad Tidskr. (Stockh.) 91: 132-147. Arvet och sexualfunktionerna. (Not seen).
- Barrett, G.R., Casida, L.E. (1946). J. Dairy Sci. 29: 556-557. Time of insemination and conception rate in artificial breeding.

- Barrett, G.R., Casida, L.E., Lloyd, C.A. (1948a).
J. Dairy Sci. 31: 682. Measuring breeding efficiency by pregnancy examination and by non-returns.
- Barrett, G.R., Lloyd, C.A., Carpenter, R.A. (1948b)
J. Dairy Sci. 31: 683. Order number of insemination and conception rate.
- Bentley, O.G., Quicke, G.V., Kastelic, J., Phillips, P.H.,
(1951). J. Dairy Sci. 34: 363-366. Certain trace elements in feeds, organs, and tissues of a selected group of repeat breeding cows in Northeastern Wisconsin.
- Berge, S. (1942) Z. Tierz. ZuchtBiol. 52: 127-167.
Fruchtbarkeitsverhaltnisse beim roten hornlosen Ostlandrind. (Anim. Breed. Abst. 10: 229).
- Beschlebov, A.V. (1938) Probl. Zivotn. 2: 73-88.
The optimal time of inseminating cows during oestrus. Abst. in Anim. Breed Abst. 6: 291.
- Blake, T.A. (1945). Nature 155: 631.
Inheritance of morphological characters in the sperms of cattle.
- Bowling, G.A., Putnam, D.N., Ross, R.H. (1940).
J. Dairy Sci. 23: 1171-1176. Age as a factor influencing breeding efficiency in a dairy herd.
- Boyd, L.J., Seath, D.M., Olds, D. (1954) J. Anim. Sci. 13: 89-93.
Relationship between level of milk production and breeding efficiency in dairy cattle.
- Brakel, W.J., Rife, D.C., Salisbury, S.M. (1952).
J. Dairy Sci. 35: 179-194. Factors associated with the duration of gestation in dairy cattle.
- Branton, C. (1949). The Artificial Breeders' Bulletin. La. St. Univ. 1: 5. Natural breeding results tell the story.
- Branton, C., Bratton, R.W., Salisbury, G.W. (1947).
J. Dairy Sci. 30: 1003-1013. Total digestible nutrients and protein levels for dairy bulls used in artificial breeding.

- Branton, C., Kellgren, H.C., Patrick, T.E., (1952). J. Dairy Sci. 35: 490. The relationship between dilution rate of bull semen or the number of motile spermatozoa and fertility.
- Bratton, R.W. (1955). Cornell Univ. Progress Report. Effect of three levels of nutrition on sexual development of young dairy animals. Mimeo.
- Bratton, R.W., Salisbury, G.W., Tanabe, T., Branton, C., Mercier, E., Loosli, J.K. (1948). J. Dairy Sci. 31: 779-791. Breeding behaviour, spermatogenesis, and semen production of mature dairy bulls fed rations low in carotene.
- Bratton, R.W., Foote, R.H., (1954). J. Dairy Sci. 37: 1439-1443. Semen production and fertility of dairy bulls ejaculated either once or twice at intervals of either four or eight days.
- Bratton, R.W., Foote, R.H. (1955). Cornell Univ. Progress Report. The effect of nutrition during early growth and development, especially the effect of prepubertal nutrition on the reproductive performance of mature dairy cattle. Mimeo.
- Bratton, R.W., Hansel, W., Bearden, H.J. (1955). Cornell Univ. Progress Report. Embryonic mortality rates of bulls having histories of either low or high fertility in artificial breeding. Mimeo.
- Brewster, J.E., May, R., Cole, C.L. (1940). Proc. Amer. Soc. Anim. Prod. 1940 : 304-310. The time of ovulation and rate of spermatozoa travel in cattle.
- Brown, L.O., Durham, R.M., Cobb, E., Knox, J.H. (1954). J. Anim. Sci. 13: 511-516. An analysis of the components of variance in calving intervals in a range herd of beef cattle.
- Burgess, T.D., (1955). Canad. J. Agric. Sci. 33: 261. The relationship between 30 -, 60 -, 90 -, and 120-day non-returns to service in the artificial insemination of dairy cattle in Ontario.

Carpenter, S.E., Johnson, P.R. (1950). Texas Agric. Exp. Sta. Progress Report 1259. Conception rate from natural breeding of dairy cows.

Casida, L.E. (1955a). Fertilization failure and embryonic death in domestic animals. Pregnancy wastage. Charles C. Thomas, Springfield, Illinois.

Casida, L.E. (1955b). Iowa St. Coll. J. Sci. 28: 119-126. Prenatal death as a factor in the fertility of farm animals.

Casida, L.E., Venzke, W.G. (1936). Proc. Amer. Soc. Anim. Prod. Nov. 1936. Observations on reproductive processes in dairy cattle and their relation to breeding efficiency.

Casida, L.E., Barrett, G.R., Lloyd, C.A., (1946). J. Dairy Sci. 29: C4 553-554. The use of pregnancy diagnosis with artificial breeding (Abstr.).

Casida, L.E., Chapman, A.B. (1951). J. Dairy Sci. 34: 1200 Factors affecting the incidence of cystic ovaries in herd of Holstein cows.

Cembrowicz, H.J. (1952). J. Agric. Sci. 42: 523-534. Fertility levels of bulls kept at an artificial insemination centre.

Chance, C.M., Mather, R.E. (1949). J. Anim. Sci. 8: 603-604. Relation of cow families to milk production, reproductive efficiency and longevity.

Chang, M.C., Pincus, G. (1951). Physiol. Rev. 31: 1-26. Physiology of fertilization in mammals.

Chapman, A.B., Casida, L.E. (1935a). Annual Report 1934-35. Agric. Exp. Sta., Univ. Wisconsin. Length of service period affects efficiency of dairy herds.

Chapman, A.B., Casida, L.E. (1935b). Proc. Amer. Soc. Anim. Prod. Nov. 1935. 66-70. Length of service period in relation to productivity and reproductive efficiency in dairy cows.

- Chapman, A.B., Casida, L.E. (1935c) Proc. Amer. Soc. Anim. Prod. 27th Ann. Mtg. :57. Factors associated with breeding efficiency in dairy cattle.
- Chapman, A.B., Casida, L.E. (1937). J. Agric. Res. 54: 417-435. Analysis of variation in the sexual cycle and some of its component phases with special reference to cattle.
- Christian, R.E., Casida, L.E. (1951). J. Dairy Sci. 34: 971. The effect of infertile insemination and individuality of bulls upon the subsequent fertility of cows returning for service.
- Christian, R.E., Ulberg, L.C., Phillips, P.H., Casida, L.E. (1951a). J. Dairy Sci. 34: 978-987. The response of low-fertility cows to chlorobutanol and ascorbic acid administration.
- Christian, R.E., Ulberg, L.C., Casida, L.E. (1951b). J. Dairy Sci. 34: 988-991. The response of low-fertility cows to insemination with semen from bulls of another breed.
- Clapp, H. (1937). Proc. Amer. Soc. Anim. Prod. 1937: 259-265. A factor in breeding efficiency of dairy cattle.
- Clarke, R. (1949). Vet. Rec. 61: 861-863. Statistical records in artificial insemination practice.
- Corley, E.L., Bayley, N.D., Hendrickson, F.A. (1952). J. Dairy Sci. 35: 963-965. The fertility of interbreed vs. intrabreed matings as determined from artificial breeding data.
- Cornell University (1955). Animal Husbandry Department Mimeo. Report. Studies on sterility in dairy cattle.
- Davis, H.P. (1951). J. Dairy Sci. 34: 495. Reproductive efficiency in a Holstein herd 1897-1950.
- Dawson, J.R., (1938). J. Dairy Sci. 21: 725-737. The breeding of proved (aged) sires.

- De Groot, T. (1950). Landbouwk. Tijdschr. 62: 60-74.
De invloed van de erfelijkheid op vruchtbaarheid
en onvruchtbaarheid. (Not seen).
- Donald, H.P. (1943). Vet. Rec. 55: 297-298.
Heat during pregnancy in dairy cows.
- Donald, H.P., Hancock, J.L. (1953). J. Agric. Sci.
43: 178-181. Evidence of gene-controlled
sterility in bulls.
- Dunbar, R.S., Jr., Henderson, C.R. (1950). J. Dairy
Sci. 33: 377. Heritability of fertility in
dairy cattle.
- Dunbar, R.S., Jr., Henderson, C.R. (1953). J. Dairy
Sci. 36: 1063-1071. Heritability of fertility
in dairy cattle.
- Eberle, A. (1953). Dissertation, Univ. Munich.
Untersuchungen über die Vererbung der
Langlebigkeit, unter gleichzeitiger
Berücksichtigung der Fruchtbarkeit, beim Allgauer
Braunvieh im Tierzuchtamtsbereich Kaufbeuren.
- Eckles, C.H., Palmer, L.S. (1916). Missouri Agric.
Exp. Sta. Res. Bull. No. 25. Influence of plane
of nutrition of the cow upon the composition and
properties of milk and butterfat. Influence of
underfeeding.
- Ellenberger, H.B., Lohmann, A.H. (1946). Vet. Agric.
Exp. Sta. Bull. No. 533. Artificial insemination
of dairy cattle.
- Elliott, F.I., (1944). Ph.D. thesis, Cornell Univ.
Studies on some problems related to the successful
artificial insemination of dairy cattle.
- Erb, R.E. (1955). Mimeo. Purdue Univ. Summary of
reproductive performance of the Purdue dairy herd.
- Fett, H. (1951). Dissertation, Munich.
Familienuntersuchungen in niederbayerischen
Fleckviehzuchtgebieten unter besonderer
Berücksichtigung erblicher Veranlagungen zu
Fruchtbarkeit und Unfruchtbarkeit. (Anim. Breed.
Abst. 21: 141).

- Fetscher, E. (1940). Dissertation, Munich.
Untersuchungen über die Vererbung von Fruchtbarkeit
und Unfruchtbarkeit beim oberbadischen Fleckvieh.
(Anim. Breed. Abst. 16. No. 513).
- Fincher, M.G. (1946). Am. Soc. Study of Sterility,
Trans. 1946: 1-17. Methods of increasing
fertility in domestic animals.
- Flerchinger, F.H., Erb, R.E. (1953). J. Dairy Sci.
36: 1072. Service sire influences on fertility
rates of repeat breedings.
- Flipse, R.J., Snyder, J.W., Thacker, D.L., Almquist, J.O.
(1953). Penn. St. Coll. Agric. Exp. Sta.
Progress Report 104. Effect of total digestible
nutrient intake on growth and reproductive
development.
- Fohrman, M.H., Graves, R.R. (1939). U.S. Dep. Agric.
Tech. Bull. No. 677. Experiments in breeding
Holstein-Friesian cattle for milk- and butterfat-
producing ability, and an analysis of the
foundation cows and on the first outbred
generation.
- Foote, R.H., Bratton, R.W. (1952). J. Dairy Sci. 35:
261-265. The influence of anti-biotics on
delayed returns in artificial breeding.
- Foote, R.H., Henderson, C.R., Bratton, R.W. (1951).
J. Dairy Sci. 34: 490. Some biases to consider
in measuring fertility in artificial insemination.
- Foote, R.H., Henderson, C.R., Bratton, R.W. (1955).
Cornell Univ. Progress Report. A study of
factors affecting breeding efficiency in 2,000
co-operating herds in artificial breeding.
- Fosgate, O.T., Smith, V.R. (1954). J. Dairy Sci. 37:
1071. Prenatal mortality in the bovine between
pregnancy diagnosis at 34-50 days post-
insemination and parturition.
- Friend, I.J.C. (1951). Brit. Cattle Breed. Club address
Jan. '51. M.M.B. Natural service investigation,
1946-8.
The results of inseminations in recorded herds.

