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Seria ANIMALIA DOMESTICA N. 4 — Sarja KOTIELÄIMET n:o 4

FERTILITY AS A BREEDING PROBLEM IN ARTIFICIALLY BRED POPULATIONS OF DAIRY CATTLE. I. REGISTRATION AND HERITABILITY OF FEMALE FERTILITY

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Agricultural Research Centre, Department of Animal Breeding
Tikkurila, Finland

Selostus:

Hedelmällisyys jalostuskysymyksenä lypsykarjan keinosiemennyspopulaatioissa
I. Naaraspuolisen hedelmällisyyden rekisteröinti ja heritabiliteetti

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To be presented, with the permission of the Faculty of Agriculture and Forestry of the University of Helsinki, for public criticism in Auditorium XIX on May 27th, 1964, at 12 o'clock.

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PREFACE

The question of how much weight should be attached to fertility and vitality traits in dairy cattle breeding has interested me since I, employed by the Finnish Ayrshire Society in 1954—55, was searching for good cows to be used as dams for bull calves. A couple of articles arising out of this interest were published while I was working as a junior research assistant at the Department of Animal Breeding of the Agricultural Research Centre in 1955—61 (MAIJALA 1959 and 1960). My interest in the subject grew and I found the opportunity to collect and analyze some data while I was working as secretary of the Central Association of Artificial Insemination Societies in 1961—63. The final analyses were performed after I had resumed my position as senior research assistant at the Department of Animal Breeding in summer 1963. At this time I also decided to restrict the study to fertility traits, and during the winter of 1963/64 it became clear that only the registration and heritability of female fertility could be treated in the first part of the study.

It is with great pleasure that I now thank Professor Viljo Vainikainen, D. Agric. and Forestry, Head of the Department of Animal Breeding, for the opportunity to concentrate on preparing the first part of my fertility studies for publication. I also wish to thank him for his indefatigable interest and for placing technical assistance at my disposal.

I also wish to express my gratitude to my senior colleague, Mikko Varo, D. Agric. and Forestry, for many helpful discussions and criticism. For the encouragement and for the methodological and mental tools given me by Professors Ivar Johansson, Alan Robertson and Jay L. Lush during my stays in Uppsala (Sweden), Edinburgh (Scotland) and Ames (Iowa), I tender my deep gratitude.

Appreciation is also extended to Professor Lauri Paloheimo, D. Agric. and Forestry, for stimulating interest and support.

It is self-evident that work of this kind could not have been done without elastic collaboration with data-processing people. In am therefore indebted to the Finnish IBM and its personnel, especially Mr. P. Malinen, Dipl. Eng., and Mr. H. Andersson, for their willing help.

During the work I had the opportunity to discuss some statistical problems with Professors G. Elfving and O. Lokki, and with Mr. P. Kerola, M. Sci., to whom I wish to express my thanks.

My special thanks are due to Mrs. Taimi Paavola, Mr. I. Kimmo, Agronomist, and Mr. R. Oja for tireless and careful technical assistance in performing the seemingly endless calculations and revisions.

The Central Association of Artificial Insemination Societies, all of its member societies and their personnel deserve my gratitude for kind help in collecting parts of the data and getting the analyses started. This also applies to all the organizations and people responsible for milk recording in Finland.

Mr. E. Risser, M.S., and Mrs. Jean Margaret Perttunen have made many valuable linguistic corrections to the manuscript. For their assistance I express my sincere thanks.

For the financial help given by the Suomen Kulttuurirahasto (Finnish Cultural Foundation) and Eemil Aaltosen Säätiö (Eemil Aaltonen Foundation) I also wish to express my deep gratitude.

To the Agricultural Research Centre I am greatly indebted for the publication of this work.

Tikkurila, April 10, 1964.

Kalle Maijala

CONTENTS

I. GENERAL INTRODUCTION

The main product of a dairy cow, its milk, was originally intended as food for its offspring. An animal which has not calved does not give any milk, and even the daily milk production of a cow which has calved gradually declines after calving. Consequently, the continuation of the utility value of a cow from year to year entirely depends on whether the animal remains fertile. It is a general experience, however, that there are many factors which often cause difficulties in getting a cow to calf or render this utterly impossible.

A. The economic importance of fertility

Lowered fertility influences the economy of milk production in at least the following ways:

1) Lengthening of the calving interval (C.I.) lowers the production per unit time. For example, among nearly 29 000 Finnish Ayrshire cows from the recording year 1957/58, the average relative milk yield of cows with a C. I. of over 15 months was about 10 % lower than that of the other cows (MAIJALA 1959). The difference becomes still larger when only cows with calving intervals of exactly 12 months are taken as a basis of comparison. In the Swedish study of JOHANSSON and ANDERSON (1945) this difference was about 22 %. Similar results were obtained by CHAPMAN and CASIDA (1935). Taking the standard deviation of the C.I. as 50 days (KORKMAN 1946) and the average decline of the annual milk yield per day's increase in C.I. as 0.1 % (JOHANSSON and ANDERSON 1945), the value of one standard deviation in C.I. equals 5 % of the annual milk yield. This is nearly 1/3 of the standard deviation of the annual milk yields.

2) Veterinary treatment and medicines to avoid delay in conception are expensive. "Sterility" and "sterility treatment" are among the commonest remarks concerning disturbances which are mentioned in the milk-recording reports. According to the statistics collected by the Veterinary Division of the Department of Agriculture, Finnish veterinarians had to treat 51 166 sterility cases in 1960, which means 17.80 % of all cattle treatments of that year, excluding infectious diseases. In addition, other disorders of the urogenital organs required 39 761 treatments, or 13.83 % of the total. In the South-West Finland A. I.

Society, where free sterility treatments are included in the benefits to be obtained with the insemination fee, the costs caused by sterility treatments to the society in the years 1961 and 1962 were about 10 new Finnmarks per treatment and ca. 1.3 marks per member cow. The number of treatments needed per 100 cows was 13.3. The respective figures from the Swedish A. I. societies are 17.0 for cows and 10.0 for heifers (SHS 1962). Obviously, the costs of these treatments can be regarded as a profitable alternative to the losses in production caused by delay in conception.

3) Repetition of inseminations during a given service period causes extra costs to the A. I. society, and hence the insemination fee has to be kept high. In Finland, each unsuccessful insemination visit means a loss corresponding to the price of about 30 kilos of milk. For example, the 579 221 cows impregnated by the Finnish A. I. societies during the year 1962 needed a total of 351 290 extra services (KSL 1962).

4) Cullings due to sterility increase the need for replacements and consequently the costs of rearing. Sterility is the main cause of culling in many countries, including Finland. The proportion of all cullings due to this cause in both Sweden and Finland is close to 40 % (Johansson and Anderson 1945, SHS 1962, Vainikainen 1939, Lonka 1960). About 5 % of all cows are culled yearly in Finland because of sterility (Korkman 1932 and 1947, Zilliacus 1937).

5) Premature culling lowers the average yield of the herd because the proportion of cows in the most productive age classes declines. According to Rendel and Robertson (1950), the economic influence of this factor is not very large.

6) Because of the increased need for replacements, sterility reduces the number of milking cows which can be maintained on a given amount of food.

7) The fact that a cow cannot be gotten to calf at the desired time may have a detrimental effect on production and income, since the annual milk production depends on the season of calving.

8) Poor fertility reduces the numbers of calves available for beef production. The importance of this factor is at present increasing with the increasing demand for high quality beef.

9) The same applies to the possibilities to sell animals for breeding.

B. Fertility and selection possibilities

Besides their direct economic importance, fertility disturbances restrict the possibilities for selection. Therefore, maintenance of fertility is also of interest from the viewpoint of improving milk-producing ability. Many individual breeders have experienced the harmful effect of sterility when it has proved impossible to get more offspring from the best cow in the herd. Calves of less productive cows have had to be saved instead.

From a more general angle, the importance of natural selection due to sterility as a restricting factor in selection becomes clear when one remembers that an average of two living offspring per cow are needed merely for maintaining the breed or species. Supposing that the standard deviation of milk yields is 15 %, the following selection differentials are made possible by different numbers of living offspring per cow:

2 calves:	selection differential	0 %
4	— » —	12 %
6	— » —	16 %
8	— » —	19 %
10	— » —	21 %

Thus, from the viewpoint of selection possibilities it is important that the cows do not become sterile before they have calved at least 5 or 6 times. Still more frequent calvings are needed if one also wants to select for other traits besides milk producing ability.

Because of the limited need for bull calves, selection of their dams is in some degree possible even when only two offspring per cow are born. It is obvious, however, that an increase in the number of calvings is also profitable from the standpoint of the selection of bull dams. When the number of offspring is optimum for selecting dams of heifer calves, there are also ample opportunities for selecting dams for bulls. In some individual cases it may seem a misfortune when a selected dam fails to calve any more, but usually she can be replaced by good cows from other herds. It is much more regrettable if an excellent progeny-tested bull loses his fertility too soon. Even this loss can be mitigated by storing so much deep-frozen semen of every young bull that some sons can be produced from selected dams if his progeny turn out to be excellent.

C. The problems

A further indication of the importance of fertility disturbances is the enormous number of investigations concerning sterility that are to be found in the literature. The overwhelming majority of these refer to pathological, nutritional and other causes of sterility and its treatment, but there is also a voluminous literature concerning the genetic aspects of fertility disturbances and the possibilities of reducing these by selective breeding. The latter kind of literature is characterized by extreme results and opinions. Some authors (e.g. BERGE 1942, VAINIKAINEN 1946, KÖRPRICH 1949 and LAGERLÖF 1951) have expressed the opinion that cows which conceive with difficulty should under no circumstances be used for breeding. On the other hand, according to several others (RENDEL and ROBERTSON 1950, ASDELL 1952 and 1958, DUNBAR and HENDERSON 1953, CARMAN 1955, LEGATES 1954, FOOTE and BRATTON 1956, BAYLEY 1959) it is unnecessary to retard the genetic progress of more strongly heritable characteristics, such as milk producing ability, by paying attention to fertility or health, whose variation, in their experience, is determined primarily by chance and environment.

This discrepancy of opinions has been an important reason for undertaking the present series of studies, the purpose of which is to throw some additional light on the question of proper weighting of fertility traits in dairy cattle breeding and to find the most effective methods of assessing the fertility of individual animals.

The importance of this study has been considerably increased by the vigorous expansion of artificial insemination (A. I.). Because of the great number of offspring an individual sire can produce by A. I., the selection of A. I. bulls has become a very responsible task, in which nothing should be left to chance or superficial knowledge. Under these circumstances it is by no means immaterial which of the above-mentioned viewpoints is more correct. If the first opinion is right, then it would be catastrophic to use bulls whose genetic faultlessness is not certain. If the second view is nearer the truth, then attention paid to fertility is only an obstruction to breeding for production ability.

The A. I. activities have actualized the problem of fertility for the further reason that fertilization is the immediate task of these activities. Unless it succeeds in this respect an A. I. unit loses its clients. Therefore, the adoption of A. I. has changed the situation so essentially that, even though the possibilities of breeding for fertility have previously been studied in Finland (VAINIKAINEN 1946, KORKMAN 1947), the problem now has to be investigated in a completely new light.

It is also important to clear up the question of whether there is any truth in the repeated claim that one-sided breeding for production ability is the cause of the generality of fertility disturbances. According to the calculations made by ROBERTSON and RENDEL (1950), which indicated that intensive selection and accurate progeny testing in A. I. may lead to progress twice as fast as natural service, it is possible that the automatic elimination of sterile individuals is no longer a sufficiently effective means for maintaining fertility. One-sided selection for production ability has in fact become possible only in the era of A. I., when the responsibilities of bull selection have been centralized in the hands of a few persons. In earlier times, when each cattle owner himself chose his bulls, such parallelism of breeding objectives was not possible. The separation of cattle breeding into thousands of small units offered a kind of insurance against catastrophes. Although progress was slow, it was safe, since an error made by one breeder had an influence only on one herd or very few herds.

Another important aspect of the problem of interrelationship between production ability and fertility concerns the question of how short the generation intervals can possibly be. If cows which produce well as young animals exhibit poor fertility, then selection decisions concerning both progeny-tested bulls and individual cows must be delayed to older age classes. This would retard genetic progress per unit time.

The question of the best measure of milk production ability is also dependent on the heritability of prolonged calving intervals. If heredity does not play any role in the variation of C. I., the lactation yield is a safe and natural measure of milk producing ability, but if the contrary is the case, then it is safest to trust in the operational year's records.

One of the practical purposes of the following series of studies is to elucidate which source of information is the more reliable and practical for collecting the data needed for assessing the fertility of individuals. For there are two sources available. One is milk recording, which is done for about 40 % of the inseminated cows in Finland (KSL 1962). The second method is the so-called A. I. statistics, based on data collected by A. I. technicians on their insemination visits. The latter statistics have two interesting features as compared with the former: (1) they concern all inseminated cows, and (2) they provide information on the fertility of all heifers, including the absolutely sterile ones. From the standpoint of the future organization of data collection, it is important to determine which of these methods gives more useful information. Depending on the results, a simplification of certain of the statistics would become possible.

Fertility — unlike milk production — is a characteristic which manifests itself in both sexes. Comparatively few studies, however, have been made on the question of whether male and female fertilities show any correlation with each other in a genetic sense. Confirmation of the observations of ERIKSSON (1939), VAINIKAINEN (1946), LAGERLÖF (1951) and AEHNELT (1958) would be important since the fertility of a bull can be assessed much earlier than that of his daughters. Therefore this question, as well as the heritability of male fertility, was also studied in the present investigation.

The primary purpose of this study is to determine the weight to be given to fertility in choosing breeding objectives. It is true that a final decision in this respect also depends on the relative economic importance of each trait, but the treatment of this aspect of the problem will — owing to lack of personal training qualifications — be restricted to what was said above. It is to be hoped, however, that a specialist in agricultural economy will become interested in this problem.

As a breeding objective, fertility is different from many other traits in that it never loses its economic importance. For this reason and to avoid possible unpleasant consequences, it is obviously of current interest to consider the fertility of dairy cattle from the standpoint of breeding work as a whole. Because the main purpose is to obtain a general picture or to map out the ground, a detailed consideration of the physiological causes of sterility cannot be included in this study. Instead, attention will be paid to certain consistent external factors causing differences between individuals and families and tending to obscure genetic differences.

In assessing fertility the main emphasis will be placed on the possibilities of progeny-testing bulls, because bulls are very important in the development of better animals with A. I. (ROBERTSON and RENDEL 1950, SKJERVOLD 1963). The genetic fertility of bulls is of special interest for the further reason that the success of an A. I. unit depends both genetically and economically on the quality of its bulls.

In fact, fertility disturbances are only part of a larger group of physiological disturbances which hamper milk production and which may be considered as phenomena due to stress. For a study of the other disturbances, such as those of metabolism, it is difficult, however, to find satisfactory material in present-day Finland. Therefore, it has been considered best to restrict the following study series to fertility, which can be measured clearly and objectively. In the title, as well as in many places in the text, the term fertility has been used as a name for the phenomenon, although in practice this is better known as sterility or disturbances of fertility. The choice of this term is based firstly on the fact that the importance of the trait will be studied especially as a breeding objective. It would be illogical to aim at a negative thing! Secondly, fertility is a more relative concept than sterility, which implies some absolute and rare condition.

In discussing the value of fertility as a breeding objective, the first task is to study whether heredity plays any part in individual differences in fertility. Therefore, the purpose of this first part of the present study series has been to find useful heritability estimates for different measures of female fertility in dairy cattle when measured on a large practical scale. The concept of heritability will be used in its narrow sense (LUSH 1945 and 1949), and the conventional h^2 will be used as its symbol in many places. On the basis of the heritability estimates to be obtained, the suitability of different measures of fertility will be preliminarily evaluated, and the relative value of the two possible channels for collecting information on fertility traits will be compared. In connection with the estimation of the heritabilities, the effects of some systematic factors on the fertility traits and their heritabilities will be examined.

II. REVIEW OF LITERATURE

It would be of interest in this connection to mention the fertility of other species, too, but for the sake of brevity this discussion will be restricted to fertility in dairy cattle. This limitation is also justified by the fact that the performances in dairy cow production probably make the whole problem of fertility in dairy cattle different from that in other species.

Even though there are several excellent reviews of the genetic aspects of dairy cattle fertility (BANE 1952, GILMORE 1949, JOHANSSON 1961, PFAU 1957, ROLLINSON 1955, VENCE 1959, YOUNG 1953), it is obviously relevant to present a survey of the different measures of fertility used in earlier studies and the heritability estimates obtained from different material.

The above studies could be divided into many different classes, since the causes of failure in reproduction are so numerous and variable. WINTERS (1954), for example, classified the causes into the following 12 groups: (1) anatomical defects, (2) mechanical injury of the genital organs, (3) infectious diseases, (4) prenatal death of the young, (5) physiological disturbances, especially improper hormone balances, (6) gametic incompatibility, (7) low vitality of gametes, (8) failure to mate at optimum time during the heat, (9) psychic disturbances, (10) malnutrition, (11) environmental disturbances, and (12) genetic causes. This list also shows how difficult it may be to make a genetic analysis of fertility when the cause varies from case to case. In the review below, the main emphasis is on the end results rather than on the causes of fertility, and the order of the different features of fertility is based on how commonly each has been used as a measure of fertility in heritability studies.

A. Calving interval and its derivatives

One of the most commonly used measures of fertility is the calving interval (C. I.). This measure has at least two important advantages. Firstly, it can be determined accurately and objectively, and secondly, it is a continuous variable. A third advantage from the practical standpoint is the fact that almost all causes of sterility have an influence on it. The accurate determination of C. I. is sometimes made difficult, however, by abortions after varying pregnancy durations. A still more important disadvantage of the C. I. is that its measurement is only possible after at least two calvings. It does not reveal the absolutely sterile heifers or young cows. The continuous variability of C. I. loses some of its value because of the skewness of its distribution. Another serious handicap is the fact that the C. I. is often dependent on human arrangements of calving times and also on carefulness in following the heats.