- Gaines, W.L. (1927). J. Dairy Sci. 10: 2.
Milk yield in relation to recurrence of conception.
- Gaines, W.L., Palfrey, J.R. (1951). J. Dairy Sci. 14: 294. Length of calving interval and average milk yield.
- Gerasimova, A.A. (1938). Probl. Zivotn. 12: 126-129.
Duration of heat and time of ovulation in the cow.
Abst. in Anim. Breed. Abst. 8: 32.
- Gilmore, L.O., (1949). J. Dairy Sci. 32: 71-91.
The inheritance of functional causes of reproductive inefficiency a review.
- Gregory, P.W., Regan, W.M., Mead, S.W. (1945).
Genetics 30: 506-517. Evidence of genes for female sterility in dairy cows.
- Gregory, P.W., Mead, S.W., Regan, W.M., Rollins, W.C. (1951). J. Dairy Sci. 34: 1047-1055. Further studies concerning sex-limited genetic infertility in cattle.
- Hafez, E.S.E. (1952). J. Agric. Sci. 42: 189-265.
Studies on the breeding season and reproduction of the ewe.
- Hafez, E.S.E. (1956). Ind. J. Vet. Sci. Anim. Husb. 26: 35-40. Control of fertility in farm animals.
- Hammond, J. (1914). J. Agric. Sci. 6: 263-277.
On some factors controlling fertility and foetal atrophy.
- Hammond, J. (1927). The Physiology of Reproduction in the Cow, Cambridge Univ. Press, London.
- Hammond, J. (1944). Vet. Rec. 56: 41-46.
Principles affecting the reproductive functions..
- Hancock, J.L. (1949). Vet. Rec. 61: 308-309.
Evidence of an inherited seminal character associated with infertility of Friesian bulls.
- Hancock, J.L., Rollinson, D.H.L. (1949). Vet. Rec. 61: 742-743. A seminal defect associated with sterility of Guernsey bulls.

- Hansel, W. (1953). Iowa St. Coll. J. Sci. 28: 1-8.
Neurogenic factors in ovulation.
- Hansel, W., Trimberger, G.W. (1951). J. Anim. Sci. 10: 719-725. Atropine blockage of ovulation in the cow and its possible significance.
- Hansel, W., Trimberger, G.W. (1952). J. Dairy Sci. 35: 65-70. The effect of progesterone on ovulation time in dairy heifers.
- Hansel, W., Trimberger, G.W., Armstrong, D.T. (1955). Cornell Univ. Progress Report. Factors controlling ovulation in the cow. Mimeo.
- Haussermann, W. (1952). Dissertation. Munich. Untersuchungen über die Vererbung von Fruchtbarkeit und Unfruchtbarkeit beim Württembergischen Hohenfleckvieh. (Anim. Breed. Abst. 21: 347).
- Hawk, H.W., Tyler, W.J., Casida, L.E. (1954). J. Dairy Sci. 37: 252-258. Some factors affecting age at puberty in Holstein-Friesian heifers.
- Hawk, H.W., Tyler, W.J., Casida, L.E. (1955). J. Dairy Sci. 38: 420-427. Effect of sire and system of mating on estimated embryonic loss.
- Henderson, C.R. (1952). Biometrics 9: 226-252. Estimation of variance and covariance components.
- Henderson, J.A. (1938). Cornell Vet. 28: 173-195. Observations on reproduction and associated conditions in a herd of dairy cattle.
- Henle, C. (1949). Dissertation, Univ. Munich. Untersuchungen über die Vererbung von Fruchtbarkeit und Unfruchtbarkeit beim Allgauer Rind. (Anim. Breed. Abst. 19. No. 1658).
- Hignett, P.G. (1952). J. Brit. Dairy Fms' Ass. 56: 1-21. Infertility in dairy cattle.
- Hignett, S.L. (1950). Vet. Rec. 62: 652-663. Factors influencing herd fertility in cattle.

- Hignett, S.L. (1951). Brit. Cattle Breed. Club.
Jan. 1951. Sterility in dairy herds.
- Hignett, S.L. (1956). Procs. III Int. Cong. Anim.
Reprod., Cambridge 1956. The influence of
calcium, phosphorus, manganese, and vitamin D
on heifer fertility.
- Hignett, S.L., Hignett P.G. (1951). Vet. Rec. 63:
603. The influence of nutrition on reproductive
efficiency in cattle. (i) The effect of calcium
and phosphorus intake on the fertility of cows
and heifers.
- Hignett, S.L., Hignett, P.G. (1952). Vet. Rec. 64:
203. The influence of nutrition on reproductive
efficiency in cattle. (ii) The effect of
phosphorus intake on ovarian activity and fertility
of heifers.
- Hignett, S.L., Hignett, P.G., (1953). Vet. Rec. 65:
21. The influence of nutrition on reproductive
efficiency in cattle. (iii) The influence of the
Vitamin D status on the effect of calcium and
phosphorus intake on the fertility of cows and
heifers.
- Hilder, R.A., Fohrman, M.H., Graves, R.R. (1944).
J. Dairy Sci. 27: 981-992. Relation of various
factors to the breeding efficiency of dairy
animals and to the sex ratio of the offspring.
- Hofstad, M.S. (1941). Cornell Vet. 31: 379-381.
A study of breeding records of one large herd of
dairy cattle. Post-partum breeding.
- Holt, A.F. (1946). Vet. Rec. 58: 309-310.
Comparison between intra-cervical and intrauterine
methods of artificial insemination.
- Holt, A.F. (1952). Vet. Rec. 64: 31-38.
Analysis of conception rates and other data in
artificial insemination.
- Hull, F.E., Dimock, W.W., Ely, F., Morrison, H.B. (1940).
Kentucky Agric. Exp. Sta. Bull. No. 402.
Reproductive efficiency in dairy cattle.

- Inchiosa, M.A., Pfau, K.O. (1954). J. Dairy Sci. 37: 667. The influence of dams and sires upon the breeding efficiency of their daughters within a Holstein-Friesian herd.
- Jafar, S.M., Chapman, A.B., Casida, L.E. (1950). J. Anim. Sci. 9: 593-601. Causes of variation in length of gestation in dairy cattle.
- Jasper, D.E. (1950). Cornell Vet. 40: 165-172. Prolonged gestation in the bovine.
- Jones, I.R., Dougherty, R.W., Haag, J.R. (1941). Ore Agric. Exp. Sta. Bull. No. 395. Reproductive performance in dairy cattle. (Anim. Breed. Abst. 11: 228).
- Joubert, D.M. (1954). J. Agric. Sci. 45: 164-172. The influence of high and low planes on the oestrous cycle and conception rate of heifers.
- Kab, E. (1937). Dissertation, Univ. Munich. Untersuchungen uber die Vererbung von Fruchtbarkeit und Unfruchtbarkeit beim gelben Frankenvieh. (Anim. Breed. Abst. 6: 200).
- Kidder, H.E., Barrett, G.R., Casida, L.E. (1952). J. Dairy Sci. 35: 436-444. A study of ovulations in six families of Holstein-Friesians.
- Kidder, H.E., Black, W.G., Wiltbank, J.N., Ulberg, L.C., Casida, L.E. (1954). J. Dairy Sci. 37: 691. Fertilization rates and embryonic death rates in cows bred to bulls of different levels of fertility.
- Kidwell, J.F., Walker, LeG., McCormick, J.A. (1954). J. Hered. 45: 142, 145. Hereditary female sterility in Holstein-Friesian cattle.
- Knapp, B., Jr., Lambert, W.V., Black, W.H. (1940). J. Agric. Res. 61: 277-285. Factors influencing length of gestation and birthweight in cattle.
- Knight, C.W., Patrick, T.E., Anderson, H.W., Branton, C. (1951). J. Dairy Sci. 34: 199-202. The relation of site of semen deposit to breeding efficiency of dairy cattle.

Knoop, C.E., Hayden, C.C. (1934). Ohio Agric. Exp. Sta. Bimonthly Bull. No.166: 8-14. A study of the length of gestation and service record of dairy cows.

Koort, P. (1948). S.R.B. Tidskr., 21: 2-17.
Om arvets inflytande på förekomsten av
fortplantnings-störningar hos kor. (Anim. Breed.
Abst. 16: 316).

Korkman, N. (1947a). Maataloust. Aikakausk, 19:
101-107. (English). On the inheritance of
female sterility in cattle.

Korkman, N. (1947b). Suom. Maataloust. Seur. Julk.
64: No.1. Om orsakerna till variationen i kornas
fruktsamhet i några ayrshirebesättningar i
södra Finland. (English summary. On the causes
of variations in the fertility of cows in some
Ayrshire herds in the south of Finland).

Lagerlof, N., Boyd, H. (1952). Rep. 2nd. Int. Congr.
Physiol. Path. Anim. Reprod. Artif. Insem. 1952
2: 164-174. Copenhagen, Postmortem examination
of the sexual organs of 6,286 cows of the Swedish
Highland breed, with special reference to ovarian
hypoplasia.

Laing, J.A. (1945a). Vet. Rec. 57: 275.
Some factors in the aetiology and diagnosis of
bovine infertility.

Laing, J.A. (1945b). J. Agric. Sci. 35: 1-24.
Observations on the characteristics of the semen
in relation to fertility in the bull.

Laing, J.A. (1945c). J. Agric. Sci. 35: 25-29.
Observations on the effect of method of management
at mating on bovine fertility.

Laing, J.A. (1945d). J. Agric. Sci. 35: 72-83.
Observations on the survival time of the
spermatozoa in the genital tract of the cow and
its relation to fertility.

- Laing, J.A. (1949). Paper presented at "Cambridge Week" on Bull Breeding, 3rd-7th January, 1949, under the auspices of the British Cattle Breeders' Club. Prevention of disease in dairy cattle.
- Laing, J.A. (1949). J. Comp. Path. & Therapeutics 59: 97-108. Infertility in cattle associated with death of ova at early stages after fertilisation.
- Lasley, J.F., Bogart, R. (1943). Mo. Agric. Exp. Sta. Res. Bull. No. 576. Some factors influencing reproductive efficiency of range cattle under artificial and natural conditions.
- Larsen, G.L., Bayley, N.D. (1955). J. Dairy Sci. 38: 549. The fertility of inseminations made in cows showing postestrous hemorrhage.
- Legates, J.E. (1950). Mimeo., North Carolina St. Coll. of Agric. Estimation of components of variance.
- Legates, J.E. (1954). J. Anim. Sci. 13: 81-88. Genetic variation in services per conception and calving interval in dairy cattle.
- Lerner, I.M. (1950). Population Genetics and Animal Improvement. Cambridge Univ. Press. 342 pp.
- Lewis, R.C. (1948). J. Anim. Sci. 7: 514. Effect of season upon spermatogenesis and fertility of dairy bulls under Michigan conditions.
- Lewis, R.C., Horwood, R.E. (1950). Quarterly Bull. Mich. Agric. Exp. Sta. 32: 4. The influence of age, level of production and management on the calving interval. Reported by Boyd et al (1954).
- Livesay, E.A., Bee, U.G. (1945). J. Anim. Sci. 4: 13-14. A study of the gestation periods of five breeds of cattle.
- Lowe, H. (1933). Kuhn-Arch. 51: 71-267. Abhangigkeit und Vererbung der Fruchtbarkeit bei den grossen landwirtschaftlichen Haustieren unter besonderer Berücksichtigung des Rindes. (Anim. Breed. Abst. 8: 32-33).

- Lush, J.L. (1948). The Genetics of Populations. Ames, Iowa. Mimeograph unpublished book, copyright by author. 381 pp.
- Mack, M. (1953). Zuchtungskunde. 25: 20-25. Grundlagen der Fruchtbarkeit beim Rind. (Anim. Breed. Abst. 22: 119).
- Marion, G.B., Smith, V.R., Wiley, T.E., Barrett, G.R. (1950). J. Dairy Sci. 33: 885. The effects of sterile copulation on time of ovulation in dairy heifers.
- McCullough, M., Seath, D.M., Olds, D. (1951). J. Dairy Sci. 34: 548-553. The repeatability and effect of age on yearly breeding efficiency of sires used in artificial breeding.
- McIntosh, R.A. (1938). Cornell Vet. 28: 107-114. Breeding problems in dairy herds.
- Mead, S.W., Gregory, P.W., Regan, W.M. (1946). Genetics 31: 574-588. Deleterious recessive genes in dairy bulls selected at random.
- Melton, A.A., Berry, R.O., Butler, O.D. (1951). J. Anim. Sci. 10: 993-1005. The interval between time of ovulation and attachment of the bovine embryo.
- Mercier, E., Salisbury, G.W. (1946). Cornell Vet. 36: 301-311. The effects of season on the spermatogenic activity and fertility of dairy bulls used in artificial insemination.
- Mercier, E., Salisbury, G.W. (1947a). J. Dairy Sci. 30: 747-756. Seasonal variations in hours of daylight associated with fertility level of cattle under natural breeding conditions.
- Mercier, E., Salisbury, G.W. (1947b). J. Dairy Sci. 30: 817-826. Fertility level in artificial breeding associated with season, hours of daylight, and the age of cattle.
- Miller, F.W., Graves, R.R. (1932). U.S. Dep. Agric. Tech. Bull. No. 321. Reproduction and health records of the Beltsville herd of the Bureau of Dairy Industry.