One of the first to use C. I. as a measure of fertility was Albrechtsen (1916), who employed it for comparing average fertilities of different herds. Schmidt (1933), Dinkhauser (1940) and Körprich (1948) used it for individual comparisons without attempting to give a quantitative estimate of heritability. Quantitative estimates have been made by many other authors, whose results are collected in Table 1.

The heritability estimates in the table are not necessarily those presented by the authors in their conclusions, but are in some cases based on their original calculations. A negative heritability is illogical according to the definition of heritability, but from the viewpoint of averaging several independent estimates, it is better to accept the results of computations at their face values. This is possible with regard to the first two rows. In spite of this, the

Table 1. Estimates of the heritability and repeatability of calving interval (C. I.) according to different investigations.

Reference	No. of cows	Heritability %	Repeatability %	Method of estim. herit.	Breed
Legates (1954)	1 016	— 3.6	13.3	DD	
Dunbar & Henderson (1953)	1 036	— 4.7		PHS	H-Friesian
Østergaard (1942)	970		13.0		Red Danish
Rennie (1954)	731	14.8	18.0	PHS	H-Friesian
„	„	3.0		DD	„
Inchiosa & Pfau (1954)	676		13.5		„
Alim (1957)	492	13.0	17.9		Buffaloes
Johansson (1947)	358		9.9		Swed. Polled
Johansson & Hansson (1940)	301		3.6		„ Red & Wh.
Asker *et al.* (1953)	345	13.0	5.4		Buffaloes
Brown *et al.* (1954)	257	0.0	0.0	PHS, DD	Ab.-Angus
Gaines & Palfrey (1931)	186		8.8		Red Danish
Weighted average		3.3	12.3		

(DD = dam-daughter regression, PHS = paternal half-sib correlation).

average estimates at the bottom of the table are not very useful, because some of the individual estimates are confounded by environmental effects or based on rather small samples. The two largest individual studies, which have also been analyzed with very modern methods, have both given negative results. Even these studies are too small, however, for studying low-heritability characteristics such as fertility. They are large enough to show that individual selection of cows with regard to fertility hardly pays, but they do not give a basis for calculating how accurately A. I. bulls can be progeny-tested as to the fertility of their daughters.

The repeatability estimates are more consistent than the heritability estimates. Their average shows that the upper limit of the heritability cannot be much above 10 %, because the repeatability also includes all dominance and espistasis deviations and permanent environmental effects, in addition to the additive gene effects included in the heritability in the narrow sense (LUSH 1949).

Several derivatives of the C. I. have been used as a measure of fertility. In the Scandinavian countries especially, it is customary to consider a calving interval of less than 15 months as normal and an interval exceeding that as abnormal (JOHANSSON and ANDERSON 1945). This abnormality is called in Swedish "överlöpning" (= over-running) and in Finnish "yliaikaisuus" (overtimedness). According to VAINIKAINEN (1946), the frequency of overtimedness is higher than average among the daughters of dams who have been overtimed at least twice. The interherd variation and age effects were not eliminated in these comparisons. The frequency of overtimed calving intervals in Finland is about 7 %, which, from the statistical point of view, is slightly too low a figure to sensitively differentiate between fertile and sterile animals. On the other hand, it corresponds very closely to the percentage of animals culled annually owing to sterility (KORKMAN 1947). Consequently, it may be effective enough in negative selection, providing that heredity is related to the underlying causes of overtimedness.

Statistically, the method recommended by RICHTER (1938), that 14 months be accepted as the line of demarcation, seems to be a more sensitive measure than the Scandinavian overtimedness.

WILLIAMS (1919) considered that an "ideal efficiency" presupposes calving every 12th month, and that a heifer must calve at the age of two years. All months after this age were called by him "breeding months", and as a measure of fertility he used the expression (No. of calvings × 12 × 100) / (No. of breeding months). SPIELMAN and JONES (1939) used an almost similar measure in which they replaced the number of "breeding months" by the number of months since the first calving as the denominator. A correlation as high as 0.546 ± 0.118 was obtained by them between the reproductive efficiencies of dams and daughters. Even if one takes into account that this measure included the fertility of several service periods, it is very likely that some positive confounding effects are involved in the correlation. Obviously these effects are concerned with time trend and breed differences.

INCHIOSA and PFAU (1954) expressed breeding efficiency as a percentage derived from the ratio of the actual average C. I. in days to the ideal of 365 days. The heritability of this figure was 0.406 on a basis of dam-daughter correlation (338 pairs). WILCOX *et al.* (1957) arrived at a heritability estimate of 0.32 based on intra-sire regression of daughters on dams (575 cows), using a measure of breeding efficiency similar to that of INCHIOSA and PFAU. Parturitions later than the sixth were not taken into account. Because the statistical procedures used in the two last-mentioned studies were relatively modern, it appers that there really are genetical differences in breeding performance between cows, especially in the older ages.

BUSCHNER *et al.* (1950) recommended the age in days at 3rd calving as a measure of reproductive efficiency. By expressing this measure in units of the standard deviation from the herd mean, an animal's relative position in the herd could be shown and comparison of animals from different herds would be facilitated.

B. The number of services per conception

Another rather commonly used measure of fertility is the number of services per conception (S/C). Although this is relatively easy to record in the herds, its reporting in the milk-recording may still be imperfect, and concealed or otherwise unreported services are difficult to detect afterwards. An advantage as compared to the C. I. is that an intentional delaying of service does not have an effect on the S/C. This may be counterbalanced, however, by the fact that even the delay caused by absence of heats cannot affect the S/C. On the other hand, the S/C can be measured one service period earlier than the C. I. However, the absolutely sterile heifers are not included at all, and likewise those service periods of cows where no conception occurs are lost. Statistically, a certain characteristic difficulty is involved in the S/C because of its one-tailed distribution.

In the literature there are several studies concerning the heritability or repeatability of the S/C. Results of these have been collected in Table 2.

Table 2. Estimates of the heritability and repeatability of the number of services per conception (S/C) according to different studies.

Reference	No. of cows	Herit-ability %	Repeat-ability %	Method of estim. herit.	Breed
OLDS & SEATH (1950)	6 509		8.4		
VANDEMARK (1954)	1 568		8.6		Several br.
LEGATES (1954)	1 129	2.6	0.0	DD	
POU *et al.* (1953)	834	7.0	12.0	DD	H-F, Jersey
CARMAN (1954)	763	— 3.5	6.0	DD	H-Friesian
KOORT (1948)	510		5.5		Swed. Red & Wh.
CARLI (1947, ref. KOORT)			10.9		„ Poll.
BRANTON *et al.* (1956)	381	9.7	10.6		H-Friesian
Weighted average		3.2	7.7		

The heritability estimate of CARMAN's (1955) study is an unweighted average of two independent estimates presented by him; this was because numbers were not available separately from the two studies in question. The averages at the bottom are slightly smaller than those on C. I. in Table 1, but it is unsafe to draw any conclusions from this small difference. In the study of LEGATES (1954), where both C. I. and S/C were investigated on the same data, S/C gave a higher heritability estimate than C. I. Unfortunately, OLDS and SEATH (1950) did not try to estimate the heritability in their extensive study. The relatively high figures of POU *et al.* (1953) and BRANTON *et al.* (1956) can be explained by the fact that they are derived from large experimental herds, where recording can be done accurately and environmental variations kept within reasonable limits.

For the average of several (2 to 12) service periods, KOORT (1948) obtained a heritability of 17.2 % on the basis of paternal half-sib correlation among 409 Swedish Red and White cows. The corresponding estimate based on intra-sire dam-daughter regression was 23.6 %. On the other hand, DONALD and ANDERSON (1953) were not able to detect any correlation between monozygous twins in the S/C.

C. Conception rate after a given number of services

In order to avoid the effect of veterinary interventions and other human arrangements on the number of services, KORKMAN (1946) used the percentage of cows conceiving at the first service as a measure of fertility. In a later study on the same data he obtained a heritability estimate of 4.72 % for this measure (KORKMAN 1947). The repeatability was almost exactly the same, namely 4.83 %. This carefully performed investigation comprised 4 009 Finnish Ayrshire cows with a total of 13 119 calvings in 38 herds. The confounding effects of herds and the age of the cows were properly eliminated. Therefore, the heritability estimate obtained by KORKMAN can be considered an ideal which can be approached by careful recording and management in individual herds. This figure cannot, however, be used as a basis for breeding plans in A. I. cattle populations, where the differences between herds may cause difficulties and where recording is inaccurate. In addition, the causes of sterility in individual herds may be more specific and thus more highly heritable than in a group of herds.

The expansion of A. I. has considerably increased the importance of conception rate at the first service as a measure of fertility, since the success of inseminations by technicians and by semen bulls is evaluated by a similar measure. Owing to the need for early determination of the success of insemination, the criterion used is the absence of return to service and not the birth of the calf. The most usual length of time for this is 60 days or 60—90 days. The percentage of cows not returning to service within the specified time period after insemination is called the nonreturn percentage, nonreturn rate or shortly NR-% (SALISBURY and VANDEMARK 1961). Usually, only the first services of cows are taken into account, since the later services are more apt to be influenced by environmental influences and human arrangements. For example, many of those cows which do not become pregnant at the first two services by A. I. are later served naturally, while others are culled as sterile without returning to service.

The use of the NR-% as a measure of the fertility of bull progeny groups is thus possible as a by-product in A. I. activities, provided that the sires of the inseminated cows are also recorded. A special advantage of the NR-% in this respect is that information can be obtained on all inseminated animals, including the absolutely sterile ones, and heifers can be judged already some months after their first service. One drawback is the fact that the losses of fertilized ova during the later stages of pregnancy do not affect the NR-%. Although the NR-% declines with the time elapsed after insemination, the differences between semen bulls remain about the same, however, and their rank order does not change (ERB and FLERCHINGER 1954).

DUNBAR and HENDERSON (1950 and 1953) analysed nonreturn data from an A. I. unit in New York State and obtained a heritability estimate of 0.04 %. The within-herds repeatability was 5.1 % if daughters of different sires were mixed, and 2.7 % within sires. The study comprised the same 1 015 cows as those in the C. I. study on the second line in Table 1. Only production-tested cows were used in the study, and the method of analysis properly took into account the nonorthogonal nature of the data. Thus it is difficult to find the reason for the disappointing estimates of heritability. It does not appear from the publication how complete and accurate was the identification of cows and their sires in this A. I. unit.

LEONARD (1950, ref. POU *et al.* 1953) used 150—180 day nonreturns as an indication of conception in a study comprising 2 610 records of breeding service from Maine state; his estimate of repeatability was 7.5 %. This is very close to the average repeatability of S/C in Table 2.

KOORT (1948) measured fertility on the basis of whether the cows had conceived at either the first or second service. The repeatability of this measure was 3.1 % among the same 510 Swedish Red and White cows as were used in his study on the S/C (Table 2). At least in this herd the S/C had a higher repeatability. Such a result seems reasonable, since a cow is sometimes served at an improper stage of estrus. Giving two chances lessens the effects of bad luck.

The measure used by BERGE (1942) is also rather closely related to the last-mentioned measures of fertility. He expressed the fertility as the number of conceptions per 100 matings and obtained 21.5 ± 5.1 % as a repeatability estimate. The data were collected during a long period in an experimental herd, and no effort was made to eliminate the time trends.

Collins *et al.* (1962) estimated the heritability of the average conception rate of 1—4 records to be about 5 %, while the heifer record alone had a heritability of about 3 %. The estimate of Inskeep *et al.* (1961) for conception rate based on birth of a live calf from first insemination was 8.5 %.

Rottensten and Touchberry (1957) analyzed the conception data of 554 young cows at 6 Danish Progeny Stations in the years 1954—56. They estimated the heritability of conception at the first service as 4 % and that of conception after one or two services as — 3.7 %.

D. Components of calving interval

The C. I. can be divided into several components, each of which could be imagined as a measure of fertility. Firstly, there is the period from parturition to the first postpartum estrus. Repeatability estimates of 19 %, 29 % and 21 % were obtained for this trait by Chapman and Casida (1937), Olds and Seath (1953) and Carman (1955), respectively. There is much less consistency, however, in the heritability estimates available. On the basis of the intra-sire dam-daughter correlations obtained by Olds and Seath, it can be calculated that the heritability of the interval from the first calving to the first subsequent heat in their material was 27.2 %. The corresponding estimate for the average of several records was 36.4 %. The correlation between paternal half-sibs gave a rather low estimate for single records, while that for the average of several records ($h^2 = 31.1$ %) agreed well with the estimate based on dam-daughter correlation. On the other hand, Carman (1955) arrived at negative estimates of heritability (—0.06 and —0.03) in the two herds studied by him. The data of both Olds and Seath and Carman originated from experimental herds and comprised 210 and 753 cows, respectively. The average heritability of a single record on the basis of these studies is a little under 10 %.

Variations in the length of the interval between two successive heats, the estrual cycle, have been studied by Chapman and Casida (1937), Berge (1942), Olds and Seath (1951) and Mares *et al.* (1961). According to Berge, the repeatibility of this trait is rather high (24.8 ± 5,4 %), while Olds and Seath estimated it as 6.9 % and Mares *et al.* as 8.5 %. Chapman and Casida showed that the inclusion of greatly abnormal cycles lowers the repeatability. When only cycles of 17—27 days were taken into account, the repeatability was 30—40 %, while only 2 % was obtained as a repeatability when longer and shorter cycles were included.

For the occurrence of estrus cycles equal to or shorter than 15 days, Erb *et al.* (1959) obtained a heritability of 11 %.

The first postpartum estrus usually occurs so early that the cow is not inseminated at that heat, but the first attempt is postponed to the second or third estrus. In 50—70 % of the cases this first insemination leads to conception, while the remaining cows return to service one or more times. The length of time between the first insemination and conception has been used as a measure of fertility by Tabler *et al.* (1951), Pou *et al.* (1953) and Carman (1955). The distribution of this measure is of course about as skew as that of the S/C. The first-mentioned authors did not estimate the heritability, but on the basis of the sire component of variance presented by them, a heritability estimate as high as 64 % can be computed. However, since the dam family component was negative, great emphasis cannot be placed on the heritability estimate. The number of cows was also small, only 369. Pou *et al.* (1953) studied 834 cows from the Beltsville dairy herd and obtained 11 % as a repeatability estimate and 7 % as a heritability estimate. These figures are almost exactly the same as were obtained for the S/C in the same herd. Carman (1955) arrived at 5 % as an estimate of repeatability and 0 % of heritability. It thus appers that the heritability of this trait is about the same as that of the other components of C. I.

Pou *et al.* (1953) investigated the regularity of estrus cycle length and estimated the heritability of it as 5 % and the repeatability as 18 %. Chapman and Casida (1935) studied the length of the interval from parturition to conception, often called the service period; they referred to the observation of Dickerson that the service period lengths of the same cow tend to be the same from one calving to another. This measure includes the interval from parturition to first estrus, from first estrus to first insemination (a trait largely dependent on human arrangements) and from first insemination to conception. If one assumes that the gestation period is of constant length, then the service period can be considered identical with the C. I. This assumption is not entirely true, however, since there are differences in the duration of gestation even if pronounced abortions are excluded. The standard deviation of gestation length is only from 5 to 6 days (Berge 1942, Mäkelä and Oittila 1955, Rendel 1959), while the standard deviation of the C. I. is ten times as much (Johansson and Anderson 1945, Korkman 1946). Thus the causes of variation in service period and C. I. are obviously mainly the same and heritability estimates obtained for the C. I. apply equally well to the service period.

In spite of this, it must be remembered that the variations in gestation period are also to a certain extent inheritable, as can be seen, for example, from the differences between breeds (Brakel *et al.* 1952, de Fries *et al.* 1958). Rollins *et al.* (1956) found that 31 % of the variation in gestation length was due to additive genetic differences between cows, while the corresponding estimate by Jafar *et al.* (1950) was 6 %. Berge (1942) estimated the repeatability of gestation length as 12.9 ± 2.0 %. It is very likely, however, that the genes causing differences in gestation period are much different from those responsible for differences in other components of the C. I.

E. Estrus symptoms

In many cases, the difficulty in getting a cow reimpregnated after calving is due to the fact that no estrus can be observed for a long time. The problem of a weak or "silent" heat is well known to most dairymen, and it is only natural that this feature has also been used as a measure of fertility. Variations in the intensity of heat symptoms were studied over 50 years ago by Weber (1911, ref. Rottensten and Touchberry 1957), who found that the intensity of the heat symptoms was determined by the individuality of the cows. Rottensten and Touchberry scored the heat symptoms of 554 first-calf heifers at six Danish progeny-testing stations in the years 1954—56 into 4 classes of different intensity. They estimated the heritability of this score as 21 % and the repeatability among unrelated animals as 29 %. Rottensten (1958) continued this study and obtained a significant difference in the intensity of heat symptoms between the Jersey and the Black and White breeds of cattle.

The suitability of the intensity of heat as a measure of fertility is questionable, especially for the reason that it must be assessed subjectively. It is also difficult to estimate the importance of this feature from the viewpoint of natural fitness, since different means of detecting the heats of cows may be available for bulls than for man.

The duration of estrus has therefore some importance in the A. I. operations since the technician can usually make only one visit to a certain farm per day. An estrus of too short duration might sometimes render it difficult for the technician to make his visit at the right time. However, this trait has been studied relatively little. As far as is known to the present writer, Hammond (1927) is the only worker who has reported individual differences in the duration of estrus. According to him, the repeatability of estrus length was 44 % among 43 cows. This observation is supported by similar results concerning other species of farm animals.

F. Occurrence of cystic ovaries

The hereditary nature of a functional disturbance of ovaries called cystic ovaries was pointed out already by RYCHNER (1851, ref. HENRICSON 1957). This opinion has subsequently been affirmed by several other workers (ZSCHOKKE 1900, ref. HENRICSON 1957, ERIKSSON 1939, WEGSCHEIDER 1939, GARM 1949, WILTBANK *et al.* 1953), although no attempt has been made to develop any theory regarding the mode of the inheritance. BERGER (1954) presented a theory of a dominant autosomal gene determining the disposition to cystic ovaries, while recessive inheritance was assumed by SONNENBRODT and RANNINGER (1949), ERIKSSON (1954) and HENRICSON (1957).

HENRICSON, however, has found it necessary to speak of either incomplete penetrance or incomplete expressivity, which implies that the effects of the gene are not fully independent of the effects of environmental factors or other genes. Obviously, it is also reasonable to treat the tendency to the disease as a quantitative, polygenic character. This has been done by ERIKSSON (1949), who estimated the heritability as 26 %, by CASIDA and CHAPMAN (1951), whose estimate was 43 %, by HENRICSON (1957), whose estimate on the basis of 1 diagnosis per service period was 5 % and on the basis of several diagnoses 11 %, and by VARO (1960), who obtained a figure of 48 %. ERB *et al.* (1959) studied this question on the basis of herds from the Carnation Milk Farms, using dam-daughter comparisons. The heritability estimate, based on 1 416 pairs, was 5 %. Although some of these figures are positively confounded by age effects, it can be concluded that the tendency to cystic ovaries is one of the most highly inheritable traits in reproduction. This fact, on the other hand, suggests that the trait may be not a very important component of natural reproductive fitness.

G. Multiple births

In normally multiparous animals such as swine and sheep, a tendency to multiple births is a desirable character, and litter size is almost the only measure of fertility in these species. In dairy cattle, the reverse is the case (KOCH 1933, VAINIKAINEN 1946, ERB and MORRISON 1959). In spite of this, an inclination to multiple births can be considered to reflect the anatomical and physiological nature of the reproductive functions of a cow. Especially the observation of ERB *et al.* (1959) that twinning is genetically associated with other reproductive disturbances, such as cystic ovaries, short estrus cycles and retained placenta, makes it reasonable to study twinning as an indicator of reproductive abnormalities and disturbances. Individual repeatability and inheritance of multiple births has been studied by HAYDEN (1922), LUSH (1925), RICHTER (1926), JOHANSSON (1932), HEWITT (1934), LÖWE (1939), KARWETZKI (1941), WEBER (1944) and PFAU *et al.* (1948). The four last-mentioned authors considered that the mode of inheritance was probably recessive. This was supported by KORKMAN (1948), who found no dam-daughter correlations in his study. The repeatability estimates obtained by KORKMAN were 6.7 % for the Finnish Ayrshire, 6.6 % for the Swedish Friesian and 4.4 % for the Swedish Red and White breeds of cattle. He pointed out, however, that certain age effects may be included in the estimate concerning the Finnish Ayrshire cattle. This also applies to the heritability estimate which can be computed from the sire component of variance in his Ayrshire data. The heritability based on the similarity of paternal half-sibs is 16,8 %. The Swedish Friesian data, where age effects were eliminated, gave a slightly lower estimate, 12.0 %, and no heritability could be found in the Swedish Red and White cattle. Each of the three croups comprised over 10 000 calvings.

ERB *et al.* (1960) estimated the heritability of twinning as 11 % on the basis of data from Carnation Milk Farms. There were 1 416 dam-daughter pairs in the material, and the method of LUSH (1950) was used in estimating the heritability. Consequently, about 10 % is the most probable value for the heritability of multiple births in cattle for the present. This agrees very closely with corresponding estimates for litter size in swine (LUSH and MOLLN 1942, KORKMAN 1947 b) and sheep (JOHANSSON and HANSSON 1943, DESAI and WINTERS 1951, RENDEL 1956).

H. Other measures

KORKMAN (1947) estimated the heritability of sterility necessitating culling in the 13 119 calvings of Finnish Ayrshire cows used by him in studies on conception rate after the first service. Multiplying the intraclass-correlation between paternal half-sibs by four, he obtained the figure 10.1 %. Age effects were not completely eliminated from the results.

Besides the previously-mentioned characters of cystic ovaries, twinning tendency and short estrus periods, ERB *et al.* (1959) also estimated heritabilities for certain additional features of fertility. The following estimates were obtained: estrus after conception 4 %, abortions 5 %, stillbirths 5 %, physiological infertility 10 %, retained placenta 16 %, pathogenic infertility 17 %. Combinations of some of the measures gave still higher heritabilities. For example, the heritability of having either cystic ovary or short estrus cycles was 16 %, although the heritabilities of these features separately were 5 % and 11 %. A similar addition of estrus after conception, cystic ovary, twinning, short estrus and retained placenta led to a heritability estimate as high as 40 %. On the basis of these interesting results, the authors suggested that the features in question are caused by a common weakness in the endocrine constitution, which in turn is partly due to genotype.

III. PRESENT STUDIES

A. Material and methods

1. The nature of the approach

Most of the economically important characters of farm animals are physiologically so complex that a polygenic interpretation of their inheritance seems most logical. This is obviously also the case with regard to fertility traits although some of them have been explained as monogenic, as for example "the white heifer disease" by GREGORY *et al.* (1945) and RENDEL (1952) and ovarian hypoplasia by ERIKSSON (1943). In any case, the present study is exclusively based on the assumption of polygenic inheritance, and no attempt will be made to determine the number of genes affecting the traits. Typical of polygenic characters is a considerable sensitivity to different kinds of environmental influences. From the standpoint of breeding studies, the environmental factors can be divided into two groups:

(a) randomly distributed environmental factors, and
(b) systematically distributed environmental factors, which fall with different probabilities on different families, known as common factors or C-effects (LERNER 1958).

While studying the possibilities of breeding for different traits, special attention has to be paid to the elimination of the C-effects, because they erroneously increase the phenotypic correlation between members of the same family. Fulfillment of this requirement has been facilitated by the A. I. procedure, since semen of bulls is used approximately at random to inseminate cows in different parts of the area served by an A. I. unit. This is at least the case in Finland at present, when deep-frozen semen is being used only to a very limited extent. It is true that some enthusiastic cattle breeders, who at the same time can usually provide a better than average environment for their cows, may to some extent choose semen doses for their cows in the bigger A. I. units, but the frequency of such breeders is relatively low. The randomness of semen distribution cannot suffer seriously from this fact, especially since about 60 % of the inseminations are done with semen of young bulls (KSL 1962), and the preferences vary from breeder to breeder. In comparisons between progeny groups of bulls of different A. I. units, the C-effects may play a noticeable role for many reasons. Among these can be mentioned the dissimilarities of soil, climate, feeding and management, accuracy of data recording, and handling and dilution of semen in different areas of the country.

The use of data from A. I. populations is especially warranted for the study of low-heritability characters and application of the results to similar populations. Both practical experience and the heritability studies presented in the literature review have shown that the fertility traits to be studied here most probably belong in this category. The distribution of the daughters of A. I. bulls with regard to different kinds of environments can be considered to represent a wide spectrum of feeding and management routine. The applicability of the results is further improved by the fact that the effects of genotype-environment interactions and genic interactions, such as dominance and epistasis, are for the most part levelled out.

2. *Material*

For the reasons mentioned above, this study is almost exclusively based on variations of different fertility traits in progeny groups of A. I. bulls. Progeny of natural service bulls have been used only in a few cases to show how important it is to eliminate the C-effects. Separation of these two gategories of progeny caused considerable difficulties, since many bulls had first been used in natural service (N. S.) — either in bull associations or individual herds — and were brought into A. I. use only when their daughters began to seem promising. By considering the year of entry into A. I., the age classes of daughters born in N. S. could, for the most part, be omitted from the data. In the most recent material, similar difficulties were caused by the fact that young bulls are often lent to private herds during the time they are waiting for the results of progeny testing. To eliminate the daughters born during the waiting years or otherwise in N. S., higher standards than those originally planned were applied to the minimum mumber of daughters per sire in each particular age class. In several cases, the results of computations in which lower minimums were used are nevertheless presented to see the effect of this factor on the heritability estimates.

There were also some difficulties in assigning the bulls to specific A. I. units, since some interchange of bulls has occurred between the units. By a careful comparison of the year of change and the age class of the daughters, the most serious errors have been avoided. The use of several different bodies of data has been considered desirable, since no one set of statistics gives an exact picture of the inheritance of a character closely associated with natural fitness. Each material has its own limitations; these either prevent the genetic differences from becoming apparent or cause misleading similarities between relatives. Several independent samples can be expected to complement each other, so that some picture of the correct situation can be seen. The use of several samples also increased the volume of the data, since the intention was not only to study the variations in the fertility traits themselves, but also the variations in their heritability estimates.

The material used can be divided into two categories according to the source of information: (1) data obtained through the official milk-recording, and (2) data obtained through A. I. technicians in connection with their insemination visits. The former group will be called recording statistics, the latter A. I. statistics.

a) Recording statistics

Punch-cards bearing data from the milk-recording reports have been accumulated at the Department of Animal Breeding of the Agricultural Research Centre since the recording year 1949/50, when VARO (1952, 1954, 1956, 1958, 1960 a) began to develop the present method of mechanical progeny-testing of bulls. The data of the first years were not suitable for studies concerning fertility, since young, sick and otherwise abnormal cows were put in the same class as those with calving intervals of longer than 15 months. After the reorganization of milk-recording in 1956, it became possible to collect specific data on "overtimedness". This possibility was utilized in punching the data from the recording year 1956/57 and the data of 10 southern agricultural societies from the year 1957/58. At the same time, data were punched on the number of services required for the last calving of each cow and on the type of birth. The latter data made it possible to study the heritability of multiple births. This feature was not part of the original plan of the work, but was included because of the studies of ERB *et al.* (1959), according to which multiple births are an expression of the same endocrine disturbances as cystic ovaries, short estrus cycles and retained placenta. In addition, records concerning disturbances of sexual functions were obtained. Only Ayrshire cows were included, since the largest A. I. populations were available from this breed.

The average annual milk yield of the 3- to 6-yr. old Ayrshire cows at this time was about 3 700 kg, live weight 420—430 kg and fat content 4.55 %. This material is called recording statistics 1956/57 — 57/58.

The second body of material was from the recording year 1961/62. In this year, the number of services was noted on the punch-cards as the sum of all services required by the individual cow during its lifetime up to the last calving. Cards for all cows recorded by two agricultural societies were punched, without regard to age, even those culled during the year and those with incomplete first records. The preceding material, on the other hand, included only cows less than 6 years old which were alive at the end of the recording year. From the Häme-Satakunta Agricultural Society enough cows were available from both Ayrshire and Finncattle breeds, while from the Nyland Agricultural Society only Ayrshire cows could be used. The A. I. units working in these areas are the Tampere and Uusimaa A. I. societies, respectively, and hence the name Tampere and Uusimaa recording statistics 1961/62 is used for this material. Since two breeds were available from the first area, there were three different populations. The traits studied were the number of services and the cullings due to sterility.

The third body of material consisted of data on Ayrshire cows from the whole country in the year 1962/63. The number of services was recorded in the same way as in the preceding year, but the culled cows and those which had more than 3 complete records were not included. In addition, the numbers of regular calving intervals and multiple births were recorded; the latter concerned only the last calving of each cow. The average annual milk yield of the 54 000 young Ayrshire cows in this material was 4 040 kg, the fat content 4.62 %, the mean age at the first calving 25.5 months, and the 305 day milk yield of the first lactation 3 650 kg. This material will be called recording statistics 1962/63.

b) A. I. statistics

The A. I. material consists mainly of the A. I. statistics of Uusimaa A. I. Society from the period 1958—62, during which the statistics were kept on punch-cards. The principal measure of fertility in these statistics is the non-return percentage within 60 days after the first insemination. The later services were not taken into account, since they seemed to give fallacious percentages, obviously owing to natural services, cullings, etc. In the year 1958, data on the intensity of estrus, retained placenta, and the type of the preceding birth were also obtained. These features were included in this study for the same reason as multiple births in the recording statistics.

From the beginning of the year 1959, these three traits were replaced by observations on the occurrence of cystic ovaries. The presence of an abnormally large, persisting follicle in the ovary was determined by the A. I. technician by rectal palpation. Originally, there were 3 different classifications — no cyst, uncertain, certain — but the first two classes were later combined in the analyses. The diagnosis was made every time the individual cow was visited. In contrast to the study of HENRICSON (1957), where most of the diagnoses were made by veterinarians, all those in the present study were made by A. I. technicians. According to them, adequate skill can be readily obtained by experience. This is supported by the preliminary analysis of the data concerning cysts in 1959 (VARO 1960). This material, comprising only Ayrshire cows, will be called Uusimaa A. I. statistics 1958—62.

Besides these Finnish data, material from the Swedish A. I. societies was used in order to see the differences between societies and to obtain additional measures for the analysis. It was also thought that the more advanced system used for numbering herds and cows in Sweden and the considerable proportion of highly qualified personnel (veterinarians) engaged in the work would show what can be achieved under ideal conditions. The data were taken from the annual reports of the Svensk Husdjursskötsel from the years 1961 and 1962 (SHS 1961 and 1962). Only Swedish Red and White (SRB) cows were used in the analyses. The material will be called Swedish A. I. statistics 1961—62.

A more detailed picture of the nature of the material will become clear in the presentation of results of the analyses.

3. Methods

The data have been analyzed mainly according to the variance analysis methods developed by FISHER (1938) and SNEDECOR (1957). The textbooks of BONNIER and TEDIN (1957) and STEEL and TORRIE (1961) have also been consulted. The average numbers of animals in the groups were used as coefficients of variance components according to WINSOR and CLARKE (1940). In some parts of the data, the more advanced methods of SNEDECOR (1957, p. 273) and KING and HENDERSON (1954) were given a trial, since the method of WINSOR and CLARKE does not lead to wholly unbiased estimates of the variance components in data where the group sizes are variable, as is almost always the case with field data on farm animals. In the Uusimaa A. I. statistics for the year 1958, the method suggested by SNEDECOR increased the component due to sires in the variance of nonreturns to the first service from 0.26 % to 0.27 %, even when the progeny group size varied from 3 to 296 and the number of progeny groups in the different age classes from 30 to 97. By omitting the daughters of natural service bulls, the corresponding component rose to 0.53 %, although the total number of daughters decreased only from 10 608 to 9 238. The method of KING and HENDERSON was applied to the fertility traits of heifers in the Swedish A. I. statistics (Table 42), but the results were practically the same as by the simpler method of WINSOR and CLARKE. Thus the errors due to the statistical procedure seem to be slight as compared with those due to the variations and inaccuracies of the data and with those due to chance. In addition, the small errors due to the procedure usually lead to too cautious rather than too high an estimate of the relative importance of a particular cause of variation. This error was further diminished when the minimum number of daughters in each age class was increased.

The heritability estimates made by the simpler method can thus be considered to be just as reliable bases for breeding plans as the estimates obtained by methods which take proper account of the variations in sample sizes. Therefore, it was not considered necessary to perform the more complicated and expensive computations required by the finer methods. The simple procedure of WINSOR and CLARKE is especially valuable because of the flexibility in combining the sums of squares according to varying needs. It seems more important to confirm the results of an analysis by analyzing additional data than by striving for statistical perfection at any price. This applies especially to the present study, where the aim is to compare the usefulness of several different measures of fertility relating to the same material with equally variable sample sizes. The rank order of the measures will not change with the method of computing the coefficients of variance components.

Another statistical problem was caused by the fact that the phenotypic variation of most of the fertility traits studied deviated essentially from the normal distribution. The distribution of nonreturn rate, multiple births, occurrence of cystic ovaries, overtimedness, etc., is binomial, although they are in all probability caused by many genes. For example, the causes of returning to service vary from case to case, and it is logical to assume that the variation of these underlying causes approaches the normal distribution. This kind of situation has been studied by LUSH *et al.* (1948), ROBERTSON and LERNER (1949) and DEMPSTER and LERNER (1950). LUSH *et al.* and DEMPSTER and LERNER called such polygenic traits "threshold characters", while ROBERTSON and LERNER called them "all-or-none" traits. The variance of such a trait depends on the mean incidence of the trait, so that at both extremes the variance approaches and even reaches zero. When groups with varying means are compared in variance analysis, the variances within the different groups are not estimates of a common error variance, as is assumed in variance analysis (EISENHART 1947). The croups with a mean near 0.5 have a larger influence on the common error variance than groups with means near 0 or 1. In most cases, this fact decreases the proportion of the total variance due to between-group variance.

If the mean incidence is close to one or other extreme and the variance correspondingly small, then the differences between groups are difficult to detect, and the estimates of heritability necessarily remain low. At mean zero or unity the heritability is zero even when there are considerable differences between individuals with regard to the underlying causes. When the same population of animals is put into conditions where the threshold divides the individuals into two equal groups, the individual predispositions can influence the overstepping of the threshold, and an estimate of heritability deviating significantly from zero can be obtained. Therefore, heritability estimates obtained under different conditions are not comparable as such, although they are useful as bases for breeding plans under the circumstances in question.

In order to be able to compare the results derived from different data, special procedures are needed. WRIGHT (1926) used a method of "inverse probability", called by BLISS (1935) probit transformation. The basis of this transformation in heritability studies is the assumption that the trait under consideration depends on normally distributed factors, a certain dose of which is needed for the manifestation of the trait. The probit value shows the quality of a group of individuals as measured in these underlying variables.