- Milk Marketing Board of England & Wales (1948).
Report to the Board of the Bureau of Records
1947-1948.
- Milk Marketing Board of England & Wales (1949).
3rd Ann. Report to the Board on artificial
insemination.
- Milk Marketing Board of England & Wales (1953).
National Milk Records. Report for year ending
September 1953.
- Milk Marketing Board of England & Wales (1956).
Report to 8th Ann. Mtg. of Chairmen on the Board's
cattle breeding centres. 25th May, 1956.
- Moeller, A.N., Van Demark, N.L. (1951). J. Anim. Sci.
10: 988-992. The relationship of the interval
between inseminations to bovine fertility.
- Morgan, R.F., Davis, H.P. (1938). Nebraska Agric.
Exp. Sta. Res. Bull. 104. Influences of age
of dairy cattle and season of year on the sex
ratio of calves and services required for
conception.
- Nalbandov, A., Casida, L.E. (1942). J. Anim. Sci.
1: 189-198. Ovulation and its relation to
estrus in cows.
- Olafson, P. (1947). Cornell Vet. 37: 277.
reported by Jasper (1950).
- Olds, D. (1950). Proc. Ass. Sth. Agric. Workers 1950
: 78. Some factors influencing breeding
efficiency in herds being bred artificially.
Reported by Trimberger (1956).
- Olds, D., Morrison, H.B., Seath, D.M. (1949).
Kentucky Agric. Exp. Sta. Bull. 539.
Efficiency of natural breeding in dairy cattle.
- Olds, D., Seath, D.M. (1950). J. Dairy Sci. 33:
721-724. Predictability of breeding efficiency
in dairy cattle.

- Olds, D., Seath, D.M. (1951). J. Dairy Sci. 34: 626-632. Repeatability of the estrous cycle in dairy cattle.
- Olds, D., Seath, D.M. (1953). J. Anim. Sci. 12: 10-14. Repeatability, heritability and the effect of level of milk production on the occurrence of first estrus after calving in dairy cattle.
- Olson, T.M. (1938). S. Dak. Agric. Exp. Sta. Bull. No. 319. The effect of sunlight on the growth, production and reproduction of dairy cattle.
- Ostergaard, P.S. (1942). Intervallert, Ugeskr. Landm. 845. Om Kaelvnings. (Anim. Breed. Abst. 14: 226).
- Phillips, R.W. (1939). U.S.D.A. Yearbook of Agriculture 1939: 476-491. Relation of diet to reproduction - reproduction failures in livestock.
- Phillips, R., Brown, E.H., Davies, J.L. (1949). J. Agric. Sci. 16: 283-300. Seasonal variations in the sale of calves in different parts of Great Britain, 1943-1947.
- Pou, J.W., Henderson, C.R., Asdell, S.A., Sykes, J.F., Jones, R.C. (1953). J. Dairy Sci. 36: 909-915. A study of the inheritance of breeding efficiency in the Beltsville dairy herd.
- Quinlan, J., Roux, L.L. (1936). Onderstepoort J. Vet. Sci. 6: 719-772. Researches into sterility of cows in South Africa. The influence of (i) dry rations, (ii) lack of exercise, and (iii) lack of sunlight on reproduction in beef heifers and cows.
- Quinlan, J., Roux, L.L., van Aswegen, W.G. (1939). Onderstepoort J. Vet. Sci. 12: 233-249. Researches into sterility of cows in South Africa. The influence of (i) dry rations, and (ii) lack of exercise on sexual maturity and the duration of the ovarian cycle in beef heifers.

- Quinlan, J., Bisschop, J.H.R., Adelaar, T.F. (1941). Onderstepoort J. Vet. Sci. 16: 213-259. Bionomic studies on cattle in the semi-arid regions of the Union of South Africa. IV The ovarian cycle of heifers during summer.
- Raps, G. (1948). North Amer. Veterinarian 29: 221-222. Relative effectiveness of two methods used in insemination of dairy cattle.
- Reid, J.T., Loosli, J.K., Turk, K.L., Trimberger, G.W., Hansel, W. (1955). Cornell Univ. Progress Report. The effect of nutrition during early growth and development, especially the effect of prepubertal nutrition, on the reproductive performance of mature dairy cattle. Mimeo.
- Rice, V.A., Andrews, F.N. (1951). Breeding and improvement of farm animals. McGraw Hill Book Co. Inc., London.
- Rife, D.C., Gerlaugh, P., Kunkle, L., Brandt, G.W., Snyder, L.H. (1943). J. Anim. Sci. 2: 50-52. Comparative lengths of gestation periods of Aberdeen-Angus and Hereford cows carrying purebred and crossbred calves.
- Roark, D.B., Herman, H.A. (1950). Mo. Agric. Exp. Sta. Res. Bull. No. 455. Physiological and histological phenomena of the bovine estrual cycle with special reference to vaginal-cervical secretions.
- Robertson, Alan, Lerner, I.M. (1949). Genetics 34: 395-411. The heritability of all-or-none traits: viability of poultry.
- Rollinson, D.H.L. (1955). Animal Breeding Abstracts 23: 215-249. Hereditary factors affecting reproductive efficiency in cattle.
- Rowson, L.E.A. (1950). Vet. Rec. 62: 190. Infertility in a bull in service at an artificial insemination centre.
- Rowson, L.E.A., Laming, G.E., Fry, R.M. (1953). Vet. Rec. 65: 335-340. The relationship between ovarian hormones and uterine function.

- Salisbury, G.W., Van Demark, N.L. (1951). J. Dairy Sci. 34: 68-74. The effect of cervical, uterine and cornual insemination on fertility of the dairy cow.
- Salisbury, G.W., Bratton, R.W., Foote, R.H. (1952a) J. Dairy Sci. 35: 250-255. The bull as one cause of delayed returns to service in artificial breeding.
- Salisbury, G.W., Bratton, R.W., Foote, R.H. (1952b) J. Dairy Sci. 35: 256-260. The effect of time and other factors on the non-return to service estimate of fertility level in artificial insemination of cattle.
- Schroter, H. (1901). Berlin. Tierarztl. Wschr. 431 reported by Jasper (1950).
- Seath, D.M., Staples, C.H., Neasham, E.W. (1943). La. Exp. Sta. Bull. No. 570. A study of breeding records in dairy herds.
- Sergin, N.P., Kuznecov, M.P., Kozlova, V.M., Nesmejanova, T.N. (1940). Dokl. Akad. Seljskhoz. Nauk. 15: 24-28. Physico-chemical condition in the genital tract of the cow and survival of spermatozoa. Abst. in Anim. Breed. Abst. 9: 18-19.
- Shannon, F.P., Salisbury, G.W., Van Demark, N.L. (1952). J. Anim. Sci. 11: 355-360. The fertility of cows inseminated at various intervals after calving.
- Snedecor, G.W. (1946). "Statistical Methods" 4th Edn. The Iowa State College Press, Ames, Iowa. 485 pp.
- Snyder, F.F. (1938). Physiological Reviews 18: 578-596. Factors concerned in the duration of pregnancy.
- Spielman, A., Jones, I.R. (1939). J. Dairy Sci. 22: 329-334. The reproductive efficiency of dairy cattle.
- Stewart, D.L. (1950). Vet. Rec. 62: 389-395. Artificial insemination of cattle. A review of the work of the Reading Cattle Breeding Centre. October 1st 1944 to September 30th 1948.

- Stewart, D.L. (1952). Vet. Rec. 64: 303.
The suppression of oestrus in dairy cattle after mating.
- Stewart, D.L., Melrose, D.R., Wilson, W.R. (1951)
Vet. Rec. 63: 609-612. The effect of streptomycin on the fertility of bull semen.
- Swanson, E.W. (1951). J. Dairy Sci. 34: 1186-1190.
The efficiency of artificial breeding with bull semen one to three days old.
- Swedish A.I. Societies (1950). Sammanställning ur seminforeningarnas årsberättelser för 1950.
- Swett, W.W., Matthews, C.A. Forhman, M.H. (1948)
U.S. Dep. Agric. Tech. Bull. No. 964. Development of the fetus in the dairy cow.
- Tabler, K.A., Tyler, W.J., Hyatt, G., Jr. (1951).
J. Dairy Sci. 34: 95-105. Type, body size and breeding efficiency of Ayrshire cow families.
- Tanabe, T., Salisbury, G.W. (1946). J. Dairy Sci. 29: 337-344. The influence of age on breeding efficiency of dairy cattle in artificial insemination.
- Tanabe, T.Y., Casida, L.E. (1949). J. Dairy Sci. 32: 237-246. The nature of reproductive failures in cows of low fertility.
- Tanabe, T.Y., Almquist, J.O. (1953). 48th Ann. Mtg. Amer. Dairy Sci. Ass. 1953. Some causes of infertility in dairy heifers.
- Taussig, S. (1946). Int. Rev. Agric. 37: 256^T-261^T.
The problem of fertility in dairy cattle and its improvement through breeding. (Anim. Breed. Abst. 15: 173).
- Taylor, G.E. (1937). Michigan Agric. Exp. Sta. Quarterly Bulletin 19: 156-159. Some factors affecting breeding efficiency in dairy cattle.

- Trimberger, G.W. (1941). J. Dairy Sci. 24: 1042-1049. 'Menstruation' frequency and its relation to conception in dairy cattle.
- Trimberger, G.W. (1948). Nebraska Agric. Exp. Sta. Res. Bull. No. 153. Breeding efficiency in dairy cattle from artificial insemination at various intervals before and after ovulation.
- Trimberger, G.W. (1954). J. Dairy Sci. 37: 1042-1049. Conception rates in dairy cattle from services at various intervals after parturition.
- Trimberger, G.W. (1956). J. Dairy Sci. 39: 448-455. Ovarian functions, intervals between estrus, and conception rates in dairy cattle.
- Trimberger, G.W., Davis, H.P. (1943). Nebraska Agric. Exp. Sta. Res. Bull. No. 129: 1-14. Conception rate in dairy cattle by artificial insemination at various stages of estrus.
- Trimberger, G.W., Davis H.P. (1945). J. Dairy Sci. 28: 659-670. Predictability of breeding efficiency in dairy cattle from their previous conception rate and from their heredity.
- Ulberg, L.C., Black, W.G., Kidder, H.E., McDonald, L.E., Casida, L.E., McNutt, S.H. (1952). J. Amer. Vet. Med. Ass. 121: 436-440. The use of anti-biotics in the treatment of low fertility cows.
- Van Demark, N.L., Hays, R.L. (1952). Amer. J. Physiol. 170: 518-521. Uterine responses to mating.
- Van Demark, N.L., Hays, R.L. (1953). Iowa St. Coll. J. Sci. 28: 107-118. Motility patterns in the female reproductive tract.
- Van Demark, N.L., Salisbury, G.W. (1950). J. Anim. Sci. 9: 807. The relation of the post-partum breeding interval to the reproductive efficiency in the dairy cow.
- Van Demark, N.L., Moeller, A.N. (1950). J. Anim. Sci. 9: 640. The influence of estrous cycle length on bovine fertility.

- Van Demark, N.L., Moeller, A.N. (1951). Amer. J. Physiol. 165: 674-679. Speed of spermatozoan transport in reproductive tract of estrous cow.
- Vainikainen, V. (1946). J. Sci. Agric. Soc. of Finland. 18: 179-181. Some points of view regarding the effect of hereditary factors on the fecundity of cattle.
- Wagner, H. (1932). Dtsch. Tierarztl. Wschr. 40: 547-550. Sterilität und Vererbung. Kann das männliche Tier Überträger einer Minderwertigkeitsanlage in Geschlechtsapparat sein?
- Weeth, H.J., Herman, H.A. (1951). J. Dairy Sci. 54: 195-198. Comparative efficiency of intracervical and intrauterine methods of insemination in dairy cattle.
- Wegscheider, A. (1939). Dissertation, Leipzig. Vererbung von Fruchtbarkeit und Fruchtbarkeitsstörungen beim niederbayerischen Fleckvieh (Anim. Breed. Abst. 14: 82).
- Werner, G.W., Casida, L.E., Rupel, I.W. (1938). Proc. Amer. Soc. Anim. Prod. 1938: 54-57. Estrus, ovulation and artificial insemination in cattle.
- Williams, E. (1956). Vet. Rec. 68: 424. Letter. Prolonged gestation.
- Willetts, E.L. (1956). J. Dairy Sci. 39: 695-711. Developments in the physiology of reproduction of dairy cattle and in artificial insemination.
- Wiltbank, J.N., Tyler, W.J., Casida, L.E. (1953). J. Dairy Sci. 36: 1077. A study of atretic large follicles in six sire-groups of Holstein Friesian cows.
- H.W.
Wiltbank, J.N., Hawk, Kidder, H.E., Black, W.G., Ulberg, L.C., Casida, L.E. (1956). J. Dairy Sci. 39: 456-461. Effect of progesterone therapy on embryo survival in cows of lowered fertility.
- Wright, J.G. (1945). Vet. Rec. 57: 313-326. Reproductive disorders and sterility in cattle.