LUSH *et al.* (1948) transformed the heritability estimates computed from the usual percentage scale into the probit scale by multiplying them by $\frac{p\,(1-p)}{z^2}$, where p is the mean incidence and z is the height of the ordinate which truncates p of the area of the normal curve. This transformation increased the heritability of mortality due to leukosis in poultry from 6.8 % to 15.6 %, while the heritability of the total mortality increased from 8.3 % to 14.5 %. Thus, the transformation made the heritability of the most important component of total mortality higher than the heritability of the total mortality itself. In the percentage scale, the heritability of mortality due to leukosis was low, because the mean incidence was only half of that of the total mortality. DEMPSTER and LERNER (1950) showed empirically the effect of the threshold level on heritability estimates by dividing hens into good and poor layers according to progressively increasing selection standards. When only 10 % of the best layers were classified as good, the heritability was 10 %, but when the hens were divided into two equal groups, the heritability was 23 %. As computed from the actual egg yields, the corresponding estimate in the same data was 36 %.

In the present study, transformations have not generally been used. It is only in cases where heritability estimates obtained for different measures from different data have been compared that the estimates have been standardized to a common incidence level by the method of LUSH *et al.* The reason for this limited use of transformations is that the main purpose of the study was to find the measures most suitable in practice as bases in breeding for fertility. Endeavors have been made to obtain realistic estimates which could be useful, especially in planning progeny testing of bulls with regard to fertility. This does not mean that the heritability of the underlying variates is without interest. On the contrary, this "theoretical heritability" could be considered an ideal heritability which can be approached when better measures of fertility are being sought.

The use of some kind of transformation also had to be considered with regard to the S/C, which has a one-sided distribution (Fig. 1). The logarithmic scale

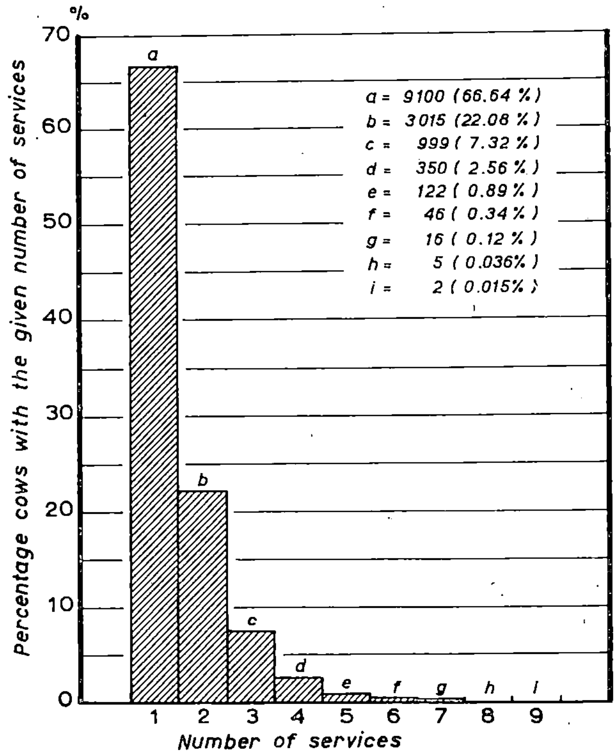

Fig. 1. Distribution of the number of services required for conception by 3- to 6-year old daughters of Ayrshire A. I. bulls in the recording year 1956/57.

obviously is one of the most suitable transformations in this kind of situation, and therefore it was tried on a small part of the data, namely that concerning services required for the second calving in three A. I. societies (Table 5). The F value for the variance between sires was 1.769, and the sire component of variance was 1.31 % of the total variance among 5 387 second-calvers, while the respective figures for the actual number of services were 1.815 and 1.39 %. Thus, the results given by the two methods seemed to be practically the same, and hence only the simpler one was used in the remaining analyses. The non-parametric method of variance analysis suggested by Kruskal and Wallis (1952) was similarly tried on a small amount of data, but the significance of the differences between sires appeared to be at the same level as in the conventional analysis of variance. Thus it was decided not to use this method further, especially since methods for estimating the relative variance components on this basis have not yet been developed.

The fourth statistical problem concerned the treatment of nonsignificant estimates of variance components. Theoretically, a negative value is not possible, but in practice such estimates can be obtained as a result of sampling.

If all negative estimates are made equal to zero, then the averages derived from several studies are biased upwards. Especially in heritability estimates this kind of procedure gives misleading results, as was stated in the literature review. For this reason, a compromise has been made in the present study, and the sire components of variance — being the most important from the viewpoint of this study — are taken at their face values, while the environmental components, when negative, are considered as zeros.

In coding the all-or-none characters for the statistical treatment, values of 1 and 0 were given to the alternative phenotypes, after which conventional analyses of variance were possible..

The most typical analyses of the present study correspond to the following hierarchical model:

$$Y_{hijkl} = \mu + s_h + t_{hi} + a_{hij} + b_{hijk} + e_{hijkl},$$

where Y_{hijkl} is the fertility record of the l^{th} daughter of the k^{th} A. I. bull in the j^{th} age class in the i^{th} year within the h^{th} A. I. society. In some cases, the order of s, t, and a was changed; some of them were omitted, and — in a very few cases — the model was altered so that an idea of the interaction component of age and bulls could be obtained.

Owing to the nature of the data used, the heritability estimates of the present study are exclusively based on the similarity of paternal half-sibs. They have been obtained by multiplying the percentage of the total variance due to sires by four. This is almost the only method possible in large data relating to a short period. ROBERTSON (1959 b) found that this method is also more effective than the parent-offspring regression at heritabilities lower than 25 %. It also facilitates the study of different age classes separately. Providing that the daughters of different A. I. bulls are distributed at random, this quadruple half-sib correlation describes the heritability in its narrow sense (LUSH 1949), which is important from the practical angle. Some epistatic effects are included in the estimates, but their importance is slight as compared with that of environmental and chance effects. A certain disadvantage can be seen from the fact that the sires are strongly selected and their variation accordingly small. The effect of this selection on the variance of their common daughter population is rather small, however, especially since it has not been possible to base their selection for A. I. use on the genotypes. With regard to a character such as fertility, where selection is necessarily very inaccurate, this aspect is not very important. The same applies to the possible danger that some sires had only been mated with certain kinds of cows.

It would have been desirable to supplement the heritability studies with repeatability estimates. However, since the data available were not suitable for repeatability studies, nothing was done on this line. Instead, heritability estimates for averages of several consecutive fertility records of individual cows were derived from the recording statistics 1961/62 and 1962/63.

As significance tests in the variance analyses, the conventional variance ratio of FISHER (1938), called the F test by SNEDECOR (1937), has been used. In addition, approximate standard errors for the heritability estimates have been computed according to the simple formula $S.E._{h^2} = (h^2 + \frac{4}{n})\sqrt{2/N}$ (ROBERTSON 1959 a), where n is the number of daughters per sire and N is the number of sires. The formula has been constructed for situations where the group size is constant, but in this study the average group size has been used as n. For this reason the standard errors of the heritability estimates and the significances of the F values do not completely agree. The disagreement is in such a direction that the F values may be significant even in cases where the standard errors do not indicate a significance. The difference is not large, however, and can be considered an additional safety marginal in drawing conclusions from the heritability estimates.

A more detailed presentation of the methods will be given in connection with each particular part of the study.

B. Results

1. Recording statistics 1956/57 — 57/58

Several studies have shown that the age of the cow is a factor affecting its fertility (HAMMOND 1927, CHAPMAN and CASIDA 1937, BOWLING *et al.* 1940, LASLEY and BOGART 1943, HILDER *et al.* 1944, TANABE and SALISBURY 1946, KORKMAN 1946, KOORT 1948, CARMAN 1954, LINDLEY *et al.* 1958, HENRICSON 1957, MORRISON and ERB 1957). Negative results have been reported by some workers (BERGE 1942, POU *et al.* 1953, BRANTON *et al.* 1956). This disagreement is partly due to the fact that different measures of fertility have been used by different authors. For example, the dependence of twinning frequency on the age of the cows is indisputable (JONES and ROUSE 1920, HEWITT 1934, JOHANSSON 1932, KORKMAN 1948, ERB and MORRISON 1959). The same applies to the occurrence of cystic ovaries (SONNENBRODT and RANNINGER 1949, CASIDA and CHAPMAN 1951, HENRICSON 1957). Thus, in the present analyses it was considered warranted to take age as a cause of variation, especially because the mean age of the progeny groups of different sires may be different. Similar systematic factors to be taken into account are the years and areas. In some cases, especially when the first daughters of a bull are served, the season of the year may also be a systematic factor, but it was not considered necessary to complicate the present study with this factor. It can be studied separately if additional refinements in the assessment of fertility become necessary.

In the recording statistics 1956/57 — 57/58, there were three different ways of measuring the age of the cows: according to (1) the year of birth, (2) the number of complete recording years in the cow's life, and (3) the number of the calving. With regard to overtimedness, all of these measures were tried, and interesting results were obtained. Therefore, the analyses concerning overtimedness will be presented first.

a) Overtimedness

According to the milk-recording regulations, which have been in force since the recording year 1956/57, a cow should be recorded as overtimed if calving has taken place more than 15 months after the preceding calving or

Table 3. Analysis of variance in the overtimedness of 3—6-yr.old Ayrshire cows in the recording statistics 1956/57—57/58.

Source of variance	Degrees of freedom	Mean square	Calculated variance		h² ± S. E.
			ð	%	%
I—V-calvers 1956/57					
Total variance	11 334	0.0683954	0.0684480	100.00	
Between calving classes	4	0.6635000(*)	0.0002018	0.29	
Between A.I. units	10	0.2060000(*)	0.0001164	0.17	
Between sires	275	0.1180655***	0.0013111	1.92	7.68±1.49
Within „	11 045	0.0668187	0.0668187	97.62	
I—IV records 1956/57					
Total variance	9 638	0.0723749	0.0723818	100.00	
Between rec. classes	3	0.1388333	0.0000057	0.01	
Between A.I. units	8	0.1251875(*)	0.0000515	0.07	
Between sires	261	0.0838379*	0.0003356	0.46	1.84±1.13
Within „	9 366	0.0719890	0.0719890	99.46	
3—6-yr.old 1956/57—57/58					
Total variance	32 829	0.0679329	0.0699090	100.00	
Between age classes	3	5.8469333***	0.0006748	0.96	
Between A.I. units	8	0.3085375	0.0000260	0.04	
Between years	12	0.2375083***	0.0001103	0.16	
Between sires	412	0.0866913***	0.0002368	0.34	1.36±0.45
Within „	32 394	0.0688611	0.0688611	98.50	

In all the tables: ***=P<0.001; **=P<0.01; *=P<0.05; (*)=P<0.20

if the age of a heifer at her first calving is more than 36 months. The records should be made in the year of the calving in question. If no calving takes place, no record of the normality of the C. I. should be made in that year. Under the older regulations, however, a certain overtimedness could cause a record to be made several times (the year the cow was becoming overtimed, the year the cow did not calve, and the year her overtimed calving occurred). The consequences of these old regulations may have had some influence on the statistics during the first years after the reform of the regulations.

In each age class, those sires which had at least 3 daughters were first accepted for the variance analysis. If there was some uncertainty as to whether all of these were born in A. I., larger numbers were required. Information on the record or calving number or birth year was lacking in many cases, and thus the bodies of data concerning these three measures of age were not equal in size. The results are shown in Table 3.

The first striking feature to be noticed is the overwhelmingly highest heritability estimate in the analysis where the computations were done within calving classes. Its deviation from zero is highly significant, five times its standard error. The estimate in the last analysis is also three times its standard error, but its numerical value is only a little over 1 %. The difference between these two estimates is also highly significant. Obviously, calving or lactation number is biologically the soundest measure of age in dairy cattle.

The differences between A. I. units were not significant in any of the analyses, although some indications of their existence could be seen in the first two analyses.

With regard to age class means, some indications of differences could be found when the age was measured by calving number. The corresponding differences were highly significant, however, when the age was measured according to the year of birth. In this latter analysis, there were also highly significant differences between the recording years. In order to find an explanation for these two kinds of differences, Table 4 was constructed, where the distribution of cows and the mean overtimedness in different age classes are presented.

Table 4. Numbers of cows and their mean overtimedness in different age classes; age measured in three different ways.

Age class			Number of cows					Average overtimedness, %				
Calving	Record	Age years	Calving	Record	Age in years			Calving	Record	Age in years		
					1956/ 1957	1957/ 1958	Total			1956/ 1957	1957/ 1958	Total
I	—	—	355	—	—	—	—	13.80	—	—	—	—
II	I	3	5375	3999	1545	3103	4648	8.07	7.68	2.65	1.55	1.91
III	II	4	3441	3059	5981	6827	12808	6.71	7.49	9.50	7.48	8.42
IV	III	5	1900	1989	4402	4813	9215	6.00	8.04	8.68	7.56	8.10
V	IV	6	264	592	2748	3411	6159	3.41	10.30	9.53	8.80	9.12
Total & ave.			11335	9639	14676	18154	32830	7.38	7.85	8.54	6.74	7.54

There were very few cows which did not have their second calving before the end of their first complete recording year. As many as 13.8 % of these were recorded as overtimed, a reflection of the old regulations. A small part of this percentage may be due to the heifers that were more than 36 months old at their first calving.

On the other hand, those cows that proceeded to their 4^th^ and 5^th^ calvings before becoming 6 years old could not have long calving intervals, and thus the mean overtimedness in these calving classes is biased downwards.

The means for 3-year-old cows are considerably lower than those for the other age classes. The difference between years in this age class is due to the fact that heifers calving during the first 3 months of the recording year (June, July, August) were included in the year 1957/58, but not in 1956/57. The yearly differences in the older age classes are more difficult to explain. They may be partly actual and partly due to the fact that the after-effects of the old regulations were less evident in the latter year's records than in the first year after the reform of the regulations.

It can be concluded from Table 4 that if the first-calvers are not considered, the effect of age on the fertility of relatively young cows is rather slight. This can also be seen from Table 5, where percentage variance components and heritability estimates are presented separately for different age classes.

The upper part of the table shows that the heritability of overtimedness per calving declined a little when the abnormal classes I and V were eliminated.

Table 5. Components of variance in the overtimedness in different age classes; age measured in three different ways. At least 3 daughters per sire per age class.

Age class	Numbers		% of total variance				Error variance	$h^2 \pm$ S. E
	Sires	Cows per sire	Betw. age classes	Between A.I. units	Between years	Between sires		%
II calving	81	66.4	—	0.02	—	2.67***	0.0722716	10.68±2.62
III —»—	70	49.2	—	0.00	—	0.20	0.0625607	0.80±1.51
IV —»—	62	30.6	—	0.00	—	0.05	0.0563999	0.20±2.38
II—IV —»—	213	50.3	0.11*	0.00	—	1.49***	0.0663773	5.96±1.35
I record ...	84	47.6	—	0.07(*)	—	0.83**	0.0702795	3.32±1.81
II —»— ...	80	38.2	—	0.16(*)	—	0.17	0.0690866	0.68±1.76
III —»— ...	69	28.8	—	0.00	—	—0.34	0.0742979	—1.36±2.60
IV —»— ...	40	14.8	—	0.10	—	0.85	0.0917466	3.40±6.81
I—IV —»— ...	273	35.3	0.01	0.07(*)	—	0.46*	0.0719890	1.84±1.13
3-yr.old	102	45.6	—	0.00	0.25*	0.14	0.0187229	0.56±1.31
4 —»—	124	103.3	—	0.00	0.33**	0.28*	0.0767331	1.12±0.63
5 —»—	111	83.0	—	0.08	0.00	0.83***	0.0737603	3.32±1.09
6 —»—	99	62.2	—	0.11	0.04	0.26(*)	0.0826362	1.04±1.06
4—6 —»—	334	84.4	0.00	0.04	0.16**	0.46***	0.0770458	1.84±0.51
Daughters of N.S. bulls 1956/57:								
4—6-yr.old	468	14.0	0.00	—	—	3.44***	0.0608989	13.76±2.77

Nevertheless it remained at an unexpectedly high level, close to 6 %. Special attention is automatically drawn to the figure of 10.68 % as the heritability of overtimedness before the second calving. If this figure can be confirmed in other studies, it obviously can be explained as a reflection of the heritability of milk yield in the first lactation. It was not possible, however, to study the influence of lactation milk yield on the heritability of overtimedness, since the milk yield was measured only on an operational year basis.

The fact that the heritability of overtimedness was not high at the later lactations obviously means that there are especially great accommodation difficulties to lactation after the first calving. This is supported by practical experience, according to which the calving season of cows is most radically changed between the first and second calvings.

In the computations where the age classes were arranged by the number of the record or by the year of birth, the second-calvers were separated into different age classes, and consequently there were not such high estimates of heritability. However, the second calving mostly takes place during the first complete recording year, and this is reflected in the corresponding heritability estimate. Generally, it does not seem to make any difference whether age is measured according to the number of the recording year or according to the birth year.

There were not many differences between the 3 A. I. units in overtimedness. This does not mean that differences between areas do not occur. In some other units, especially in Ostrobothnia, the average overtimedness was essentially lower than in the 3 units in question, but there were not enough data to warrant their inclusion in the study.

The yearly differences seen in Table 4 were small enough in the data of 5- and 6-years old cows to be explained by differences between sires.

Table 6. Components of variance in the overtimedness (at least 20 daughters per sire in each age class).