- Wright, J.G. (1955). N.A.A.S. Conference, Bangor, reported in 'Farmer & Stockbreeder' for 27th December, 1955, p.37.
- Yeates, N.T.M. (1949). J. Agric. Sci. 39: 1-40. The breeding season of the sheep with particular reference to its modification by artificial means using light.
- Young, G.B. (1953). Vet. Rec. 65: 271-278. Genetic aspects of fertility and infertility in cattle.
- Zschokke, E. (1900). Die Unfruchtbarkeit des Rindes, ihre Ursachen und Bekämpfung. Zurich: Orell-Fussli-Verlag. p.126 (quoted by Garm, 1949).

Appendix 1.

Overall "conception" rates for all first inseminations during each calendar month in Somerset.

	JAN.	FEB.	MAR.	APR.	MAY	JUN.	JUL.	AUG.	SEP.	OCT.	NOV.	DEC.	Annual Mean	Diff. from Overall mean
1946	-	60.3	61.0	61.3	55.7	63.5	59.3	61.0	56.2	68.4	70.0	69.5	62.4	- 3.1
1947	65.0	65.4	62.6	61.3	63.8	55.9	63.4	67.5	65.4	66.9	65.3	63.5	63.8	- 1.7
1948	63.7	60.2	63.5	62.9	67.0	68.9	69.8	58.9	63.7	66.7	65.6	68.4	65.1	- 0.4
1949	69.7	69.6	65.9	67.9	71.8	73.1	67.1	66.3	66.3	67.5	70.3	-	68.7	+ 3.2
1950	67.8	70.0	66.4	68.9	67.3	69.4	70.5	68.0	66.7	-	-	-	68.3	+ 2.8
Month mean	66.8	65.0	64.0	64.4	65.2	66.2	66.0	64.4	63.6	67.5	67.8	67.3	65.5	-
Diff. from overall mean.	+1.3	-0.5	-1.5	-1.1	-0.3	+0.7	+0.5	-1.1	-1.9	+2.0	+2.3	+1.8	-	-
Quarter means	65.1			65.3			64.7			67.5				

Appendix 2.

Overall "conception" rates for all first inseminations during each calendar month at Cambridge.

	JAN	FEB	MAR	APR	MAY	JUN	JUL	AUG	SEP	OCT	NOV	DEC	Annual mean	Diff. from overall mean
1944	-	-	-	-	-	67	62	50	62	67	67	67	63.1	- 1.5
1945	69	71	71	69	71	77	64	73	-	-	74	67	70.6	+ 6.0
1946	57	63	60	63	66	64	66	59	66	50	64	62	61.7	- 2.9
1947	58	61	56	67	57	67	74	70	56	53	53	56	60.7	- 3.9
1948	58	66	61	63	60	63	58	65	70	63	60	62	62.4	-2.2
1949	68	62	53	60	63	69	65	62	70	66	70	68	64.7	+ 0.1
1950	71	73	73	71	68	74	73	70	69	-	-	-	71.3	+ 6.7
Month mean	63.5	66.0	62.3	65.5	64.2	68.7	66.0	64.1	65.5	59.8	64.7	63.7	64.6	-
Diff. from overall mean	-1.1	+1.4	-2.3	+0.9	-0.4	+4.1	+1.4	-0.5	+0.9	-4.8	+0.1	-0.9	-	-
Quarter mean	63.9			66.3			65.2			62.9				

Analysis of Variance of months.				
	d.f.	s.s.	ms.	F.
Total	73	2711		
Years	6	1129	188.17	8.32 ^{XX}
Months	11	315	28.64	1.27 ^{NS}
Error	56	1267	22.63	

Analysis of Variance of Quarters.				
	d.f.	s.s.	ms.	F.
Total	73	2711		
Years	6	1129	188.17	8.22 ^{XX}
Quarters	3	117	39.00	1.70 ^{NS.}
Error	64	1465	22.89	

Appendix 3.

Overall "conception" rates for all first inseminations during each calendar month at Reading.

	Oct.	Nov.	Dec.	Jan.	Feb.	Mar.	Apr.	May	Jun.	Jul.	Aug.	Sep.	Annual Mean	Diff. from overall mean
1944-45	59.7	61.7	60.4	64.0	63.3	63.6	68.4	63.5	62.4	69.9	67.1	65.8	64.2	+ 0.7
1945-46	70.1	71.2	68.6	66.7	64.2	65.5	65.0	61.6	63.3	72.8	54.7	63.2	65.6	+ 2.1
1946-47	60.8	67.9	64.6	72.4	73.7	66.3	69.9	61.7	70.0	61.2	63.5	64.3	66.4	+ 2.9
1947-48	72.8	69.3	62.1	64.8	62.8	57.5	59.2	50.2	53.0	53.2	57.7	62.3	60.4	- 3.1
1948-49	55.9	55.2	60.0	58.5	62.9	61.0	55.6	59.9	62.5	64.0	57.7	65.8	59.9	- 3.6
1949-50	71.6	61.3	61.4	64.1	67.9	62.0	61.6	67.4	64.4	62.4	61.5	68.8	64.6	+ 1.1
Month Mean	65.2	64.5	62.9	65.1	65.8	62.7	63.3	60.7	62.6	63.9	60.4	65.0	63.5	-
Diff. from overall mean	+1.7	+1.0	-0.6	+1.6	+2.3	-0.8	-0.2	-2.8	-0.9	+0.4	-3.1	+1.5	-	-
Quarter mean	64.2			64.5			62.2			63.1				

Appendix 4.

Overall "conception" rates for all first inseminations during each calendar month at Dumfries

	JAN.	FEB.	MAR.	APR.	MAY	JUN.	JUL.	AUG.	SEP.	OCT.	NOV.	DEC.	Annual Mean	Diff. from overall mean
1948	58.4	63.5	55.6	64.5	61.3	64.6	55.6	65.8	60.3	60.0	65.0	65.7	61.7	- 1.5
1949	63.4	69.5	65.6	59.6	61.4	60.3	61.2	58.8	60.4	68.2	65.7	57.6	62.6	- 0.6
1950	68.6	60.3	64.5	63.6	63.4	60.9	62.4	62.2	65.5	72.3	68.1	70.6	65.2	+ 2.0
Month mean	63.5	64.4	61.9	62.6	62.0	61.9	59.7	62.3	62.1	66.8	66.3	64.6	63.2	-
Diff. from overall mean	+0.3	+1.2	-1.3	-0.6	-1.2	-1.3	-3.5	-0.9	-1.1	+3.6	+3.1	+1.4	-	-
Quarter Mean	63.8			62.2			61.4			65.9				

Appendix 5.

Monthly mean "conception" rates for first inseminations of 12 consistently used bulls during a twelve-month period in Somerset.

BULL	BREED	'47 OCT.	'47 NOV.	'47 DEC.	'48 JAN.	'48 FEB.	'48 MAR.	'48 APR.	'48 MAY	'48 JUN.	'48 JUL.	'48 AUG.	'48 SEP.	Mean & 5 % f.i.
FBK	Shorthorn	67.3	66.7	65.6	60.7	63.1	67.2	65.5	64.4	64.4	63.9	62.5	69.0	65.19 ± 1.50
WLY	"	64.4	65.2	55.9	62.4	65.6	57.0	72.8	66.2	65.2	68.9	47.9	76.9	64.03 ± 4.90
EMC	"	58.1	68.1	67.6	65.2	67.9	59.6	53.6	67.0	58.4	63.0	55.6	58.4	61.88 ± 3.31
SLC	"	68.6	67.7	68.8	64.4	63.8	66.1	57.6	57.6	58.6	56.1	64.1	72.7	63.84 ± 3.38
EMF	"	70.0	69.2	57.3	66.1	58.5	62.3	66.2	66.4	64.7	59.3	58.7	66.2	63.74 ± 2.78
KD	Friesian	62.8	66.4	59.5	47.5	40.6	45.8	65.2	74.6	62.7	62.1	88.3	-	61.41 ± 9.05
LW	"	65.6	71.4	66.7	65.2	65.2	67.5	70.6	67.6	66.8	61.5	59.8	64.7	66.05 ± 2.08
CPW	"	72.2	64.7	67.1	65.8	66.5	65.3	56.6	64.4	60.0	49.2	60.0	62.9	62.89 ± 3.74
BF	"	65.8	74.4	72.8	70.1	65.3	62.5	63.8	65.8	64.7	72.0	64.9	69.7	67.65 ± 2.51
RJ	"	64.7	80.0	68.8	66.0	64.9	65.3	71.5	48.3	64.3	62.6	58.4	66.7	65.13 ± 4.75
BPD	Guernsey	56.3	59.8	66.3	65.0	67.7	69.7	59.0	63.5	61.5	63.6	69.1	60.9	63.53 ± 2.67
HD	"	62.4	67.1	67.3	66.4	55.0	56.4	60.6	58.6	53.2	52.0	68.1	70.2	61.44 ± 4.04
Overall month mean		64.9	68.4	65.3	63.7	62.0	62.1	63.6	63.7	62.2	61.2	63.1	67.1	63.92
Quarter-mean		66.2			62.6			63.2			63.7			
Diff. from overall mean		+1.0	+4.5	+1.4	-0.2	-1.9	-1.8	-0.3	-0.2	-1.7	-2.7	-0.8	+3.2	

Appendix 6.

"Conception rates" resulting from first inseminations carried out at different "service periods" post-partum, and classified by artificial insemination centre.

Service Period (Days)	Somerset		Cambridge		Reading		Dumfries		Hampshire			
	No. of insems.	Concept. rates.	No. of insems.	Concept. rates.	No. of insems.	Concept. rates.	No. of insems.	Concept. rates.	No. of insems.	Concept. rates.	No. of insems.	Conception rates.
11-20	8	12.50	15	6.67	4	50.00	2	0.00	3	0.00	6	0.00
21-26	40	15.00	30	13.33	20	25.00	6	50.00	8	0.00	10	50.00
27-32	68	30.88	33	33.33	28	42.86	12	33.33	10	30.00	20	40.00
33-38	87	36.78	45	26.67	29	44.83	15	33.33	16	37.50	16	43.75
39-44	91	45.05	59	35.59	45	44.44	26	57.69	11	45.45	15	46.67
45-50	126	52.38	77	46.75	53	52.83	33	45.45	16	37.50	19	57.89
51-56	117	58.12	63	41.27	57	59.64	42	54.76	27	44.44	28	64.28
57-62	114	55.26	(57-60)		59	62.71	39	51.28	23	52.17	23	69.57
63-68	101	62.38	18	44.44	64	56.25	52	82.69	22	40.91	21	71.43
69-74	131	68.70	(61-90)		53	54.72	50	60.00	25	56.00	29	48.28
75-80	92	71.74			54	48.15	37	59.46	18	16.67	20	45.00
81-86	93	67.74			54	57.41	43	69.77	22	50.00	17	70.59
87-90	59	62.71			39	58.97	21	66.66	5	80.00	8	62.50
91-120	218	56.42	103	37.86	131	57.25	97	67.01	44	52.27	43	60.47
121-150	64	59.38	34	38.24	47	57.45	34	58.82	16	43.75	9	55.56
151-200	85	50.59	38	39.47	19	57.89	24	50.00	3	66.67	13	61.54
TOTAL	1494		753		756		533		269		297	
Percentage inseminated <50 days	28.11 %		34.40 %		23.68 %		17.64 %		23.79 %		28.96 %	

Appendix 7.

Estimations of incidence of insemination failures, among cows submitted for insemination, classified according to the number of seasons during which the cows have been inseminated.