Age class	Numbers		% of total variance				Error variance	$h^2 \pm$ S. E.
	Sires	Cows per sire	Betw. age classes	Between A. I. units	Between years	Between sires		%
II calving	40	82.5	—	0.00	—	1.50***	0.0708674	6.00±2.43
III —»—	38	60.6	—	0.00	—	0.24	0.0626637	0.96±1.73
IV —»—	26	48.8	—	0.00	—	—0.33	0.0544566	—1.32±2.64
II—IV —»—	104	66.1	0.07(*)	0.00	—	0.80***	0.0651043	3.20±1.28
I—IV record	150	57.2	0.00	0.04	—	—0.02	0.0707095	—0.08±0.82
3—6-yr.old	393	82.0	0.95***	0.03	0.16***	0.32***	0.0690610	1.28±0.44
4—6 —»—	307	90.5	0.00	0.03	0.17**	0.41***	0.0770716	1.64±0.49
4 —»—	118	107.7	—	0.00	0.33***	0.30**	0.0769903	1.20±0.64
5 —»—	104	87.6	—	0.06	0.02	0.70***	0.0736383	2.80±1.02
6 —»—	85	70.3	—	0.09	0.03	0.22(*)	0.0824921	0.88±1.01

The last row in Table 5 has been derived from daughters of natural service bulls and is comparable with the row just above it. The comparison shows very clearly how important it is to eliminate the systematic environmental factors from the analyses. Obviously, much of the overemphasis which many non-statisticians place on heredity as a cause of variation in fertility is due to overlooking this fact. It should also be considered as a factor tending to bias upwards the results concerning daughters of A. I. bulls. In order to determine the magnitude of this bias, the computations were also made using only daughter groups of at least 20 daughters for the analyses of each particular age class. These results are presented in Table 6.

When the figures of Table 6 are compared with those of Table 5, a certain decline can be seen in the heritability estimates as a result of the elimination of the small progeny groups. Although this could be explained as due to a reduction of the genetic variability between the bulls, this is unlikely to be the case, because of the inaccuracy of the assessment of fertility. On the other hand, this explanation might be valid if the whole heritability of overtimedness is only a reflection of the heritability of milk producing ability.

With regard to the computations where age grouping was done according to the number of the yearly records, there was a radical effect: no heritability remained. There was also a change in the values concerning different calvings, but certain significant estimates remained. For example, the estimate of the heritability of overtimedness in the first lactation was not less than 6 %, and the combined estimate for the first 3 lactations was 3.2 %. This latter figure is biased downwards because it includes the IV-calvers. As can be seen from the error variance of the IV-calvers in Tables 5 and 6 and the means in Table 4, this class does not contain enough unfertile animals. The same also applies in a certain degree to the III-calvers. It thus appears that if all the overtimed animals were included, the combined estimate would be higher than 3.2 %, probably over 4 %.

No essential change occurred in the estimates where age had been reckoned from the year of birth. Nevertheless, the pooled estimate was lower than the corresponding estimate concerning calving classes.

Table 7. Components of variance in the overtimedness of II—IV-calvers in three A. I. units. A=at least 3 daughters per sire per age class, B=at least 20 daughters.

A. I. unit	Numbers				Error variance		$h^2 \pm$ S. E., %	
	A		B					
	Sires	Cows/sire	Sires	Cows/sire	A	B	A	B
South-west Finland	90	65.5	49	79.7	0.066792	0.066469	2.52±1.29	3.32±1.68
Lahti	51	46.2	27	49.8	0.071005	0.067880	3.56±2.42	1.52±2.60
Uusimaa	72	34.2	28	57.9	0.060908	0.059508	17.52±4.87	4.40±3.02

Although the means of different A. I. units did not differ essentially from each other, it is possible that the heritabilities do vary from area to area. Therefore the results are presented by A. I. units in Table 7.

No valid conclusions can be derived from the differences between the heritability estimates from different areas, although the values from the Uusimaa area tend to be higher than those from the others.

b) Number of services

The number of services required for the calving taking place during a given recording year should — according to the regulations — be reported for each individual cow in each annual milk-recording report. Services made during one heat are then considered as one service. Several different measures of fertility can be derived from these records. For example, the proportion of cows conceiving at the first service can be used. There are, however, many environmental factors which may cause failure in the first service, and consequently it is reasonable to expect that the heritability may become higher if the cows are given more chances to conceive. The question of the best measure can only be solved empirically. Therefore, heritability estimates concerning four different measures based on the number of services are presented in Table 8. The computations have here been made only within calving classes, since the number of calvings seemed to be the most natural measure of age in the studies concerning overtimedness in the same data.

The total number of services required for a conception proved to have the highest heritability in both series of computations, while the rank order of the other measures varied slightly in the two series. The results of the latter series are evidently more accurate. The heritability of conception after 2 or 3 services is low, since the means and variances of these measures are so close to zero.

The differences between calving classes which could not be explained by differences between sires were found only in the upper part of Table 8. These

Table 8. Components of variance in the conception after 1, 2 and 3 services and in the number of services per conception (S/C).

Calving class	Minim. no. of cows/sire	Measure of fertility	Numbers		% of total variance			Error variance	$h^2 \pm$ S. E.
			Sires	Cows per sire	Between calving classes	Between A. I. units	Between sires		%
I—V	3	C. 1 serv.	314	36.1	0.08(*)	0.00	0.48*	0.225123	1.92±1.04
»	3	C. 2 »	314	36.1	0.07(*)	0.00	0.63**	0.104982	2.52±1.09
»	3	C. 3 »	314	36.1	0.25**	0.00	0.64**	0.039823	2.56±1.09
»	3	S/C	314	36.1	0.11(*)	0.00	1.11***	0.808445	4.44±1.24
II—IV	20	C. 1 serv.	128	76.0	0.00	0.00	0.43*	0.226773	1.72±0.87
»	20	C. 2 »	128	76.0	0.02	0.00	0.41*	0.106388	1.64±0.86
»	20	C. 3 »	128	76.0	0.02	0.00	0.13	0.040120	0.52±0.72
»	20	S/C	128	76.0	0.02	0.00	0.51**	0.807950	2.04±0.91

Table 9. Means and heritabilities of the S/C in different calving classes. A = at least 3 daughters per sire per age class, B = at least 20.

Calving	Numbers A Sires	Numbers A Cows/sire	Numbers B Sires	Numbers B Cows/sire	Means A	Means B	Error variance A	Error variance B	h² ± S. E. % A	h² ± S. E. % B
I	47	7.6	—	—	1.556	—				
II	93	57.9	54	93.7	1.525	1.524	0.782280	0.774144	5.56±1.83	3.60±1.51
III	80	42.9	45	69.0	1.534	1.535	0.819320	0.820631	1.56±1.72	—0.72±1.32
IV	66	28.8	29	54.0	1.553	1.575	0.853359	0.892839	0.32±2.47	2.40±2.58
V	28	9.3	—	—	1.437	—	—	—	—	—
II—IV	239	44.9	128	76.0	1.531	1.536	0.806566	0.807950	3.36±1.12	2.04±0.91

differences are due to the extreme classes I and V, as can be seen from Table 9. If the extreme classes are excluded, only very small age differences remain. This was also the case with regard to overtimedness.

There were no differences at all between the means of different A. I. units which could not be explained by sire differences.

A comparison of the heritability estimates concerning overtimedness (Tables 5 and 6) and S/C (Table 8) reveals that the former measure has a somewhat higher heritability. The difference between the estimates of II- to IV-calvers from the most reliable computations is 1.16 ± 1.57 %, which is far from significance. This difference may be due to the different inclusion of silent heats in the two measures. In spite of this small difference, surprisingly similar results were obtained from the two measures. The similarity is still more evident in Table 9, where the heritability of S/C is estimated separately for the second, third and fourth conceptions. Just as with regard to overtimedness in Tables 5 and 6, the second conception definitely showed the highest heritability in S/C. The difference between the two measures at this point (2.40 ± 2.86 %) is not significant.

In Table 10, the heritability of S/C in different A. I. units is shown.

Although there are no significant differences, the low values of the South-West Finland A. I. unit are noteworthy. If these results could be accepted as

Table 10. Means and heritabilities of the S/C of II—IV-calvers in three A. I. units. A = at least 3 daughters/sire/age class, B = at least 20.

A. I. unit	Calving class	Sires A	Sires B	Cows per sire A	Cows per sire B	Means A	Error variance A	Error variance B	h² ± S. E., % A	h² ± S. E., % B
SW. Finl.	II—IV	97	63	60.2	88.1	1.540	0.829746	0.819092	0.92±1.09	1.36±1.05
Lahti	»	65	34	37.1	63.9	1.534	0.805209	0.820519	6.88±3.10	2.32±2.08
Uusimaa	»	77	31	32.0	64.7	1.513	0.752090	0.763377	6.56±3.07	3.92±2.57
SW. Finl.	II	40	—	73.9	—	1.529	0.797951	—	3.76±2.05	—
Lahti	»	23	—	49.3	—	1.552	0.867084	—	5.88±4.13	—
Uusimaa	»	30	—	43.3	—	1.493	0.672049	—	10.32±5.05	—

valid, the most natural explanation for them would be the free sterility treatment in this unit. By treating a cow in due time one can avoid many unsuccessful services. It was not possible to study whether any of the heritability of the S/C remains when variations in the lactation milk yield are eliminated.

c) Multiple births

Causes of variation in the frequency of multiple births were also studied in the data of the recording year 1956/57. The results are presented in Table 11.

Table 11. Components of variance in the frequency of multiple births of Ayrshire cows in the recording year 1956/57.

Age class	Minim. no. of cows/ sire	Numbers		% of total variance			Error variance	$h^2 \pm$ S.E.
		Sires	Cows per sire	Between age classes	Between A. I. units	Between sires		%
I—V calv.	3	290	38.8	0.10(*)	0.05	0.19	0.0133648	0.76±0.92
II—IV »	20	104	65.8	0.31(*)	0.10(*)	0.52*	0.0131594	2.08±1.13
I—IV rec.	20	136	54.3	0.11(*)	0.00	0.52*	0.0135581	2.08±1.15

In contrast to the overtimedness and the S/C, where exclusion of the small daughter groups tended to decrease the heritability estimates, higher values were obtained for the heritability of multiple births when only the large progeny groups were used in the analyses. In addition, the result was the same whether the computations were made according to calving sequence or record sequence. These two differences indicate that the causes of multiple births are different from the causes of overtimedness or number of services. This is also reflected in the effect of age on the frequency of multiple births, as can be seen from Table 11 and from the following average frequencies in the data where the minimum number of daughters per sire was three:

II-calvers:	50	multiple births among	5 370	calvings,	or	0.931 %
III- —»—	59	—»—	3 400	—»—		1.735 »
IV- —»—	36	—»—	1 890	—»—		1.905 »

It should also be mentioned that the heritability of multiple births at the second calving was not higher than that at the other calvings.

d) Frequency of fertility disturbances

In the milk-recording report form there is a column for remarks concerning different kinds of disturbances and veterinary treatments. The intention is that every treatment should be recorded. A recent analysis of these records from the years 1956/57 — 57/58 showed that the proportions of different diseases in these remarks is in agreement with the official veterinary statistics, but that

Table 12. Analysis of variance in the fertility disturbances of 4—6-yr. old Ayrshire cows according to remarks in milk-recording reports, 1956/57 — 1957/58. At least 20 daughters/sire/age class.

Source of variance	D. f.	Mean square	Calculated variance		$h^2 \pm$ S. E.
			δ	%	%
Total variance	30203	0.00533494	0.00533571	100.00	
Between age classes	2	0.02870000(*)	0.00000187	0.04	
Between A. I. units ..	9	0.00986667	0.00000100	0.02	
Between sires	188	0.00736170**	0.00001352	0.25	1.00±0.37
Within »	30004	0.00531932	0.00531932	99.69	

only 10—20 % of the veterinary treatments are noted in the milk-recording reports (Maijala 1964). In spite of this, it was considered to be of interest to analyze the data concerning fertility disturbances. The results are shown in Table 12.

The analysis indicated significant differences between sires, so that a heritability estimate of 1 % was obtained. The differences between years were not eliminated, but the data of the two successive years were combined for each sire. Consequently, there may be some upward bias in the heritability estimate. On the other hand, the age of the cows was measured according to the year of birth, a procedure which in regard to overtimedness yielded a markedly lower value for heritability than grouping based on lactation number. It is obvious that this fact more than counterbalances the bias due to the year effects.

There were 13 674 records of 4-year old cows, 0.53 % of which were reported as disturbed by sterility. The respective figures for 5- and 6-year old cows were 0.39 % and 0.77 %. It can be mentioned that the frequency of sterility treatment in the South-West Finland A. I. Society is about 13 %. Consequently, hardly 10 % of them are reported in the milk recording.

The heritability of the reported fertility disturbances was highest among the 4-year old cows, namely 1.88 ± 0.67 %, while the estimate was only 0.24 % for the 5-year old and 0.12 % for the 6-years old animals. It thus appears that also in this measure, the hereditary differences mainly concern the first lactation. The estimate on the South-West Finland A. I. unit did not deviate essentially from the general estimate (1.12 % — 1 %).

2. *Recording statistics 1962/63*

a) Overtimedness

In the material of the recording year 1962/63, data on overtimedness were punched as the total number of regular calvings during the life of the cows. The first calving was considered as regular if it had taken place before the age of 3 years. Since the total number of calvings was also recorded, it was

Table 13. Numbers of Ayrshire cows, sires and calvings in data from the recording statistics 1962/63.

A. I. unit	Min. no. of cows per sire	No. of sires in different calving classes				Number of cows in different calving classes				Cumulative number of calvings			
		I	II	III	IV	I	II	III	IV	I	II	III	IV
SW. Finland	10	38	103	87	64	727	5 816	5 244	4 552	727	11 632	15 732	18 208
Tampere	10	1	8	9	9	10	313	325	267	10	626	975	1 068
Lahti	10	19	39	37	33	596	3 422	3 258	2 508	596	6 844	9 774	10 032
Uusimaa	10	28	72	62	52	568	4 117	4 070	3 537	568	8 234	12 210	14 148
Oulu	10	1	4	4	5	10	130	98	94	10	260	294	376
S. Ostrobothnia	10	11	28	23	22	214	1 860	1 628	1 616	214	3 720	4 884	6 464
Pieksämäki	10	5	5	3	2	100	422	364	74	100	844	1 092	296
Satakunta	10	1	8	8	9	13	175	194	201	13	350	582	804
A. I. total	10	104	267	233	196	2 238	16 255	15 181	12 849	2 238	32 510	45 543	51 396
—»—	20	44	217	182	152	1 455	15 529	14 476	12 229	1 455	31 058	43 428	48 916
N.S. total	10	2	76	90	102	21	1 037	1 313	1 454	21	2 074	3 939	5 816
A. I. + N. S.	10	106	343	323	298	2 259	17 292	16 494	14 303	2 259	34 584	49 482	57 212

Table 14. Average number of regular calvings per cow and calving in data from the recording statistics 1962/63.

A. I. unit	Min. no. of cows per sire	Regular calvings per cow in different calving classes				Regular calvings per calving in different calving classes			
		I	II	III	IV	I	II	III	IV
SW. Finland	10	1.003	1.878	2.815	3.818	1.003	0.939	0.938	0.955
Tampere	10	1.000	1.859	2.818	3.816	1.000	0.930	0.939	0.954
Lahti	10	1.000	1.884	2.824	3.825	1.000	0.942	0.941	0.956
Uusimaa	10	1.002	1.901	2.810	3.824	1.002	0.951	0.937	0.956
Oulu	10	1.000	1.923	2.867	3.798	1.000	0.962	0.956	0.949
S. Ostrobothnia	10	1.019	1.899	2.836	3.851	1.019	0.950	0.945	0.963
Pieksämäki	10	1.030	1.896	2.827	3.838	1.030	0.948	0.942	0.959
Satakunta	10	1.000	1.880	2.747	3.736	1.000	0.940	0.916	0.934
A. I. total	10	1.005	1.888	2.818	3.824	1.005	0.944	0.939	0.956
—»—	20	1.003	1.888	2.816	3.824	1.003	0.944	0.939	0.956
N. S. total	10	1.000	1.916	2.834	3.867	1.000	0.958	0.945	0.967
A. I. + N. S.	10	1.004	1.890	2.819	3.828	1.004	0.945	0.940	0.957

possible to get an idea of the proportion of regular calvings — or of its complement, the proportion of overtimed calvings. Because the total also included the earlier calvings of the cows, the data were actually from several recording years. For instance, in the case of a cow which had her third complete record year in 1962/63 and which had calved the fourth time during that year, the first calving must already have taken place during the recording year 1959/60. For cows which were culled during the recording year 1962/63, data were taken from the previous report (1961/62).

The results were calculated only for those progeny groups of Ayrshire breed in each calving class having at least 10 daughters for which there was information on overtimedness. After preliminary analyses it was found appropriate to perform the analyses on two different minimum group sizes, namely 10 and 20 daughters. The volume of the data can be seen from Table 13.

The total number of calvings on which information was available was thus 143 537. Rather small numbers of I-calvers were available. The reason for this is the same as in the previous material. Increasing the minimum group size from 10 to 20 did not reduce the data very much. The average numbers of regular calving intervals per cow and calving are shown in Table 14.

The means of the I-calvers are somewhat illogical, presumably because of errors in reporting the number of calvings. The comparison of the other means with those in Table 4 is made difficult by the inclusion of the results of first calving in the figures in Table 14, but no major changes can have taken place. For the difference between the III-calvers and II-calvers is 0.929, which means an overtimedness of 7.1 %. The corresponding figure for III-calvers in Table 4 is 6.71 %. The means of the IV-calvers are abnormally high, since only the most fertile cows can have their fourth calving before the end of their complete recording year. In spite of this, analyses have also been made on the IV-calvers.

The figures concerning the daughters of N. S. bulls seem to be a little higher than those of A. I. populations, but the minimum group size did not affect the means of the A. I. cows.

In the analysis of variance, the number of regular calving intervals was used as a variable in each calving class. Since the error variances in the different classes were not estimates of a common variance, a pooling of the results was not possible. The results are therefore presented separately for each calving class in Table 15.

Only the two uppermost entries in each calving class deserve serious attention. Even they can be disregarded as far as concerns the abnormal data from the first calving. Attention is first paid to the fact that the minimum group size applied did not affect the heritability estimates as in the data of the recording year 1956/57. Secondly, the estimates of II-calvers are surprisingly low. It is difficult to find reasons for this other than the fact that overtimedness before the first calving may bear no relation at all to overtimedness

Table 15. Components of variance in the cumulative number of regular (< 15 months) calving intervals of I—IV-calvers of Ayrshire breed in the recording statistics 1962/63.

Nature of data			Numbers			% of total var.		Error variance	h² ± S. E. %
Calving no.	A. I. or N. S.	Minim. no. of cows/sire	A. I. units	Sires	Cows per sire	Between A. I. units	Between sires		
I	A. I.	20	5	44	33.1	1.54**	—0.75	0.0027286	—3.00±3.22
»	»	10	5	101	21.8	1.26***	0.45	0.0044487	1.80±2.84
II	A. I.	20	8	317	71.6	0.09*	0.49***	0.102505	1.96±0.72
»	»	10	8	267	60.9	0.07*	0.53***	0.102959	2.12±0.75
»	N. S.	10	—	76	13.6	—	1.57(*)	0.081426	6.28±5.79
III	A. I.	20	8	182	79.5	0.00	1.04***	0.183890	4.16±0.96
»	»	10	8	233	65.2	0.00	1.08***	0.183202	4.32±0.97
»	N. S.	10	—	90	14.6	—	0.75	0.188986	3.00±4.53
IV	A. I.	20	8	152	80.5	0.03	0.43**	0.174703	1.72±0.77
»	»	10	8	196	65.6	0.07(*)	0.59***	0.174853	2.36±0.85
»	N. S.	10	—	102	14.2	—	8.61***	0.129749	34.44±8.77

before the second calving. When the two unrelated measurements are combined, a low heritability may be the result. The heritability is increased when the results of the 3rd calving are added. This suggests that overtimedness during the 2nd lactation is related to that either before the first calving or during the first lactation. It seems to be more logical to assume that it is related to the latter. In any case, the heritability of cumulative overtimedness up to and including the third calving appears to be about 4 %.

The estimates at the fourth calving are greatly lowered as a result of the fact that no unfertile animals could be included in the data. This is also seen from the error variances: those concerning the IV-calvers are even smaller than those of the III-calvers. The effect is still more radical in the N. S. material, but here it obviously is distributed systematically among the different daughter groups, so that an excessively high heritability estimate is obtained.

The differences between A. I. units were highly significant in the abnormal class I and significant in class II, while their importance in the other classes was negligible.

Table 16. Heritability of the cumulative number of regular calving intervals in four A. I. units. At least 10 daughters/sire.

A.I. unit	Error variance			Heritability ± standard error (%)		
	II calving	III calving	IV calving	II calving	III calving	IV calving
SW. Finland	0.111582	0.189319	0.184160	2.32±1.31	4.04±1.62	0.68±1.12
Lahti	0.105457	0.172698	0.176073	1.08±1.28	3.20±1.80	3.80±2.23
Uusimaa	0.092633	0.189064	0.175047	2.84±1.64	5.68±2.12	0.64±1.28
S. Ostrobothn.	0.091299	0.163445	0.137033	1.16±1.92	5.08±3.16	3.28±2.63

In Table 16, heritabilities have been estimated separately for the four largest A. I. units.

Excluding the abnormal data concerning IV-calvers, there seem to be no large differences between the units. However, the rank order in class III is the same as that of the II- to IV-calvers in Table 7, the Uusimaa unit having the highest heritability.

b) Number of services

The number of services required by each cow was recorded in the same way as the regularity of calving intervals, that is, cumulatively since the very first service. Precisely the same cows were available for this analysis as for the overtimedness. The averages of different calving classes in the data are shown in Table 17.

Table 17. Average numbers of services per cow and calving in data from the recording statistics 1962/63.

A. I. unit	Min. no. of cows per sire	Number of services/cow in different calv. classes				Number of services/calving in different calv. classes			
		I	II	III	IV	I	II	III	IV
SW. Finland	10	1.444	2.848	4.353	5.533	1.444	1.424	1.451	1.383
Tampere	10	1.100	2.958	4.348	5.562	1.100	1.479	1.449	1.390
Lahti	10	1.413	3.048	4.559	5.778	1.413	1.524	1.520	1.444
Uusimaa	10	1.452	2.989	4.472	5.647	1.452	1.494	1.491	1.412
Oulu	10	1.400	2.677	4.214	5.245	1.400	1.338	1.405	1.311
S. Ostrobothnia	10	1.355	2.839	4.243	5.257	1.355	1.420	1.414	1.314
Pieksämäki	10	1.800	3.147	4.505	5.905	1.800	1.573	1.502	1.476
Satakunta	10	1.462	2.840	4.412	5.587	1.462	1.420	1.471	1.397
A. I. total	10	1.444	2.933	4.421	5.579	1.444	1.467	1.474	1.395
—»—	20	1.438	2.938	4.424	5.585	1.438	1.469	1.475	1.396
N. S. total	10	1.524	2.803	4.225	5.244	1.524	1.402	1.408	1.311
A. I. + N. S.	10	1.444	2.926	4.405	5.545	1.444	1.463	1.468	1.386

The picture given by the means is about the same as that of overtimedness in Table 14. However, the first-calvers here are rather similar to the other age classes. The average number of services per calving does not seem to change much from age class to age class. The lower figure of the IV-calvers was already explained in connection with overtimedness. The fact that the general level in the present data is slightly lower than in the data from the recording year 1956/57 may indicate that not all of the services are included in the cumulative figures.

The results of the variance analysis are presented in Table 18.

Just as with regard to overtimedness, the heritability estimates did not depend on the minimum group size applied in the A. I. data, except in the data on the I-calvers. The estimates are somewhat higher in each age class

Table 18. Components of variance in the cumulative number of services of I—IV-calvers of Ayrshire breed in the recording statistics 1962/63.

Nature of data			Numbers			% of total var.		Error variance	$h^2 \pm$ S E. %
Calving no.	A. I. or N.S.	Minim. no. of cows/ sire	A. I. units	Sires	Cows per sire	Betw. A. I. units	Between sires		
I	A. I.	20	5	44	33.1	0.46(*)	0.45	0.768214	1.80±2.96
»	»	10	5	101	21.8	0.82**	0.92	0.765779	3.68±3.10
II	A. I.	20	8	217	71.6	0.53***	1.00***	1.587603	4.00±0.92
»	»	10	8	267	60.9	0.56***	1.05***	1.578478	4.20±0.93
»	N. S.	10	—	76	13.6	—	6.23***	1.557898	24.92±8.81
III	A. I.	20	8	182	79.5	0.36***	1.52***	2.560885	6.08±1.16
»	»	10	8	233	65.2	0.35***	1.60***	2.543195	6.40±1.16
»	N. S.	10	—	90	14.6	—	4.72***	2.100818	18.88±6.90
IV	A. I.	20	8	152	80.5	0.99***	0.85***	2.668890	3.40±0.96
»	»	10	8	196	65.6	0.92***	1.01***	2.665758	4.04±1.02
»	N. S.	10	—	102	14.2	—	8.94***	1.851820	35.76±8.95

than the corresponding estimates on overtimedness. For instance, at the second calving the difference is 2.04 ± 1.17 %, and at the third 1.92 ± 1.51 %. The differences are not fully significant, but because the data were independent of each other, the results confirm one another, and the existence of a real difference seems to be very probable. In any case it appears that cows can be judged for genetic fertility with an accuracy of 4—6 % at the time of their third calving. The fact that the heritability estimates increased with the number of calvings indicates that still better accuracies may be obtained at the later ages.

The estimate on the II-calvers is again low as compared with the heritability of the number of services required for the second calving separately (Table 9). It is not known what the heritability of the cumulative number of services would be if the services before the first calving were excluded. On the basis of the data available, it is not possible to determine this, but the problem obviously deserves to be studied as soon as possible.

The heritability estimates obtained from the N. S. data show how illogical estimates of heritability can be obtained by the uncritical use of statistical methods on field data. The fact that the corresponding estimates on overtimedness were not so illogical suggests that the excessively high estimates are to a considerable extent due to errors in the recording of services. These errors are obviously distributed systematically among the different areas, as is also shown by the significant differences between A. I. unit means. In this respect, overtimedness seems to be less liable to error than the number of services.

Table 19 has been constructed to see whether there are differences between the A. I. units in the heritability of the number of services.

Table 19. Heritability of the cumulative number of services in four A. I. units. At least 10 daughters per sire.

A. I. unit	Error variance in different calving classes			Heritability ± standard error (%) in different calving classes		
	II	III	IV	II	III	IV
SW. Finland	1.399690	2.399050	2.554737	4.64±1.63	6.32±1.96	5.52±1.97
Lahti	1.851918	2.980559	3.174020	3.44±1.81	7.88±2.89	3.92±2.26
Uusimaa	1.642719	2.595921	2.677498	6.36±2.23	6.12±2.19	1.96±1.54
S. Ostrobothnia	1.435218	2.080280	2.127992	1.36±1.97	0.64±1.85	3.40±2.67

This table does not agree with Table 10, according to which the heritability is lower in the South-West Finland unit than in the other units. Instead, in Table 19 the estimates for the Southern Ostrobothnia unit seem to deviate considerably from the general level. The fact that a similar deviation could not be seen in the heritability of overtimedness gives additional support to the assumption that in some areas the services may not be properly reported.

c) Multiple births

Only data on the last calving of Ayrshire cows having their first complete record in the recording years 1960/61, 1961/62 or 1962/63 were included in the material on multiple births. The numbers and averages as well as the results of variance analyses are shown in Table 20.

Table 20. Averages and components of variance in the frequency of multiple births of Ayrshire cows in the recording statistics 1962/63.

Nature of data			Numbers			% mult. births	% of total variance			Error variance	$h^2 \pm$ S. E. %
Calving no.	A. I. or N. S.	Min. no. of cows per sire	A. I. units	Sires	Cows per sire		Between calvings	Between A. I. units	Between sires		
I	A. I.	20	5	56	36.0	0.595	—	0.00	—0.20	0.005936	—0.80±2.25
»	»	10	8	131	23.3	0.460	—	0.02	—1.36	0.004639	—5.44±2.79
II	A. I.	20	8	237	80.1	1.348	—	0.02	0.91***	0.013179	3.64±0.79
»	»	10	8	285	68.9	1.339	—	0.04(*)	0.79***	0.013099	3.16±0.75
»	N. S.	10	—	95	13.8	0.913	—	—	—1.08	0.009146	—4.32±4.83
III	A. I.	20	8	195	85,4	2.241	—	0.01	0.70***	0.021752	2.80±0.76
»	»	10	8	238	72.5	2.233	—	0.01	0.68***	0.021680	2.72±0.76
»	N. S.	10	—	106	14.5	2.014	—	—	1.90*	0.019377	7.60±4.84
IV	A. I.	20	7	157	87.2	2.582	—	0.00	0.81***	0.024929	3.24±0.88
»	»	10	8	207	69.7	2.622	—	0.00	0.77***	0.025337	3.08±0.87
»	N. S.	10	—	118	14.3	1.836	—	—	0.28	0.017988	1.12±3.79
II—IV	A. I.	20	23	589	83.7	1.991	0.20***	0.00	0.78***	0.019336	3.12±0.46
»	»	10	24	730	70.3	2.000	0.21***	0.02	0.73***	0.019422	2.92±0.45
»	N. S.	10	—	319	14.2	1.629	0.13(*)	—	0.70	0.015905	2.80±2.45

The numbers of cows are slightly greater than in the data on overtimedness and the number of services. This was because the information on multiple births had also been collected for cows culled during the recording year 1961/62, and because the reporting of multiple births was more complete.

The average frequency of multiple births in the different calving classes seems to be somewhat higher in the present statistics than in those from the year 1956/57, the difference being about 0.4 — 0.6 %-units. It is not possible to tell whether this increase in the frequency is real or due only to an improvement in reporting. The two statistics agree, however, in the tendency to more frequent multiple births with age. The frequency is only about a half percent at the first calving, but at the second calving it is 1.3 %, at the third 2.2 % and at the fourth calving 2.5 %. From the pooled results of the II- to IV-calvers at the bottom of the table it can be seen that the differences between calvings are significant even when the first calving is not considered.

No heritability could be found at the first calving. The heritability at the later calvings did not vary according to the average freguency of multiple births but was about the same (3 %) at all calvings after the first. The pooled estimate on the second to fourth calvings is more than six times its standard error. This is in reasonable agreement with the estimate obtained from the recording year 1956/57 (Table 11). It can alco be seen that the fourth calving is of equal value to the second and third calvings, even though only selected animals are represented in this group.

Attention is also paid to the fact that the estimates obtained from the N. S. data were not higher than those from the A. I. data. The impression that the multiple births are not as liable to systematic errors as the other traits is further confirmed by the fact that there were no significant differences between the A. I. units. It thus appears that the age of the cow is the only systematic factor to be seriously considered in comparing different progeny groups with regard to the frequency of multiple births. It is true that KORKMAN (1948), for instance, found seasonal variation in the trait, and that the intensity of feeding and production may also influence the frequency, but in most cases these factors are distributed quite at random among the different progeny groups.

Table 21. Means and heritabilities of the frequency of multiple births of Ayrshire cows in different A. I. units. At least 20 daughters per sire.

A. I. unit	Multiple births (%) at different calvings				Heritability ± standard error (%) at different calvings			
	II	III	IV	II-IV	II	III	IV	II-IV
SW. Finland	1.689	2.327	2.718	2.176	0.76±0.92	3.00±1.35	2.52±1.34	2.08±0.68
Lahti	0.911	1.850	2.208	1.583	11.68±3.71	2.24±1.48	2.48±1.79	4.48±1.21
Uusimaa	1.431	3.281	2.874	2.289	3.88±1.65	2.36±1.39	4.84±2.03	3.52±0.95
S. Ostroboth.	1.167	1.821	2.434	1.769	4.16±2.32	3.92±2.48	2.16±1.98	3.24±1.28

In Table 21 the dependency of the level of heritability on the A. I. unit can be seen.

At first sight it appears that there are considerable differences between the units in the mean frequency of multiple births, but the results of variance analysis in Table 20 showed that these differences can be explained by differences between the sires in the different units. The heritability estimates in Table 21 are fairly consistent, although the difference between the pooled estimates of South-West Finland and of Lahti is significant at the $P < 0.10$ level of probability. Thus, the recording of the type of birth is about equally accurate in each area. However, the heritability estimates are only about half of those obtained by KORKMAN (1948) from individual herds.

3. *Tampere and Uusimaa recording statistics 1961/62*

a) Number of services

This material complemented the preceding material, since it comprised data of all cows which had been alive at the beginning of the recording year. Consequently, an idea of the effect of culled cows on the average fertility could be obtained, and the age trend was not as greatly disturbed by the upper age limit as in the preceding material. Even the I-calvers were all included without regard to the length of the time they had been in milk during the recording year.

Because of the small size of the material, daughter groups of A. I. bulls comprising at least 3 daughters were accepted for the analysis in each calving class. The analysis was also tried with a minimum of 10 daughters per group, but since these results were almost the same, only those from the former computations are presented. Table 22 gives the numbers of sires and daughters

Table 22. Number of A. I. bulls and their daughters used in the Tampere and Uusimaa recording statistics 1961/62, and the average number of services in each calving class.

Calving	Number of sires				Number of cows				Average number of services					
	Uusim.	Tampere		Total				Total	per cow				per. calv.	
	Ay	Ay	Finnish		U Ay	T Ay	T F		U Ay	T Ay	T F	Total	Diff.	Total
I	54	17	30	101	593	381	632	1 606	1.42	1.34	1.31	1.36	1.36	1.36
II	58	24	32	114	835	310	491	1 636	2.89	2.77	2.65	2.80	1.44	1.40
III	45	16	26	87	663	254	466	1 383	4.34	4.25	3.91	4.18	1.38	1.39
IV	41	16	20	77	475	166	318	959	5.92	5.68	5.27	5.67	1.49	1.42
V	29	16	22	67	385	150	252	787	7.25	7.29	6.58	7.04	1.37	1.41
VI	22	14	16	52	287	108	169	564	8.65	8.47	7.98	8.41	1.37	1.40
VII	17	6	10	33	175	44	84	303	10.22	9.48	9.48	9.91	1.50	1.42
VIII	14	4	8	26	104	23	44	171	11.94	10.13	10.71	11.38	1.47	1.42
I—VIII	280	113	164	557	3 517	1 436	2 456	7 409						1.39
IX—XIV								663						1.38

(Diff. = increment in the average number of services per cow from one calving to another.)