(SOMERSET DATA)

No. of insems seasons "z"	DAMS GROUP (selected breeders)					DAUGHTERS GROUP (unselected)				
	No. of cows having		% of cows having			No. of cows		% of cows having "z"		
	"z" or more		"z" or more seasons			having		or more seasons		
	"z" seasons	"z" or more seasons	"barren" during season "z"	"failed to conceive during season "z"	Total unsucc- essful	"z" seasons	"z" or more seasons	"barren"	"fai- led to con- ceive" during season "z"	Total unsuc- cess- ful.
1	171	887	-	2.37	2.37	399	571	3.50	3.15	6.65
2	237	716	2.24	1.96	4.20	138	172	4.65	1.74	6.39
3	221	479	3.97	3.13	7.10	29	34	5.88	-	5.88
4	153	258	7.36	2.71	10.07	4	5	-	-	-
5	69	105	2.86	0.95	3.81	1	1	-	-	-
6	29	36	5.56	-	5.56					
7	7	7	14.30	-	14.30					
Regressions of % failures on insemination seasons			b=+0.533 ±2.195NS		b= +0.291 ±1.491NS			b= +1.190		b= -0.385

Appendix 8.

Estimations of incidence of insemination failures, among cows submitted for insemination, classified according to the number of seasons during which the cows have been inseminated.

(CAMBRIDGE DATA)

No. of insem. seasons "2"	DAMS GROUP (selected breeders)					DAUGHTERS GROUP (unselected)				
	No. of cows having		% of cows having "2" or more seasons			No. of cows having		% of cows having "2" or more seasons		
	"2"	"2" or more seasons	"barren"	"failed to conceive"	Total unsuc- cessful	"2"	"2" or more seasons	"barren"	"failed to conceive"	Total unsuccessful
	seasons		- during season "2"			seasons		during season "2"		
1	31	293	-	1.37	1.37	126	256	5.86	4.20	10.06
2	68	262	2.29	0.76	3.05	78	130	7.70	0.77	8.47
3	52	194	2.06	2.06	4.12	37	52	3.85	-	3.85
4	60	142	5.64	2.11	7.75	12	15	-	-	-
5	45	82	4.38	2.44	6.82	3	3	-	-	-
6	23	37	5.41	8.11	13.52					
7	9	14	7.15	-	7.15					
8	4	5	20.00	-	20.00					
over 8	1	1	-	-	-					
Regressions of % failures on insem- ination seasons			b = +0.856 ^{NS} ±1.187		b = +1.241 ^{NS} ±1.722			b = -1.005		b = - 3.055

Appendix 9.

Estimations of incidence of insemination failures, among cows submitted for insemination, classified according to the number of seasons during which the cows have been inseminated.

(READING DATA)

No. of insem. sea- sons "z"	DAMS GROUP (selected breeders)					DAUGHTERS GROUP (unselected)				
	No. of cows having		% of cows having "z" or more seasons			No. of cows having		% of cows having "z" or more seasons		
	"z" sea- sons	"z" or more seasons	"barren"	"failed to conceive"	Total unsuc- cessful	"z" sea- sons	"z" or more seasons	"barren"	"failed to conceive"	Total unsuccessful
1	27	211	-	0.47	0.47	79	218	0.46	1.84	2.30
2	38	184	-	1.63	1.63	75	139	3.60	1.44	4.04
3	47	146	-	2.74	2.74	50	64	4.69	1.56	6.25
4	37	99	-	5.06	5.06	13	14	-	-	-
5	36	62	4.84	3.23	8.07	1	1	-	-	-
6	14	26	-	3.85	3.85					
7	6	12	-	8.33	8.33					
8	5	6	-	-	-					
over 8	1	1	-	-	-					
Regressions of % failure on insem- ination seasons					b = +0.652 ±1.242 ^{NS}			b = +2.115		b = +1.975

Appendix 10.

Annual means of monthly-mean conception rates (first services, third month non-returns) of the principal bulls used each year at the Cambridge centre.

Year	Bull	No. of months used	Annual Mean of monthly C.Rs	Change from previous year.	Age
1944	KH	7	60.9 $\pm$ 7.1	-	6
	TF	7	69.3 $\pm$ 9.8	-	4
	HRL	7	67.6 $\pm$ 3.5	-	?
	HDK	6	60.7 $\pm$ 12.9	-	3
1945	KH	10 ^x	68.2 $\pm$ 5.3	+ 7.3	7
	TF	10 ^x	74.9 $\pm$ 4.1	+ 5.6	5
	HRP	10 ^x	69.8 $\pm$ 3.6	-	5
	TOP	7 ^x	71.9 $\pm$ 6.7	-	2
	OSB	10 ^x	66.3 $\pm$ 5.4	-	9
1946	TF	12	63.2 $\pm$ 4.0	- 5.0	6
	TOP	12	58.4 $\pm$ 3.3	-13.5	3
	OSB	12	64.0 $\pm$ 3.9	$\pm$ 2.3	10
	HP	12	68.6 $\pm$ 5.6	-	?
1947	TF	12	62.2 $\pm$ 5.8	- 1.0	7
	TOP	12	61.5 $\pm$ 6.7	+ 3.1	4
	OSB	12	56.4 $\pm$ 4.1	- 7.6	11
	HP	12	63.0 $\pm$ 5.1	- 5.6	?
	LH	12	63.2 $\pm$ 6.8	-	4
	OWE	12	59.8 $\pm$ 10.7	-	10
	BB	7	53.9 $\pm$ 13.8	-	4

cont....

Appendix 10 - continued.

1948	TF	11	62.7 ± 6.9	+ 0.5	8
	TOP	7	64.0 ± 10.8	+ 2.5	5
	OWE	11	64.2 ± 7.9	+ 4.4	11
	TN	10	59.9 ± 8.4	-	5
	LS	8	64.5 ± 5.0	-	4
	FA	12	70.1 ± 5.1	-	3
	HWP	10	63.7 ± 3.1	-	6
	HDD	7	61.0 ± 7.2	-	4
1949	TF	8	46.0 ± 16.5	- 16.7	9
	OWE	12	61.8 ± 5.4	- 2.4	12
	FA	12	71.3 ± 7.5	+ 1.2	4
	BB	9	69.0 ± 4.6	-	6
	BSJ	8	64.8 ± 12.1	-	2
	ICL	10	69.3 ± 3.1	-	7
	TSC	8	67.4 ± 8.0	-	3
1950	OWE	9	75.6 ± 4.5	+ 13.8	13
	BB	9	71.3 ± 6.9	+ 2.3	7
	ICL	8	65.6 ± 11.6	- 3.7	8
	TSC	9	67.8 ± 4.8	+ 0.4	4
	FM	6	73.8 ± 8.2	-	2
	SIS	8	70.1 ± 9.1	-	3
	LS	10	73.4 ± 2.9	-	6
	HDK	10	70.0 ± 4.6	-	9
	HL	6	70.5 ± 6.5	-	5

x 2 months' records missing.

Appendix 11.

Annual means of monthly-mean conception rates (first services, 16 weeks non-returns) of the principal bulls used each year at the Reading centre.

Year	Bull	No. of months used	Annual mean of monthly C.Rs.	Change from previous year.	Age
1945	BLW	7	68.7 $\pm$ 10.0	-	3
	LMP	9	66.6 $\pm$ 8.1	-	6
	LC	7	60.9 $\pm$ 8.3	-	2
	WR	9	71.7 $\pm$ 4.7	-	2
	DS	8	69.6 $\pm$ 5.6	-	5
	BA	9	70.9 $\pm$ 8.1	-	2
	GDGR	10	66.7 $\pm$ 9.9	-	3
1946	LMP	12	65.7 $\pm$ 3.9	- 0.9	7
	LC	8	55.9 $\pm$ 15.7	- 5.0	3
	WR	11	64.8 $\pm$ 4.7	- 6.9	3
	DS	11	61.1 $\pm$ 5.3	- 8.5	6
	BA	10	69.0 $\pm$ 3.9	- 1.9	3
	GDGR	10	65.3 $\pm$ 3.3	- 3.4	4
	MLD 20	7	64.6 $\pm$ 10.6	-	4
	RF	11	56.1 $\pm$ 8.3	-	7
	SCJ	11	65.4 $\pm$ 9.5	-	7
1947	LMP	11	69.1 $\pm$ 3.8	+ 6.6	8
	WR	12	69.8 $\pm$ 3.5	$\pm$ 5.0	4
	DS	11	71.5 $\pm$ 5.6	+ 10.4	7
	BA	12	71.7 $\pm$ 5.7	+ 2.7	4
	GDGR	11	66.8 $\pm$ 6.3	+ 3.5	5
	RF	11	62.7 $\pm$ 7.6	+ 6.6	8
	SCJ	12	62.1 $\pm$ 8.9	- 3.1	8
	MLD 15.	9	69.3 $\pm$ 4.8	-	7
	KCr	8	57.1 $\pm$ 10.2	-	2

Appendix 11 (cont.)

1948	LMP	12	64.0 ± 3.4	- 5.1	9
	WR	12	68.0 ± 3.3	- 1.8	5
	DS	7	50.3 ± 12.3	- 21.2	8
	BA	10	58.8 ± 10.9	- 12.9	5
	RF	8	42.4 ± 15.4	- 20.3	9
	MLD 15.	11	61.8 ± 5.2	- 7.5	3
	SRA	8	48.1 ± 10.6	-	3
	HA	8	40.4 ± 8.0	-	5
	TRD	11	51.6 ± 6.7	-	2
	KGM	12	48.7 ± 6.1	-	6
	RBT	7	68.6 ± 8.6	-	1
	GI	7	44.3 ± 16.6	-	5
1949	LMP	12	65.9 ± 6.4	+ 1.9	10
	WR	12	70.8 ± 2.7	+ 2.8	6
	BA	7	58.9 ± 7.8	+ 0.1	6
	MLD. 15.	12	68.1 ± 6.2	+ 6.3	9
	SRA	11	55.8 ± 7.8	+ 7.7	4
	TRD	8	57.3 ± 11.8	+ 5.7	3
	KGM	11	50.8 ± 5.9	+ 2.1	7
	RBT	11	65.0 ± 5.1	- 5.6	2
	RD. 8	10	64.6 ± 11.3	-	2
	HBC	12	65.4 ± 8.0	-	4
	SN	12	55.4 ± 8.8	-	5
	WVO	8	53.6 ± 11.3	-	4
1950	WR.	9	71.6 ± 3.0	+ 0.8	7
	BA	7	64.3 ± 8.9	+ 5.4	7
	MLD. 15.	9	63.1 ± 10.9	- 5.0	10
	RBT	8	72.9 ± 5.0	+ 7.9	3
	RD. 8.	9	65.6 ± 11.5	+ 1.0	3
	HBC	7	59.6 ± 5.8	- 5.8	5
	SN	8	69.4 ± 11.8	+ 13.6	6
	WVO	8	65.9 ± 10.9	+ 12.3	5
	HVP	8	61.3 ± 10.0	-	6

Appendix 12.

Effect of interval between time of first observation of oestrus and insemination on the 90-day "non-return" rate for first inseminations at the Dumfries centre.

1950-51	Intervals from notification of oestrus to insemination															Total			
Month	1-4 hours			5-8 hours			9-12 hours			13-16 hours			17-20 hours			21-24 hours			of angles
	Insems	C.R.	Angle	Insems	C.R.	Angle	Insems	C.R.	Angle	Insems	C.R.	Angle	Insems	C.R.	Angle	Insems	C.R.	Angle	
	%			%			%			%			%			%			
B L O C K N O. 1																			
Feb.	59	64.1	53.19	155	62.6	52.30	38	57.9	49.54	15	53.3	46.89	50	62.0	51.94	46	52.2	46.26	300.12
Mar.	30	36.7	37.29	131	68.0	55.55	39	66.7	54.76	31	64.5	53.43	50	70.0	56.79	36	55.6	48.22	306.04
Apr.	30	53.4	46.95	92	72.8	58.56	50	64.0	53.13	26	65.4	53.97	46	54.4	47.52	39	61.6	51.71	311.84
May	30	66.7	54.75	118	68.6	55.92	188	61.7	51.77	81	61.7	51.77	92	64.1	53.19	78	59.0	50.18	317.58
Jun.	54	53.0	46.72	92	64.2	53.25	227	57.3	49.20	86	67.5	55.24	82	62.2	52.06	39	64.1	53.19	309.66
Jul.	28	46.5	42.99	72	61.1	51.41	201	60.7	51.18	69	68.1	55.61	53	71.7	57.86	24	62.5	52.24	311.29
Aug.	21	71.4	57.67	54	53.7	47.12	169	62.7	52.36	59	67.8	55.43	57	61.4	51.59	13	53.8	47.18	311.35
Sep.	14	42.8	40.86	45	68.9	56.11	113	64.6	53.49	42	66.7	54.76	44	70.5	57.10	6	66.7	54.76	317.08
Sum	226		380.42	759		430.22	1025		415.43	409		427.10	474		428.05	281		403.74	2484.96
Mean		54.3	47.55		65.0	53.78		62.0	51.93		64.4	53.39		64.5	53.51		59.4	50.47	
B L O C K N O. 2.																			
Oct.	9	66.7	54.76	44	77.3	61.55	98	71.4	57.67	37	73.0	58.69	52	73.1	58.76	20	65.0	53.73	345.16
Nov.	13	76.9	61.27	104	75.0	60.00	121	71.9	57.99	68	73.6	59.08	61	68.9	56.11	21	61.9	51.88	346.33
Dec.	48	68.8	56.04	184	73.4	58.95	148	71.0	57.42	57	73.7	59.15	58	62.1	52.00	56	67.9	55.49	339.05
Jan.	42	78.6	63.44	226	77.9	61.96	145	71.7	57.86	85	62.4	52.18	77	70.1	56.85	66	74.2	59.47	351.76
Feb.	33	72.7	58.50	147	75.5	60.33	112	68.7	55.98	54	74.1	59.41	60	73.3	58.89	40	60.0	50.77	343.88
Mar.	25	56.0	48.45	141	71.6	57.80	100	70.0	56.79	25	64.0	53.13	63	69.8	56.66	30	66.7	54.76	327.59
Sum	170		342.46	846		360.59	724		343.71	326		341.64	371		339.27	233		326.10	2053.77
Mean		69.9	57.08		75.1	60.10		69.1	57.29		70.1	56.94		69.5	56.55		65.9	54.35	
B L O C K S N O S. 1 & 2.																			
Overall sum	396		722.8	1605		790.81	1749		758.14	735		768.74	845		767.32	514		729.84	4537.73
Overall mean		61.6	51.63		69.6	56.49		65.7	54.15		65.7	54.91		66.9	54.81		63.0	52.13	
Distribution of inseminations		6.8%			27.6%			28.3%			11.8%			13.9%			8.8%		2.8% over 24 hours.

Appendix 15.

Analyses of Variance and Covariance among daughters (NOT AGE CORRECTED) and their dams, of the mean number of inseminations required to achieve conception during all recorded seasons of the daughters and the first two recorded seasons of their dams.

Source of variation	d.f.	Dams' s.s.	Dams x Daughters s.p.	Daughters'			Dams'	
				S.S.	M.S.	F.	M.S.	F.
Total	948	470.4256	+ 3.1588	514.5043				
Centres	5	4.9677	+ 5.8566	13.2914	2.6583	5.474 XX	0.9935	2.057 NS
Breeds	3	0.7051	- 0.0044	4.2924	1.4308	2.946 X	0.2350	0.487 NS
Bulls	55	39.7504	+ 7.8546	69.8179	1.2694	2.614 XX	0.7227	1.496 X
Cows within subgroups	880	425.0024	-10.5480	427.1026	0.4853		0.4830	
Regression Daughters within sub- groups adjusted for regression.	1 879			0.2617 426.8409	0.2617 0.4856	0.539 NS		
Regression of daughters on dams within subgroups $b = - 0.0248 \pm 0.0664$ (5 % fiducial limits) $S_b = 0.0338$								
	Estimated k.	Variance	Percentage of variance		Heritability Estimates			
			within breeds & centres.	in general				
Centres	140.289	0.0099	1.823	-	From daughter-dam regression Nil From paternal half-sibs. $h^2 = \frac{8.656}{2.57} = 33.68 \%$			
Breeds	210.495	0.0008	0.147	-				
Bulls	16.692	0.0470	8.656	8.830				
Cows		0.4853	89.374	91.170				
Total		0.5430	100.000	100.000				

Appendix 14.

Analyses of Variance and Covariance among daughters (NOT AGE-CORRECTED) and their dams, of the mean number of inseminations required to achieve conception during all recorded seasons of the daughters and the first three recorded seasons of their dams.

Source of variation	d.f.	Dams' s.s.	Dams x Daughters s.p.	Daughters			Dams'	
				s.s.	m.s.	F.	m.s.	F.
Total	577	201.9483	+ 21.8417	335.1922				
Centres	5	6.5258	+ 5.6615	6.0424	1.2085	2.188 NS	1.3052	3.933 XX
Breeds	3	0.8816	+ 0.7245	3.8546	1.2849	2.326 NS	0.2939	0.886 NS.
Bulls	44	20.5006	+ 5.8204	35.2767	0.8017	1.451 X	0.4614	1.390 NS.
Cows within subgroups	525	174.2403	+ 9.6355	290.0185	0.5524		0.3319	
Regression	1			0.5328	0.5328	0.964 NS		
Daughters within subgroups adjusted for regression	524			289.4857	0.5525			
Regression of daughters on dams within subgroups $b = + 0.0553 \pm 0.1107$ (5 % fiducial limits) Sb = 0.0563								
	Estimated k	Variance	Percentage of variance		Heritability Estimates			
			within breeds & centres.	in general				
Centres	82.050	0.0050	0.866	-	From daughter-dam regression $h^2 = 11.06 \%$ From paternal half-sibs $h^2 = \frac{2.822}{0.261} = 10.81 \%$			
Breeds	121.698	0.0040	0.692	-				
Bulls	12.700	0.0163	2.822	2.866				
Cows		0.5524	95.621	97.154				
Total		0.5777	100.001	100.000				

Appendix 15.

Analyses of Variance and Covariance among daughters (NOT AGE-CORRECTED) and their dams, of the mean number of inseminations required to achieve conception during all recorded seasons of the daughters and four or more recorded seasons of their dams.

Source of variation	d.f.	Dams' s.s.	Dams x Daughters s.p.	Daughters			Dams	
				s.s.	m.s.	F.	m.s.	F.
Total	289	64.7188	+ 9.2328	151.6502				
Centres	2	2.0235	+ 0.8615	0.7886	0.3943	0.747 NS	1.0118	4.667 ^K
Breeds	2	0.5033	- 0.2727	0.6950	0.3475	0.658 NS	0.2517	1.161 NS
Bulls	29	6.7014	+ 0.7547	14.9754	0.5164	0.978 NS	0.2311	1.066 NS
Cows within subgroups	256	55.4906	+ 7.8893	135.1912	0.5281		0.2168	
Regression	1			1.1216	1.1216	2.133 NS.		
Daughters within subgroups adjusted for regression	255			134.0696	0.5258			
Regression of daughters on dams within subgroups $b = + 0.1422 + 0.1918$ (5 % fiducial limits) $S_b = 0.0973$								
	Estimated k	Variance	Percentage of variance		Heritability Estimates			
			within breeds & centres.	in general				
Centres	86.279	- 0.0016 (Nil)	Nil	-	From daughter-dam regression $h^2 = 28.44 \%$			
Breeds	83.217	- 0.0022 (Nil)	Nil	-				
Bulls	9.585	- 0.0012 (Nil)	Nil	Nil	From paternal half-sibs Nil.			
Cows		0.5281	100.000	100.00				
Total		0.5281	100.00	100.000				

Appendix 16.

Analyses of Variance and Covariance among daughters (AGE CORRECTED) and their dams, of the number of inseminations required to achieve conception during their first seasons of insemination.

Source of variation	d.f.	Dams' s.s.	Dams x Daughters s.p.	Daughters'			Dams'	
				s.s.	m.s.	F.	m.s.	F.
Total	1230	941.7401	+15.7700	898.9057				
Centres	5	4.6054	+ 0.0019	15.2561	3.0512	4.370 ^{xx}	0.9211	1.2145 NS.
Breeds	3	1.1346	+ 1.3300	4.2186	1.0729	1.537 ^{NS}	0.3782	0.4987 NS
Bulls	56	51.7159	+ 6.5500	65.3335	1.1667	1.671 ^{xx}	0.9235	1.218 NS
Cows within subgroups	1166	884.2842	+ 7.8881	814.0975	0.6982		0.7584	
Regression Daughters within subgroups adjusted for regression	1			0.0704	0.0704	0.101 ^{NS}		
	1165			814.0271	0.6987			
Regression of daughters on dams within subgroups b = + 0.0089 ± 0.0551 (5% fiducial limits) Sb = 0.0281								
	Estimated k	Variance	Percentage of variance		Heritability Estimates			
			within breeds and centres.	in general				
Centres	181.018	0.0104	1.424	-	From daughter dam regression			
Breeds	276.725	-0.0003 (Nil)	Nil	-	h ² = 1.78 %			
Bulls	21.370	0.0219	2.998	3.041	From paternal half-sibs			
Cows		0.6982	95.578	96.959	h ² = $\frac{2.998}{.255}$ = 11.76 %			
Total		0.7305	100.000	100.000				

Appendix 17.

Analyses of Variance and Covariance among daughters (AGE CORRECTED) and their dams, of the mean number of inseminations required to achieve conception during all recorded seasons of the daughters and the first two recorded seasons of their dams.

Source of variation	d.f.	Dams'	Dams x Daughters	Daughters'			Dams'	
		S.S.	S.P.	S.S.	m.s.	F.	m.s.	F.
Total	945	470.4256	+ 2.5822	511.0390				
Centres	5	4.9677	+ 5.3986	10.7058	2.1412	4.500 ^{xx}	0.9935	2.057 NS
Breeds	3	0.7051	+ 0.0306	4.7928	1.5976	3.209 ^x	0.2350	0.487 NS
Bulls	55	39.7504	+ 8.2373	57.3908	1.0435	2.096 ^{xx}	0.7227	1.496 x
Cows within subgroups	880	425.0024	-11.0843	458.1496	0.4979		0.4830	
Regression Daughters within subgroups adjusted for regression	1			0.2890	0.2890	0.580 ^{NS}		
	879			437.1026	0.4981			
Regression of daughters on dams within subgroups. $b = -0.0261 \pm 0.0672$ (5% fiducial limits) $S_b = 0.0342$								
	Estimated k.	Variance	Percentage of variance		Heritability Estimates			
			within breeds & centres.	in general				
Centres	140.289	0.0078	1.442		From daughter-dam regression Nil. From paternal half-sibs $h^2 = \frac{6.044}{2.57} = 23.52 \%$			
Breeds	210.495	0.0026	0.481					
Bulls	16.692	0.0327	6.044	6.163				
Cows		0.4979	92.033	93.837				
Regression								
Total		0.5410	100.000	100.000				

Appendix 18.

Analyses of Variance and Covariance among daughters (AGE CORRECTED) and their dams, of the mean number of inseminations required to achieve conception during all recorded seasons of daughters and the first three recorded seasons of their dams.

Source of variation	d.f.	Dams' s.s.	Dams x Daughters S.D.	Daughters'			Dams'	
				s.s.	m.s.	F.	m.s.	F.
Total	577	202.5828	+ 15.1508	343.0758				
Centres	5	6.3094	+ 5.1975	4.8848	0.9770	1.709 ^{NS}	1.2619	3.772 ^{XX}
Breeds	3	0.7621	+ 0.7949	4.3105	1.4368	2.514 ^{NS}	0.2540	0.759 ^{NS}
Bulls	44	19.8815	+ 6.4278	33.8429	0.7692	1.359 ^{NS}	0.4519	1.351 ^{NS}
Cows within subgroups	525	175.6298	+ 2.7306	300.0376	0.5715		0.3345.	
Regression Daughters within subgroups adjusted for regression	1			0.0424	0.0424			
	524			299.9952	0.5725			
Regression of daughters on dams within subgroups				b = + 0.0155 ± 0.1122 (5 % fiducial limits) Sb = 0.0571				
	Estimated k	Variance	Percentage of variance		Heritability Estimates			
			within breeds and centres	in general				
Centres	82.030	0.0025	0.420	-	From daughters-dam regression $h^2 = 3.10 \%$			
Breeds	121.698	0.0055	0.924					
Bulls	12.700	0.0156	2.621	2.657	From paternal half-sibs $h^2 = \frac{2.621}{0.261} = 10.04 \%$			
Cows		0.5715	96.034	97.343				
Total		0.5951	99.999	100.000				

Appendix 19.