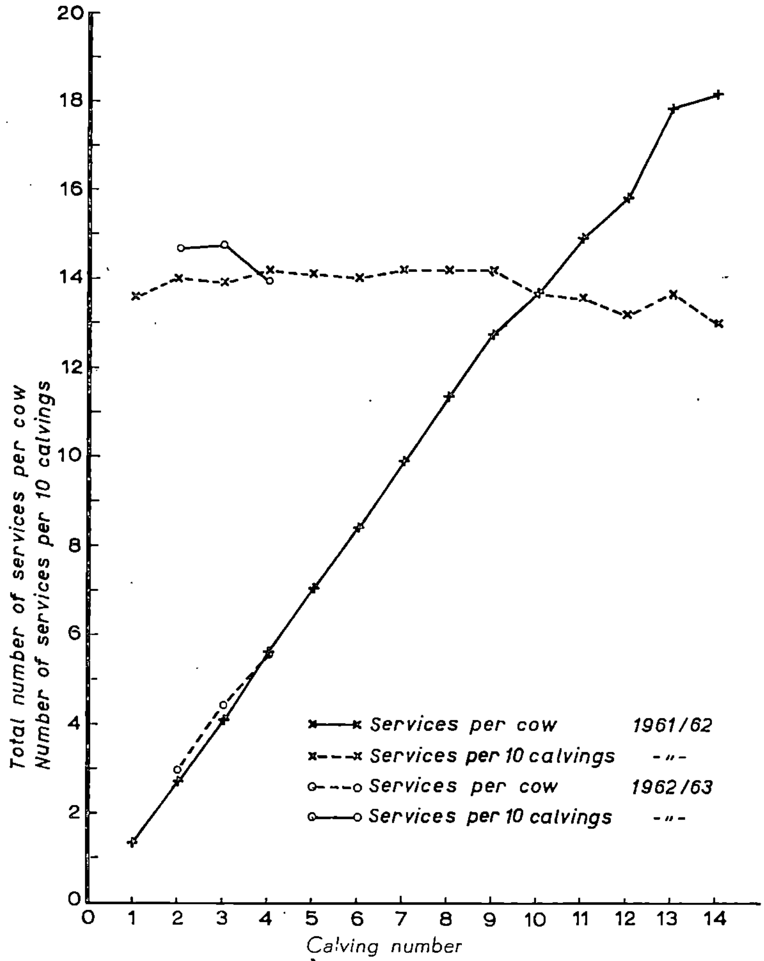

Fig. 2. The number of services required by cows for different numbers of calvings in the recording years 1961/62 (Tampere and Uusimaa) and 1962/63.

included in the analyses as well as the average numbers of services per cow and conception.

The averages are shown in Fig. 2, together with corresponding averages from the recording statistics 1962/63 from Table 17.

The averages of the Tampere + Uusimaa statistics are slightly lower than the means of the other statistics, but the difference is not very large. It is evident, however, that the inclusion of all the I-calvers lowered the mean of the I-calvers.

In the table there seems to be a slight difference between the Ayrshire cows in the two areas, more services being required in Uusimaa than in Tampere. This difference may be due wholely to differences in the accuracy of the recording of services in the two agricultural societies. On the other hand, the breed difference in the Tampere area is very likely real.

It is surprising that the average number of services per conception does not change essentially with age in the Tampere + Uusimaa material. Obviously, the natural effect of age is cancelled by the continuous culling of sterile individuals. Another reason for the smaller number of services in the older age classes is the fact that the collecting of all individual services in milk-recording only started in the year 1956/57. It is probable that some of the earlier services are not included in the older age classes. Only the cows in the first 5 or 6 classes have been included in this cumulative system since their first calving. The effect of age becomes a little more apparent when the averages are expressed as differences between the numbers of inseminations per cow in successive calving classes, but these fluctuations are rather inconsistent and difficult to explain.

The results of variance analyses on the cumulative number of services per cow are presented in Table 23.

This table shows that the differences between populations were significant in each calving class. The sire component of variance tended to increase with the number of calvings, as was to be expected. The tendency was in fact greater than expected, and the heritability estimates were surprisingly high in the older age classes. From the viewpoint of breeding for fertility, this would be encouraging, but because the material was small and the separation of A. I. daughters from other cows was difficult, positive conclusions from these statistics should be made with care. However, the results can be regarded as an indication that the question deserves further study, especially since KOORT (1948) obtained roughly similar estimates on the basis of averages of 2—12 records ($h^2 \approx$ 20 %).

b) Culling due to sterility

Excluding the cows sold for breeding there were 24 355 Ayrshire and Finncattle cows milking a shorter or longer time during the recording year 1961/62

Table 23. Components of variance in the cumulative number of services in the Tampere and Uusimaa recording statistics 1961/62.

Calving	Numbers		% of variance within calving classes		Error variance	$h^2 \pm$ S. E.
	Sires	Cows per sire	Betw. populations	Betw. sires		%
I	101	15.9	0.47*	—1.25	0.511714	—5.00±4.24
II	114	14.4	1.06**	2.24*	1.255256	8.96±4.87
III	87	15.9	2.34***	0.52	2.149252	2.08±4.13
IV	77	12.5	3.68***	2.55*	2.931474	10.20±6.80
V	67	11.7	2.16**	4.87***	3.925278	19.48±7.08
VI	52	10.8			5.761035	
VII	33	9.2	3.91*	10.42***	4.939481	41.68±16.88
VIII	26	6.6			7.451586	

Table 24. Components of variance in cullings due to sterility in the Tampere and Uusimaa recording statistics 1961/62.

Data		% culled steril.	Numbers		% of total variance			Error variance	$h^2 \pm$ S. E.
Birth years	Min. no. of cows/ sire		Sires	Cows per sire	Betw. age classes	Betw. popul.	Betw. sires		%
1952—59	3	3.35	477	20.2	0.96**	0.37***	0.01	0.0320936	0.04±1.29
1952—59	10	3.38	306	28.5	1.06**	0.35**	0.53*	0.0321158	2.12±1.31
1952—53	10	8.48	33	20.7	0.00	0.80(*)	0.72	0.0767578	2.88±5.47
1954—55	10	4.04	57	29.1	0.00	0.00	0.43	0.0386464	1.72±2.90
1956—57	10	3.66	87	30.8	0.07	0.34*	−0.27	0.0352577	−1.08±2.13
1958—59	10	1.95	129	28.6	0.93*	0.08	1.37**	0.0187485	5.48±2.42

in the two agricultural societies. A total of 4 135 cows or 16.98 % of them were culled before the end of the recording year. The reason for culling was known in 66.87 % of these cows. If the remaining 33.13 % are divided between the different culling categories in the same proportion as they were among the cullings with known reasons, the cullings due to sterility amount to 39.22 %, while the corresponding figure for poor production and old age together is 24.17 % and for udder troubles 11.78 %. The role of sterility was maximal in the age class born in 1951, where 57 % of the cullings were due to this cause. About 16 % of the cows born in the years 1948—51 and starting the recording year 1961/62 were removed from the herds because of sterility before the end of that year. Assuming sterility to have been the only cause for discarding, about 15 % of cows would be culled before the age of 6 years and the cumulative risk at the age of 10 years would be about 50 %.

The results of variance analyses of sterility cullings are shown in Table 24. Cows born in 1951 or earlier were excluded from the analyses. Two minimum sizes of progeny groups were used, namely 3 and 10.

In contrast to the results obtained for overtimedness and service numbers, the material having progeny groups as small as 3 cows did not give any high estimate of heritability with regard to sterility cullings. On the other hand, the material where only progeny groups of 10 or more cows were accepted gave an estimate of 2.12 ± 1.31 %. This is at about the same level as the estimates concerning other fertility traits in the recording statistics. It is considerably lower than the estimate (10 %) obtained by Korkman (1947) from accurate recording of 38 Finnish Ayrshire herds.

There were significant differences between age classes and the three different populations in the combined data. In the pairwise grouping, the difference between adjacent classes was significant only between cows born in 1958 and 1959. These two classes also showed the highest heritability in spite of the low frequency of cullings. Although the differences between the heritability estimates are not significant, the tendencies in Table 24 are obviously similar to those in Tables 6 and 9.

4. *Uusimaa A. I. statistics 1958—1962*

a) Frequency of data concerning sires and birth years

The value of the A. I. statistics from the viewpoint of breeding for fertility depends partly on how regularly the sire and the year of birth of the inseminated cow are recorded by the technician. To elucidate this problem Table 25 has been constructed. It concerns all cows inseminated by the Uusimaa A. I. Society during the years 1958—1961 without regard to breed. Most of the cows belonged to the Ayrshire breed.

Table 25. Frequency of cows with known sire and birth year among the cows inseminated in the Uusimaa A. I. Society in 1958—1961.

Year	No. of cows inseminated		Sire and birth year known			
			No. of cows		%	
	record. herds	unrec. herds	record. herds	unrec. herds	record. herds	unrec. herds
1958	27 034	21 191	13 278	3 231	49.1	14.8
1959	27 755	22 716	13 896	4 090	50.1	18.0
1960	32 674	27 056	18 380	5 346	56.3	19.8
1961	33 989	29 208	19 307	6 024	56.8	20.6

It can be seen from the table that obtaining information on sire and age causes difficulties to the technicians even in milk-recorded herds, not to speak of unrecorded herds. Thus, the A. I. statistics do not help to the expected degree in obtaining data from unrecorded herds for progeny-testing bulls with regard to fertility traits. In addition, fewer data have been obtained even from the recorded herds through the A. I. technicians than through the milk-recorders. The low figures are due partly to the fact that data concerning older cows in the archives of A. I. technicians are deficient. The situation has improved year by year as the old cows born before the A. I. activity have fallen out of the statistics. However, much time must still elapse before the unrecorded herds can add significantly to the number of daughters available for progeny testing. The data obtained from these herds should not be interpreted as useless ballast, however, until the quality of the data has also been determined.

The age distribution of the inseminated Ayrshire cows with a known sire is shown in Table 26.

The oldest age class in the table is 16 years, but among the cows with unknown sires the corresponding limit was 19 years. From the average ages at the bottom of the table it is evident that increasing numbers of older cows are included year after year, as the cows born in A. I. have become older. In the data from unrecorded herds the mean age has been a year less than the mean of recorded cows.

Table 26. The numbers of Ayrshire cows with known sire inseminated by the Uusimaa A. I. Society in 1958—1962, according to age.

Age yrs.	No. of cows inseminated in recorded herds						Number of cows inseminated in unrecorded herds					
	1958	1959	1960	1961	1962	Total	1958	1959	1960	1961	1962	Total
16			2			2						
15			2			2						
14	4	4	4	5		17				1		1
13	10	8	14	2	14	48			1		2	3
12	9	19	26	45	67	166				3	7	10
11	38	27	77	116	168	426	2	1	4	15	15	37
10	55	111	225	250	320	961	3	12	29	18	54	116
9	145	288	382	420	493	1 728	9	27	38	73	72	219
8	378	398	585	725	848	2 934	31	53	83	90	160	417
7	559	653	943	1 147	1 104	4 406	62	92	132	222	213	721
6	820	933	1 446	1 447	1 339	5 985	116	157	264	283	378	1 198
5	1 252	1 459	1 832	1 714	1 846	8 103	199	303	363	474	621	1 960
4	1 762	1 725	2 124	2 292	2 677	10 580	355	419	585	780	961	3 100
3	2 076	2 021	2 749	3 068	3 005	12 919	529	636	1 007	1 109	1 156	4 437
2	1 171	1 334	1 876	1 964	2 106	8 451	385	567	753	822	850	3 377
2 h	1 196	1 367	1 867	1 634	1 865	7 929	447	549	692	649	781	3 118
1 h	1 858	2 189	2 759	2 967	3 213	12 986	848	1 123	1 198	1 241	1 706	6 116
?	1 598	2 354	1 019	2 854	3 446	11 271	598	688	602	1 018	1 251	4 157
Total	12 931	14 890	17 932	20 650	22 511	88 914	3 584	4 627	5 751	6 798	8 227	28 987
Mean age, yr.	3.58	3.64	3.74	3.81	3.84	3.74	2.69	2.75	2.94	3.12	3.14	2.98

(Age=year of insemination minus year of birth; h=heifer)

b) Nonreturn percentage

The effect of age of the cows on the nonreturn percentage within 60 days after the first service can be seen from Table 27, which is based on the same cows as Table 26.

Firstly, it can be seen that the NR-% varies from year to year, and secondly, that the NR-% is also dependent on the age of the cows. This age effect seems to vary somewhat from year to year, partly because of the small numbers. This effect can be seen more clearly from the combined results of the five years, presented graphically in Fig. 3.

In the recorded herds, the NR-% is highest for the heifers, decreases about 1 % after the first calving, and then increases slightly at the following lactations up to the age of 4 or 5 years. After that it starts a steady decline. It is not at all clear whether this age trend is due to different conception rates at different ages or whether it is only due to a statistical bias, caused, for instance, by different culling rates or some other factors. In any case, the variations caused by age cannot be considered large up to the age of 6 years.

The curve obtained from the unrecorded herds deviates from that for the recorded cows not only with regard to the direction of the age effects but also with regard to general level. On the average, it is about 4 % above

Table 27. The average NR-% within 60 days after the first service of Ayrshire cows in the Uusimaa A. I. Society in 1958—1962.

Age yrs.	Nonreturn percentage							
	Recorded herds						Unrec. herds 1958 -62	Unrec. minus rec.
	1958	1959	1960	1961	1962	1958 -62		
≧10	56.9	58.0	56.3	57.2	62.6	58.9	64.7	+ 5.8
9	66.2	60.8	59.4	64.8	64.9	63.1	70.3	+ 7.2
8	61.9	66.8	65.1	62.1	65.0	64.1	75.8	+11.7
7	61.0	67.1	66.8	62.9	67.8	65.3	75.5	+10.2
6	66.0	68.6	64.5	64.6	68.0	66.1	72.0	+ 5.9
5	65.2	68.6	66.6	66.6	68.6	67.2	71.5	+ 4.3
4	67.5	68.3	65.4	66.9	67.8	67.2	73.5	+ 6.3
3	67.0	66.6	65.5	65.6	68.2	66.6	70.2	+ 3.6
2	67.3	67.9	64.0	65.3	67.6	66.3	69.4	+ 3.1
2 h	69.7	68.3	68.6	65.5	67.2	67.8	69.0	+ 1.2
1 h	67.5	67.1	66.0	66.7	68.7	67.2	67.9	+ 0.7
?	65.5	69.4	67.2	65.9	68.3	67.4	71.1	+ 3.7
Rec.	66.48	67.72	65.60	65.48	67.75	66.60	—	—
Unrec.	70.23	69.66	69.12	69.01	72.65	—	70.32	—
Unrec-rec.	3.75	1.94	3.52	3.53	4.90	—	—	+ 3.72

the curve for the recorded cows. The reasons for this are also difficult to find, but obviously they arise from human and statistical factors rather than from biological ones. In any case, these different results from the two groups of herds show that they must be studied separately.

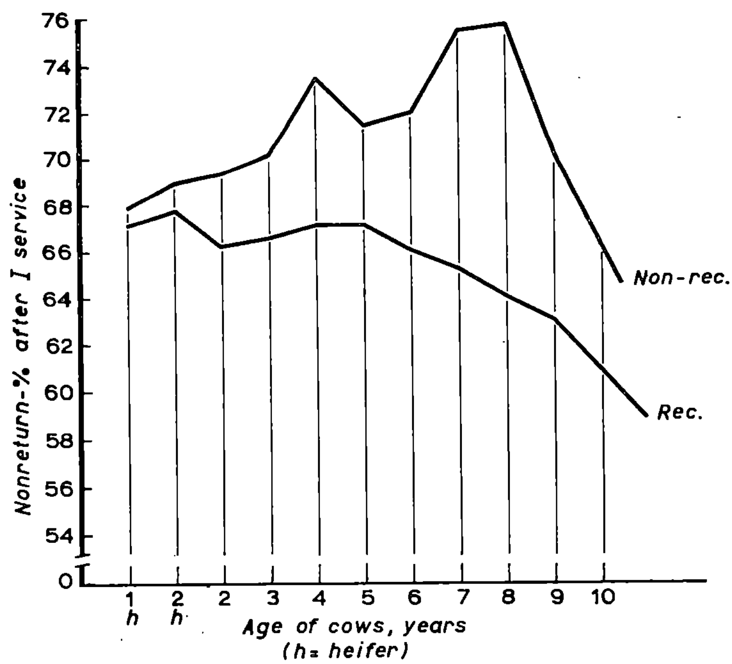

Fig. 3. The effect of age of Ayrshire cows on the NR-% after the 1st service in the Uusimaa A. I. Society in 1958—62.

The relative importance of both age and years as causes of variation in NR-% becomes clearer from the results of variance analyses presented in Table 28. Here again, two different lower limits for the group sizes in each age class were used. The age classes were the same as in Table 27, with the exception that cows with an unknown birth year or older than 9 years were excluded, while the 6- and 7-year old cows were treated as one group and the 8- and 9-year old cows as another. Consequently, 8 different age groups were used in each year. The pooled results of the 5 years were also computed from both groups of material.

The similarity of the pooled estimates from the two groups of data shows that the separation of daughters of A. I. bulls from other cows is not a serious problem in the A. I. statistics. However, the heritability estimates from the larger progeny groups are more consistent from year to year. The mean of the five yearly estimates in this material is 1.336 + 0.178 %, while the corresponding average from the smaller groups is 1.360 ± 0.282 %. The standard error of the latter mean is thus larger, in spite of the larger numbers of cows. The results would have been still more variable if daughter groups of N. S. bulls had been accepted in the analyses, but the general level of the estimates did not increase as in the recording statistics.

The estimate concerning the year 1962 is only about one-half of the average of the four previous years. Although this could be attributed to chance alone, it is possible that the replacement of punching personnel in the middle of the year 1962 by inexperienced persons may have had an effect on the accuracy of the data. Familiarity with and careful checking of the data to be punched are essential for good results in statistical work where the basic data are written by numerous persons in varying manners.

Table 28. Components of variance in the NR-% after the first service of recorded daughters of Ayrshire A. I. bulls in the Uusimaa A. I. Society in the years 1958—1962.