Analyses of Variance and Covariance among daughters (AGE CORRECTED) and their mean/
dams, of the/number of inseminations required to achieve conception during all recorded seasons of the daughters and four or more recorded seasons of their dams.

Source of variation	d.f.	Dams' s.s.	Dams x daughters s.p.	Daughters			Dams'	
				s.s.	m.s.	F	m.s.	F.
Total	289	64.7188	+ 10.4368	164.1311				
Centres	2	2.0235	+ 0.7007	0.7504	0.3752	0.659 ^{NS}	1.0118	4.667 ^X
Breeds	2	0.5033	+ 0.3082	0.8663	0.4332	0.761 ^{NS}	0.2517	1.161 ^{NS}
Bulls	29	6.7014	+ 2.1387	16.6849	0.5753	1.011 ^{NS}	0.2311	1.066 ^{NS}
Cows within subgroups	256	55.4906	+ 7.2892	145.8295	0.5691		0.2168	
Regression Daughters within subgroups adjusted for regression	1			0.9575	0.9575	1.685 ^{NS}		
	255			144.8720	0.5681			
Regression of daughters on dams within subgroups				b = + 0.1314 ± 0.1993 (5% fiducial limits) Sb = 0.1012				
	Estimated k	Variance	Percentage of variance		Heritability Estimates			
			within breeds and centres	in general				
Centres	86.279	-0.0023(N11)	-	-	From daughter-dam regression $h^2 = 26.23 \%$			
Breeds	83.217	-0.0017(N11)	-	-				
Bulls	9.585	0.0006	0.105	0.105				
Cows		0.5691	99.895	99.895	From paternal half-sibs $h^2 = \frac{0.105}{0.268} = 0.39 \%$			
Total		0.5697	100.000	100.000				

Appendix 20.

Analyses of Variance and Covariance among daughters (AGE CORRECTED) and their dams, of the mean number of inseminations required to achieve conception during all recorded seasons of the daughters and the single recorded season available for their dams.

Source of variation	d.f.	Dams'	Dams x	Daughters'			Dams'	
		s.s.	Daughters s.p.	s.s.	m.s.	F	ms.	F.
Total	241	152.4339	+13.6645	163.9430				
Centres	5	3.2748	- 0.3241	3.4355	0.6871	0.989 ^{NS}	0.6550	1.104 ^{NS}
Breeds	3	7.2114	+ 2.3343	2.5893	0.8631	1.242 ^{NS}	2.4038	4.050 ^{xx}
Bulls	26	19.1000	+ 4.9960	14.4598	0.5561	0.801 ^{NS}	0.7346	1.238 ^{NS}
Cows within sub-groups	207	122.8477	+ 6.6583	143.4584	0.6930		0.5935	
Regression Daughters within subgroups adjusted for re-gression	1			0.3608	0.3608	0.519 ^{NS}		
	206			143.0976	0.6946			
Regression of daughters on dams within subgroups $b = + 0.0542 \pm 0.1483$ (5% fiducial limits) $S_b = 0.0752$								
	Estimated k	Variance	Percentage of variance		Heritability Estimates			
			within breeds & centres	in general				
Centres	29.1769	- 0.0002(Nil)	Nil	-	From daughter-dam regression $h^2 = 10.84 \%$			
Breeds	55.2727	0.0031	0.445	-				
Bulls	8.8430	- 0.0155(Nil)	Nil	Nil	From paternal half-sibs.			
Cows		0.6930	99.555	100.000				
Total		0.6961	100.000	100.000				

Appendix 21.

Analyses of Variance and Covariance among daughters (AGE CORRECTED) and their dams, of the mean number of inseminations required to achieve conception during all recorded seasons of the daughters and the two recorded seasons available for their dams.

Source of Variation	d.f.	Dams' ~~xxx~~ s.s.	Dams x Daughters s.p.	Daughters'			Dams'	
				s.s.	m.s.	F	m.s.	F.
Total	303	164.1242	+14.8251	152.6039				
Centres	5	2.2585	+ 2.9242	6.4677	1.2935	3.127 ^{xx}	0.4517	0.833 ^{NS}
Breeds	3	0.6741	- 0.2156	0.5899	0.1966	0.475 ^{NS}	0.2247	0.414 ^{NS}
Bulls	33	19.6274	+ 8.2640	17.4870	0.5299	1.281 ^{NS}	0.5948	1.097 ^{NS}
Cows within subgroups	262	141.5642	+ 3.8525	108.0593	0.4124		0.5424	
Regression Daughters within subgroups adjusted for regression	1			0.1048	0.1048	0.253 ^{NS}		
	261			107.9545	0.4136			
Regression of daughters on dams within subgroups $b = + 0.0272 \pm 0.1065$ (5% fiducial limits) $S_b = 0.0541$								
	Estimated k	Variance	Percentage of variance		Heritability Estimates			
			within breeds and centres.	in general				
Centres	44.6803	0.00171	3.862	-	From daughter-dam regression $h^2 = 5.44 \%$			
Breeds	71.0241	-0.0047(N11)	N11	-				
Bulls	8.8551	0.0133	3.004	3.124	From paternal half-sibs $h^2 = \frac{3.004}{3.124} = 12.02 \%$			
Cows		0.4124	93.135	96.876				
Total		0.4428	100.001	100.000	0.25			

Appendix 22.

Analyses of Variance and Covariance among daughters (AGE CORRECTED) and their dams, of the mean number of inseminations required to achieve conception during all available seasons of the daughters and the three recorded seasons available for their dams.

Source of Variation	d.f.	Dams' s.s.	Dams x Daughters s.p.	Daughters'			Dams'	
				~~XXXXX~~ S.S.	m.s.	F.	m.s.	F.
Total	215	103.1801	+9.7422	147.0521				
Centres	4	9.4344	+8.4226	10.0209	2.5052	4.364 ^{XX}	2.3586	5.662 ^{XX}
Breeds	3	0.4173	+0.5524	2.4787	0.8262	1.439 ^{NS}	0.1393	0.334 ^{NS}
Bulls	24	16.6745	+5.1217	23.9345	1.2056	2.100 ^{XX}	0.6943	1.668 ^X
Cows within subgroups	184	76.6534	-4.3545	105.6180	0.5740		0.4166	
Regression Daughters with- in subgroups adjusted for regression	1			0.2473	0.2473	0.429 ^{NS}		
	183			105.3707	0.5758			
Regression of daughters on dams within subgroups $b = -0.0568 \pm 0.1710$ (5% fiducial limits) $s_b = 0.0867$								
	Estimated k	Variance	Percentage of variance		Heritability Estimates			
			within breeds & centres.	in general				
Centres	32.4259	0.0401	5.826	-	From daughter-dam regression $h^2 = \text{Nil}$			
Breeds	48.9599	-0.0077(Nil)	Nil					
Bulls	8.5116	0.0742	10.780	11.447	From paternal half-sibs. $h^2 = \frac{10.780}{.2558} = 42.14 \%$			
Cows		0.5740	83.394	88.553				
Total		0.6883	100.000	100.000				

Appendix 25.

Distribution of daughters by bull, breed of sire, and centre, shewing number of daughters per bull, total number of seasons recorded for all daughters of each bull and the mean number of inseminations required per insemination season for conception of all the daughters of each bull.

	Somerset				Cambridge				Reading				Dumfries				Hampshire				Worcester				Breed Totals				
SHORTHORN	Bull	Drs.	Seasons	Mean	Bull	Drs.	Seasons	Mean	Bull	Drs.	Seasons	Mean	Bull	Drs.	Seasons	Mean	Bull	Drs.	Seasons	Mean	Bull	Drs.	Seasons	Mean	Bulls	Drs.	Seasons	Mean	
	HPG	68	92	1.25	TOP	25	34	1.38	GP	28	49	1.43					RWR	12	16	1.37	RBP	15	35	1.57					
	WLY	53	70	1.39	HRP	24	35	1.57	BLW	19	41	1.34					WRD	8	11	1.82	WPP	15	38	1.18					
	EMC	48	57	1.33	HRL	22	39	1.59	MLD20	13	26	1.46					WWD	13	16	1.63									
	EMF	27	29	1.10	OSB	20	32	1.75	RF	11	22	1.45					BWE	10	15	1.27									
	MLF	25	31	1.32	HDK	11	28	1.61	WR	23	32	1.44																	
	WGD	24	40	1.55	OWE	7	9	1.44	MWP	5	14	1.36																	
	BWI	25	32	1.47	HP	10	11	1.82																					
	YGD	17	22	1.32																									
	FBK	6	7	1.14																									
	9	293	380	1.33	7	119	188	1.59	6	99	184	1.41					4	43	58	1.50	2	30	73	1.37	28	584	912	1.37	
FRIESIAN	KD	58	85	1.27	LH	7	7	1.00	BA	15	30	1.83									EER	24	69	1.41					
	CPW	42	53	1.43	KH	47	100	2.01													BB	9	25	1.20					
	BF	6	6	1.50	TF	43	76	1.47																					
	LW	79	99	1.44																									
	RJ	6	6	1.50																									
	TB	7	10	1.40																									
	6	198	259	1.39	3	100	183	1.75	1	15	30	1.83									2	33	94	1.35	12	346	566	1.52	
GUERNSEY	BPD	26	31	1.35					LMP	38	74	1.66					SDRL	8	9	1.56									
	HD	21	22	1.32					LC	10	14	1.86					TR	21	32	1.41									
									GDGR	13	17	1.76					DCC	24	39	1.64									
	2	47	53	1.34					TML	5	15	1.60																	
									4	66	120	1.69					3	53	80	1.54					9	166	253	1.57	
AYRSHIRE									BWF	21	36	1.72									HM	9	14	1.64					
									UTD	57	107	1.42									DS	5	6	2.67					
									BV	23	42	1.36																	
									LK	28	53	1.38																	
									HR	24	42	1.67																	
									RBI	24	39	1.62																	
									6	177	319	1.43									2	14	20	1.95	8	191	339	1.46	
Centre Totals	17	538	692	1.35	10	219	371	1.67	11	180	334	1.55	6	177	319	1.43	7	96	138	1.52	6	77	187	1.42	57	1287	2041	1.47	

Appendix 24. Mean number of inseminations required per conception by groups of daughters of individual bulls, and by their dams, during their first season of insemination. Grouped by centres and breed of sire.

	Somerset				Cambridge				Reading				Dumfries				Hampshire				Worcester				
	Mean				Mean				Mean				Mean				Mean				Mean				Breed
	Bulls	No.	Dms	Drs	Bulls	No.	Dms	Drs	Bulls	No.	Dms	Drs	Bulls	No.	Dms	Drs	Bulls	No.	Dms	Drs	Bulls	No.	Dms	Drs	Totals
SHORTHORN	HPG	68	1.24	1.51	TOP	30	1.20	1.52	GP	26	1.50	1.55					RWR	9	1.11	1.44	RBP	15	1.53	1.55	28 bulls
	WLY	53	1.62	1.34	HRP	24	1.71	1.79	BLW	19	1.53	1.32					WBD	5	1.40	2.40	WPP	15	1.33	1.00	569 pairs
	EMC	48	1.48	1.57	HRL	22	1.27	1.59	MLD	20	1.62	1.46					WWD	10	1.50	1.60				1.47 dams	
	EMF	27	1.37	1.11	OSB	20	1.80	1.55	RF	11	1.64	1.27					BWE	7	1.86	1.00				1.40 daughters	
	MLF	25	1.56	1.28	HDK	11	1.09	1.36	WR	23	2.00	1.35													
	WGD	24	1.46	1.46	OWE	7	1.14	1.57	MWP	4	3.50	1.75													
	BWI	25	1.48	1.40	HP	10	1.10	1.90																	
	YGD	17	1.18	1.41																					
	FBK	6	1.67	1.17																					
	9	293	1.43	1.33	7	119	1.59	1.61	6	96	1.74	1.36					4	31	1.45	1.55	2	30	1.33	1.27	
FRIESIAN	KD	58	1.41	1.26	LH	7	1.43	1.00	BA	15	1.80	1.80								EER	24	1.46	1.17	12 bulls	
	CPW	42	1.57	1.45	KH	47	1.45	2.02												BB	9	1.67	1.11	346 pairs	
	BF	6	2.00	1.50	TF	46	1.57	1.52																1.54 dams	
	LW	79	1.51	1.47																				1.49 daughters	
	RJ	6	2.00	1.50																					
	TB	7	2.29	1.43																					
6	198	1.55	1.40	3	100	1.50	1.72	1	15	1.80	1.80								2	33	1.52	1.15			
GUERNSEY	BPD	26	1.54	1.38					LMP	38	1.45	1.63					SDRL	6	1.83	1.50					9 bulls
	HD	21	1.38	1.33					LC	10	1.60	2.10					TR	15	1.40	1.67					44 pairs
									GDGR	12	1.50	1.33					DCC	23	1.61	1.74					1.57 dams
2	47	1.47	1.33					4	64	1.45	1.61					3	44	1.57	1.68					1.68 daughters.	
AYRSHIRE									BWF	20	1.75	1.80								HM	9	1.78	1.67	8 bulls	
									UTD	47	1.62	1.43								DS	5	1.20	3.00	161 pairs	
									BV	20	1.50	1.25												1.50 dams	
									LK	21	1.19	1.48												1.50 daughters.	
									HR	18	1.28	1.22													
									RBI	21	1.43	1.48													
									6	147	1.49	1.44								2	14	1.57	2.14		
Centre Totals	17	538	1.48	1.36	10	219	1.44	1.66	11	175	1.64	1.49	6	147	1.49	1.44	7	75	1.52	1.63	6	77	1.45	1.38	57 bulls 1231 pairs 1.50 dams 1.46 daughters.

Appendix 25.

Mean number of inseminations required per conception by groups of daughters of individual bulls (age-corrected and uncorrected), and by their dams, during all recorded seasons of the daughters and during the first two recorded seasons of their dams. Grouped by centres and breed of sire.

	Somerset	Cambridge	Reading	Dumfries	Hampshire	Worcester	Breed Totals
	Bulls Mean No.Dms. Drs. Drs.C	Bulls Mean No.Dms Drs Drs.C	Bulls Mean No.Dms Drs Drs C.	Bulls Mean No.Dms Drs Drs C.	Bulls Mean No. Dms Drs Drs C.	Bulls Mean No. Dms Drs Drs C.	
SHORTHORN	HPG 47 1.51 1.27 1.36 WLY 35 1.56 1.35 1.47 EMC 40 1.40 1.29 1.40 EMF 20 1.52 1.15 1.28 MLF 14 1.54 1.45 1.54 WGD 19 1.47 1.60 1.66 BWI 15 1.43 1.37 1.48 YGD 9 1.22 1.22 1.28 FBK 5 1.40 1.20 1.33	TOP 21 1.29 1.43 1.50 HRP 22 1.61 1.58 1.66 HRL 19 1.29 1.49 1.55 OSB 18 1.69 1.72 1.78 HDK 9 1.33 1.78 1.83 OWE 7 1.21 1.50 1.62 HP 8 1.31 1.31 1.41	GP 21 1.62 1.37 1.46 BLW 16 1.59 1.43 1.51 MLD 11 1.50 1.42 1.51 RF 11 1.91 1.38 1.46 WR 21 1.74 1.35 1.47 MWP 4 2.63 1.33 1.39		RWR 6 1.17 1.33 1.34 WBD 4 1.12 2.42 2.43 WWD 8 1.38 1.63 1.63 BWE 7 1.57 1.12 1.16	RBP 11 1.09 1.60 1.68 WPP 10 1.20 1.14 1.23	28 bulls 438 pairs 1.46 dams 1.40 daughters 1.56daughters(C)
	9 204 1.43 1.32 1.42	7 104 1.43 1.55 1.62	6 84 1.71 1.38 1.47		4 25 1.34 1.54 1.56	2 21 1.14 1.38 1.47	
FRIESIAN	KD 46 1.44 1.22 1.32 CPW 31 1.39 1.37 1.47 BF 6 2.08 1.50 1.64 LW 54 1.35 1.42 1.53 RJ 5 1.50 1.40 1.51 TB 6 1.50 1.42 1.51	LH 7 1.79 1.00 1.14 KH 41 1.61 2.07 2.15 TF 40 1.81 1.47 1.56	BA 13 1.77 1.40 1.47			EMR 20 1.25 1.37 1.45 BB 8 1.44 1.13 1.21	12 bulls 277 pairs 152 dams 1.46 daughters 1.56 daughters(C)
	6 148 1.45 1.35 1.45	3 88 1.71 1.71 1.80	1 13 1.77 1.40 1.47			2 28 1.30 1.30 1.38	
GUERNSEY	BPD 23 1.61 1.46 1.58 HD 16 1.31 1.31 1.45		LMP 36 1.29 1.64 1.73 LC. 9 1.50 2.18 2.30 GDGR 10 1.50 1.65 1.77 TML 4 1.12 1.50 1.57		DCC 16 1.56 1.69 1.75 TR. 11 1.77 1.68 1.74 ~~SPR 10 1.50 1.35 1.37~~ ~~TAT 12 1.12 1.30 1.33~~		8 bulls 125 pairs 1.46 dams 1.61 daughters 1.71 daughters(C)
	2 39 1.49 1.40 1.53		4 59 1.35 1.72 1.81		2 27 1.65 1.69 1.75		
AYRSHIRE			BWF 10 1.90 1.75 1.84 UTD 33 1.50 1.37 1.47 BV 13 1.38 1.17 1.27 LK 9 1.17 1.09 1.17 HR 15 1.30 1.13 1.24 RBI 12 1.25 1.67 1.77			HM 8 1.94 1.64 1.76 DS 4 1.50 3.00 3.14	8 bulls 104 pairs 1.47 dams 1.44 daughters 1.54daughters(C)
			6 92 1.43 1.36 1.45			2 12 1.79 2.09 2.22	
Centre Totals	17 391 1.45 1.34 1.44	10 192 1.56 1.62 1.70	11 156 1.58 1.51 1.60	6 92 1.43 1.36 1.45	6 52 1.50 1.62 1.65	6 61 1.34 1.48 1.57	56 bulls 944 pairs 1.48 dams 1.45 daughters 1.54 daughters(C)

Appendix 26.

Mean number of inseminations required per conception by groups of daughters of individual bulls, and by their dams, during all recorded seasons of the daughters and during the first three recorded seasons of their dams. Grouped by centres and breed of sire.

(Daughters age-corrected and uncorrected)

(Daughters age-corrected and uncorrected)																																
	Somerset					Cambridge					Reading					Dumfries					Hampshire					Worcester					Breed Totals	
	Bulls	No.	Dms	Drs	Drs C.	Bulls	No.	Dms	Drs	Drs C.	Bulls	No.	Dms	Drs	Drs C.	Bulls	No.	Dms	Drs	Drs C.	Bulls	No.	Dms	Drs	Drs C.	Bulls	No.	Dms	Drs	Drs C.		
SHORTHORN	HPG	26	1.32	1.25	1.33	TOP	16	1.44	1.38	1.44	GP	13	1.64	1.21	1.50						RWR	5	1.20	1.40	1.40	RBP	4	1.08	1.49	1.56	26 bulls. 288 pairs 1.50 dams 1.40 daughters 1.48 drs.(C)	
	WLY	18	1.56	1.56	1.67	KRP	18	1.76	1.60	1.69	BLW	9	1.37	1.17	1.25						WWD	5	1.60	1.40	1.43	WPP	4	1.34	1.23	1.32		
	EMC	25	1.33	1.26	1.36	HRL	13	1.38	1.45	1.51	MLD	9	1.41	1.41	1.49						BWE	4	1.50	1.00	1.00							
	EMF	12	1.50	1.17	1.30	OSB	14	1.93	1.32	1.39	RF	10	1.70	1.28	1.36																	
	HLF	9	1.45	1.56	1.64	EDK	9	1.44	1.73	1.33	WR	19	1.65	1.53	1.45																	
	WGD	12	1.56	1.64	1.68	OWE	4	1.42	1.38	1.50	MWP	4	2.16	1.33	1.39																	
	BWI	11	1.42	1.32	1.43	HP	6	1.45	1.42	1.50																						
	YGD	7	1.14	1.29	1.55																											
	8	120	1.41	1.36	1.45	7	80	1.59	1.56	1.64	6	64	1.62	1.29	1.38						3	14	1.43	1.29	1.50	2	8	1.21	1.56	1.44		
FRIESIAN	KD	32	1.41	1.24	1.34	LH	7	1.72	1.00	1.14	RA	13	1.69	1.40	1.47											EMR	4	1.33	1.64	1.72	8 bulls 180 pairs 1.55 dams 1.49 drs. 1.58 drs(C)	
	CPW	22	1.41	1.43	1.53	KH	31	1.65	2.12	2.19																						
	LF	33	1.39	1.44	1.55	TF	33	1.84	1.56	1.45																						
	3	92	1.40	1.37	1.47	3	71	1.74	1.66	1.74	1	13	1.69	1.40	1.47											1	4	1.33	1.64	1.72		
GUERNSEY	BPD	15	1.80	1.43	1.55						LMP	31	1.59	1.62	1.71						DCC	9	1.59	1.78	1.84						8 bulls 92 pairs 1.51 dams 1.62 drs. 1.72 drs(C)	
	HD	11	1.33	1.27	1.41						LC	7	1.53	2.09	2.21						TR	7	1.66	1.86	1.94							
												GDGR	8	1.54	1.69	1.80																
	2	26	1.61	1.37	1.49						4	50	1.41	1.69	1.78						2	16	1.62	1.81	1.88							
AYRSHIRE																UTD	8	1.42	1.22	1.51											8 bulls 20 pairs 1.35 dams. 1.35 drs. 1.45 drs(C)	
																HR	6	1.33	1.25	1.36												
																RBI	6	1.28	1.63	1.75												
																3	20	1.55	1.35	1.45												
Centre Totals	13	233	1.43	1.36	1.46	10	151	1.66	1.61	1.69	11	127	1.54	1.46	1.55	3	20	1.35	1.35	1.45	5	30	1.53	1.57	1.61	3	12	1.25	1.45	1.53	45 bulls 578 pairs 1.51 dams 1.46 drs 1.55 drs(C)	

Appendix 27.

Mean number of inseminations required per conception by groups of daughters of individual bulls, and by their dams, during all recorded seasons of the daughters and during four or more seasons of their dams. Grouped by centre and breed of sire.

(Daughters age-corrected and uncorrected)

Somerset					Cambridge				Reading				Breed Totals			
SHORTHORN	Mean				Mean				Mean							
	Bulls	No.	Dms	Drs	Drs C.	Bulls	No.	Dms	Drs	Drs(C)	Bulls	No.	Dms	Drs	Drs (C)	
	HPG	15	1.34	1.20	1.30	TOP	12	1.54	1.33	1.43	GP	8	1.73	1.08	1.18	19 bulls
	WLY	11	1.52	1.91	2.01	HRP	11	1.53	1.56	1.46	BLW	7	1.38	1.21	1.28	163 pairs
	EMC	12	1.46	1.42	1.51	HRL	10	1.64	1.55	1.60	MLD	8	1.31	1.46	1.54	1.55 dams
	EMF	4	1.75	1.50	1.62	OSB	9	1.75	1.66	1.75	RF	8	1.76	1.35	1.42	1.43 daughters
	MLF	4	1.40	1.25	1.36	HDK	7	1.68	1.64	1.69	WR	16	1.63	1.21	1.32	1.51 daughters(C)
	WGD	9	1.51	1.78	1.83	HP	4	1.50	1.63	1.68	MWP	4	1.98	1.33	1.39	
	BWI	4	1.21	1.25	1.36											
7	59	1.45	1.49	1.59	6	53	1.61	1.50	1.58	6	51	1.61	1.28	1.35		
FRIESIAN	KD	14	1.44	1.14	1.24	LH	5	1.58	1.00	1.14	BA	8	1.76	1.52	1.62	7 bulls
	CPW	13	1.36	1.58	1.66	KH	20	1.75	1.96	2.03						88 pairs
	LW	11	1.55	1.42	1.51	TF	17	1.68	1.32	1.41						1.60 dams
																1.49 daughters
	3	38	1.44	1.37	1.46	3	42	1.70	1.59	1.67	1	8	1.76	1.52	1.62	1.58 daughters(C)
GUERNSEY	BPD	5	1.55	1.50	1.60						LMP	22	1.41	1.55	1.64	4 bulls
	HD	6	1.46	1.33	1.47						GDGR	6	1.55	1.92	2.02	39 pairs
	2	11	1.50	1.41	1.53						2	28	1.44	1.63	1.72	1.46 dams
Centre Totals	12	108	1.45	1.44	1.54	9	95	1.65	1.54	1.62	9	87	1.57	1.42	1.49	1.57 daughters
																1.67 daughters(C)