Data			Numbers			% of total variance			Error variance	h²±S. E.
Min. no. of cows. /sire	Age classes yrs.	Year of insem.	Age class-es	Sires	Cows per sire	Betw. years	Betw. age classes	Betw. sires		%
3	1—9	1958	8	276	33.4	—	0.09(*)	0.44*	0.222913	1.76±1.17
3	1—9	1959	8	315	32.7	—	0.00	0.54*	0.219756	2.16±1.15
3	1—9	1960	8	395	35.1	—	0.11**	0.21	0.226322	0.84±0.87
3	1—9	1961	8	447	33.6	—	0.00	0.35*	0.225693	1.40±0.89
3	1—9	1962	8	519	31.1	—	0.00	0.16	0.217245	0.64±0.84
3	1—9	1958—62	8	1 952	33.1	0.06***	0,03*	0.31**	0.222380	1.24±0.43
10	1—9	1958	8	179	48.7	—	0.05(*)	0.40*	0.223099	1.60±1.04
10	1—9	1959	8	212	45.9	—	0.00	0.42*	0.220444	1.68±1.01
10	1—9	1960	8	281	47.3	—	0.11*	0.29*	0.225445	1.16±0.81
10	1—9	1961	8	306	46.5	—	0.00	0.38*	0.225590	1.52±0.82
10	1—9	1962	8	351	43.4	—	0.00	0.18	0.217269	0.72±0.75
10	1—9	1958—62	8	1 329	46.0	0.06***	0.02(*)	0.32***	0.222451	1.28±0.39

There seemed to be significant differences between the yearly averages of NR-%, since the variance component was 0.06 % of the total. This was mainly due to the year 1962, without which the corresponding component was only 0.01 (*) %.

The differences between age classes were of minor importance, although two stars could be attached to the variance component of age classes in the year 1960. The inclusion of a class consisting of cows 10 years old and older increased the importance of age in the combined material to 0.08*** %, while the exclusion of cows more than 5 years old decreased it to 0.01(*) %. The interaction of years and age classes was zero in both cases. Thus it can be concluded that the effect of age on the NR-% is about the same from year to year. The variations seen in Table 27 can thus be explained by the small sample sizes.

Because of the unimportance of annual differences in the data for the years 1958—1961, it was also possible to combine corresponding age classes from the four years for each sire. In addition, the age classes were combined pairwise, all heifers being treated as one group, 2- and 3-yr. old cows as another, and 4- and 5-yr. old cows as a third group, while the 6- and 7-yr. old cows formed a fourth. The results of this analysis, where an interaction component between the sires and age classes was also estimated, are shown in Table 29. There was considerable variation in the numbers of daughters in the sire × age groups, but at least 10 daughters were required in each group.

Noteworthy are the significant interaction components, especially in the first three rows, where heifers and cows have been compared. At the same time, the sire component has become almost zero. These results indicate quite strongly that a good conception rate as a heifer is not genetically related to the conception rate as a cow. This could explain the relatively low heritability of the cumulative number of services required for the first two conceptions in Table 18 as compared with the heritability of the number of services required for the second calving alone.

Table 29. Components of variance in the NR-% in the years 1958—1961 (year effects not considered).

Age groups compared	Degrees of freed.				% of total variance		
	Total	Betw. age groups	Between sires	Age x sire	Between age groups	Between sires	Age x sire interact.
Heifers and 2—3 year old cows ...	26 899	1	77	77	0.07*	0.02	0.34**
—»— 4—5 —»— ...	20 832	1	53	53	0.01(*)	0.00	0.35**
—»— 6—7 —»— ...	8 949	1	21	21	0.05(*)	0.19(*)	0.19(*)
2—3 year old and 4—5 year old cows	23 747	1	63	63	0.00	0.30***	0.01
2—3 —»— 6—7 —»—	12 311	1	31	31	0.01	0.22(*)	0.11(*)
4—5 —»— 6—7 —»—	15 070	1	35	35	0.02(*)	0.20(*)	0.18(*)
Heifers, 2—3, 4—5, 6—7 —»—	23 807	3	21	63	0.00	0.21***	0.12*

Table 30. Components of variance in the NR-% after the first service in different age classes. At least 10 daughters per sire/age class.

Age groups	Numbers		% of total variance			Error variance	h² ± S. E. %
	Sires	Cows per sire	Betw. age classes	Betw. years	Betw. sires		
Heifers, 1 and 2 years	433	42.1	0.00	0.00	0.44**	0.219428	1.76±0.77
Cows, 2 and 3 —»—	403	44.5	0.00	0.09*	0.42**	0.223748	1.68±0,75
—»— 4 and 5 —»—	298	49.8	0.00	0.02	0.26(*)	0.221268	1.04±0.74
—»— 6—7 and 8—9 —»—	195	52.3	0.04	0.11*	0.02	0.227275	0.08±0.78

The interaction does not seem so marked when heifers are compared with the 6- to 7-yr. old daughters, but this material was so small that no positive conclusions can be drawn concerning the deviating nature of the components for 6- to 7-yr. old cows. However, this difference finds some support from the interaction existing between the 6- to 7-yr. old cows on the one hand and the 2- to 3-yr. old and 4- to 5-yr. old cows on the other. In any case, the interaction component in these comparisons does not lower the sire component as much as in the comparisons where heifers and the younger cow classes were paired. These relationships will be studied more closely in subsequent papers.

In Table 30 the results of variance analyses are grouped according to the age of the cows. The table is based on the same sums of squares as Table 28.

It appears from this table that the heritability of NR-% is highest at the young ages and thereafter declines. The difference between the estimates for heifers and 4- to 5-yr. old cows is not significant, but the probability of a difference larger than that between the estimates for 2- to 3-yr. old and 6- to 9-yr old cows is smaller than 0.15. The decline of the heritability estimates in the older ages may, however, be due to the fact that the older age classes were born at a time when the herds were not included in the A. I. activity. This may have caused inaccuracies in the cards kept by the A. I. technicians. On the other hand, the higher heritability at the age of 2—3 years as compared with that at the age of 4—5 years agrees with the results obtained from the recording statistics 1956/57, where conception during the first lactation proved to have an exceptionally high heritability. Unfortunately, only the time of birth has been recorded in the A. I. statistics, so that the number of calving was not known for any of the inseminated cows.

The results for the unrecorded herds are presented in Table 31. The analyses were performed in the same way as with regard to the recorded herds in Table 28. In pooling the estimates, cows older than 5 years were excluded.

Exclusion of progeny groups of less than 10 daughters led to slightly higher estimates than for the whole material, but still the values were at a lower level than in the recorded herds, and no significant deviations from zero were obtained. However, the yearly estimates showed some tendency to increase, the two last years being at least at the same level as the corresponding values

Table 31. Components of variance in the NR-% of unrecorded daughters of Ayrshire A. I. bulls in the Uusimaa A. I. Society in 1958—62. At least 3 daughters/sire/age/class.

Data			Numbers		% of total variance				Error variance	$h^2 \pm$ S. E. %
Min. no. of cows per sire	Age classes yrs.	Years of insem-ination	Sires	Cows per sire	Between years	Between age classes	Year x age	Between sires		
3	1—9	1958—62	1 433	15.3	0.14***	0.19***	0.00	0.07	0.209194	0.28±0.98
3	1—5	1958—62	1 260	15.7	0.14***	0.13***	0.00	0.20	0.210548	0.80±1.01
10	1—9	1958—62	791	23.2	0.12*	0.18**	—	0.12	0.208676	0.48±0.89
10	1—5	1958—62	711	23.5	0.12*	0.11	—	0.23	0.210283	0.92±0.95
10	1—9	1958	99	22.6	—	0.02	—	—1.13	0.212331	—4.52±3.16
10	1—9	1959	120	23.9	—	0.05	—	0.50	0.209411	2.00±2.42
10	1—9	1960	158	24.1	—	0.29*	—	—0.32	0.216038	—1.28±2.01
10	1—9	1961	189	22.7	—	0.11(*)	—	0.40	0.213750	1.60±1.98
10	1—9	1962	225	23.1	—	0.27*	—	0.56(*)	0.197118	2.24±1.84

for recorded herds in Table 28. This gives some hope that the situation is improving and that it may be possible in future to obtain useful information from the unrecorded herds through the A. I. technicians.

The differences between years and age classes appeared to be more significant in the unrecorded herds than in the recorded herds. It is difficult to find any biological reasons for this strong age effect.

c) Intensity of heat symptoms

Data concerning the intensity of heat symptoms were available from the year 1958. They were collected by the A. I. technicians in connection with insemination operations. The heats were classified subjectively into 3 groups: 0 = no symptoms, 1 = a weak heat, and 2 = a strong, distinct heat. Because

Table 32. Average intensity of heat symptoms of Ayrshire cows in recorded and unrecorded herds in the Uusimaa A. I. Society in 1958.

Age yrs.	Recorded herds			Unrecorded herds			Total		
	No. of cows	Distinct heat		No. of cows	Distinct heat		No. of cows	Distinct heat	
		no.	%		no.	%		no.	%
≥10	116	102	87.9	5	4	80.0	121	106	87.6
9	145	126	86.9	9	8	88.9	154	134	87.0
8	373	319	85.5	31	24	77.4	404	343	84.9
7	557	466	83.7	61	52	85.2	618	518	83.8
6	814	680	83.5	116	107	92.2	930	787	84.6
5	1 246	1 047	84.0	199	180	90.5	1 445	1 227	84.9
4	1 748	1 476	84.4	355	301	84.8	2 103	1 777	84.5
3	2 063	1 691	82.0	527	440	83.5	2 590	2 131	82.3
2	1 169	1 001	85.6	385	337	87.5	1 554	1 338	86.1
2 h	1 220	1 019	83.5	452	387	85.6	1 672	1 406	84.1
1 h	1 844	1 613	87.5	843	731	86.7	2 687	2 344	87.2
?	1 543	1 371	88.9	583	507	87.0	2 126	1 878	88.3
Total	12 838	10 911	85.0	3 566	3 078	86.0	16 404	13 989	85.3

Table 33. Components of variance in the frequency of distinct heat symptoms of Ayrshire cows in the Uusimaa A. I. Society in 1958.

Data				Numbers			% of total variance			Error variance	h² ± S. E.
A. I. or N. S.	Rec. or unrec.	Min. no. of cows sire	Age classes	Age cl.	Sir-es	Cows per sire	Betw. age classes	Between sires	Age x sire		%
A. I.	Rec.	10	Cows 5—8	4	46	40.5	0.00	1.89**	—	0.135961	7.56±3.64
»	»	10	» 2—4	3	76	52.7	0.18(*)	0.64*	—	0.137104	2.56±1.65
»	»	10	Heif. 1—2	2	64	41.8	0.57**	0.56(*)	—	0.119912	2.24±2.09
»	»	10	C&H 1—8	9	186	45.9	0.18*	0.88***	—	0.131487	3.52±1.27
»	»	3	» 1—8	9	241	36.7	0.19**	0.75**	—	0.131438	3.00±1.27
»	»	3	» 1—8	2	23	30.7	0.00	—0.10	0.55**	0.129348	—0.40±3.96
»	Unrec.	3	» 1—8	9	194	13.6	0.02	—0.48	—	0.118336	—1.92±3.18
N. S.	Rec.	3	» 1—8	9	283	4.5	0.00	0.76	—	0.132997	3.04±7.73

there were very few cows in class 0 (VARO 1959), they were combined with class 1, there being thus 2 classes: 0 = imperfect symptoms, and 1 = distinct symptoms.

The effect of the age of the cows on the heat symptoms at the first service is to be seen in Table 32.

The age effect does not seem very large. The most strongly deviating group is the class of 3-yr. old cows, which lies under both 2- and 4-yr. old cows. This appears not only in the recorded herds, but also in the unrecorded ones. A variance analysis performed on the data of Table 32 showed that the differences between age classes were significant on the whole, the variance component being 0.23* %. The interaction between age and recording class was insignificant (0.04 %), and the difference between the recording classes (recorded vs. unrecorded) formed only 0.04(*) % of the total variance.

Further results of variance analyses concerning the heat symptoms are shown in Table 33.

Because data were only available from one year, the cows were divided into fewer age classes than in the previous analyses, but the computations were still performed within age classes defined with an accuracy of one year. The oldest group gave a slightly higher heritability estimate than the younger groups, but the difference is not significant. The pooled estimate was 3.52 %, which is significantly different from zero. The estimate did not change much when progeny groups smaller than 10 daughters were included in the analysis. However, when all cows and heifers were combined according to sire, the sire differences disappeared. On the other hand, a significant interaction component was obtained between age and sire. This means that the intensity of heat symptoms as a heifer may be genetically unrelated to such symptoms as a cow. This is in accord with the results on the nonreturn percentage shown in Table 29.

A negative but insignificant heritability estimate was obtained from the artificially bred cows in unrecorded herds, while the naturally bred cows in recorded herds gave an estimate similar to that of the daughters of A. I. bulls in recorded herds. The estimate is not significant, but it shows that the heat symptoms as judged by the A. I. technicians are not as liable to systematic effects as are the fertility data from milk recording.

d) Multiple births

The type of birth preceding the insemination in question was recorded by the technicians in the year 1958. The number of cows studied and the average frequency of multiple births can be seen in Table 34.

Table 34. Average frequency of multiple births in Ayrshire cattle in the Uusimaa A. I. unit in 1958.

Age yrs.	Recorded herds			Unrecorded herds			Total		
	No. of births	Multiple births		No. of births	Multiple births		No. of births	Multiple births	
		no.	%		no.	%		no.	%
≧ 10	114	3	2.63	5	1	20.00	119	4	3.36
8—9	510	12	2.35	40	0	0.00	550	12	2.18
6—7	1 348	30	2.23	173	4	2.31	1 521	34	2.24
4—5	2 927	41	1.40	534	3	0.56	3 461	44	1.27
2—3	3 128	15	0.48	882	5	0.57	4 010	20	0.50
?	1 479	23	1.56	552	4	0.72	2 031	27	1.33
Total	9 506	124	1.30	2 186	17	0.78	11 692	141	1.21

The average frequency seems to be at the same level as in the recording statistics of 1956/57, but because older age classes were also represented in the A. I. statistics, it appears that not all of the multiple births were recorded by the A. I. technicians. In the unrecorded herds the frequency of reported multiple births was still lower.

The results of variance analyses are shown in Table 35.

It can be seen from the table that no heritability could be detected in the data collected by the A. I. technicians, although the heritability was 2 or 3 % on the basis of data collected by milk recorders (Tables 11 and 20). On the other hand, there were no systematic factors either, since the small progeny

Table 35. Components of variance in the frequency of multiple births of Ayrshire cows according to the Uusimaa A. I. statistics in 1958.

Data				Numbers			% of tot. var.		Error variance	$h^2 \pm$ S. E.
A. I. or N. S.	Rec. or unrec.	Min. no. of cows/sire	Age yrs.	Age cl.	Sires	Cows per sire	Betw. age classes	Betw. sires		%
A. I.	Rec.	10	2—8	7	118	48.0	0.47***	0.08	0.0111217	0.32±1.13
»	»	3	2—9	8	169	35.3	0.46***	—0.53	0.0108041	—2.12±1.46
»	Unrec.	3	2—8	7	113	12.4	0.07	—0.63	0.0057322	—2.52±3.76
N. S.	Rec.	3	2—11	10	274	4.4	0.07	—0.19	0.0164087	—0.76±7.83

groups, the unrecorded cows, and the naturally bred cows did not give positive estimates of heritability. However, the age effect was significant in the data consisting of the larger progeny groups.

e) Retained placenta

During the year 1958, the A. I. technicians in the Uusimaa A. I. unit also recorded whether the afterbirth had been delivered normally or not. The incidence of retained placenta according to these records is shown in Table 36.

Table 36. Average frequency of retained placenta in Ayrshire cows in the Uusimaa A. I. unit in 1958.

Age yrs.	Recorded herds			Unrecorded herds			Total		
	No. of births	Retained placenta		No. of births	Retained placenta		No. of births	Retained placenta	
		no.	%		no.	%		no.	%
≧ 10	114	1	0.88	5	0	0.00	119	1	0.84
8—9 ..	511	14	2.74	40	0	0.00	551	14	2.54
6—7 ..	1 355	30	2.21	176	8	4.55	1 531	38	2.48
4—5 ..	2 929	48	1.64	542	9	1.66	3 471	57	1.64
2—3 ..	3 143	56	1.78	894	24	2.68	4 037	80	1.98
?	1 414	24	1.70	533	11	2.06	1 947	35	1.80
Total	9 466	173	1.83	2 190	52	2.37	11 656	225	1.93

The frequency of retained placenta increases slightly with age, but this tendency is not at all as clear as in the case of multiple births. The frequency was not lower in the unrecorded herds than in the recorded ones.

The results of variance analyses concerning retained placenta are presented in Table 37.

These results do not differ much from those on multiple births in Table 35, but it appears that there are more systematic factors which tend to increase the similarity of half-sibs. On the other hand, the differences due to age were not so important as in the multiple births.

Table 37. Components of variance in the frequency of retained placenta among Ayrshire cows in the Uusimaa A. I. unit in 1958.

Data				Numbers			% of tot. var.		Error variance	$h^2 \pm$ S. E.
A. I. or N. S.	Rec. or unrec.	Min. no. of cows/sire	Age yrs.	Age cl.	Sires	Cows per sire	Betw. age classes	Betw. sires		%
A. I.	Rec.	10	2—8	7	119	47.8	0.00	0.20	0.0189213	0.80±1.19
»	»	3	2—9	8	168	35.6	0.00	—0.05	0.0192069	—0.20±1.25
»	Unrec.	3	2—8	7	112	12.7	0.00	2.88**	0.0241319	11.52±5.74
N. S.	Rec.	3	2—11	10	276	4.4	0.45(*)	1.34	0.0151625	5.36±8.19

f) Cystic ovaries

Since the beginning of the year 1959, the technicians have recorded the presence of abnormally large and persistent, unruptured follicles in the ovaries. The diagnosis has been made by rectal palpation. From the data of the first two years (1959—1960), only the follicles observed at the first service were included in this study. In the years 1961—62 a cow was considered cystic even if the cysts were found only at the later services. Each cow was included only once, so that if a cyst had already been observed at the first service, those found at the repeat services were not considered. Correspondingly, a cyst observed at the third service was neglected if the cow had had a cyst at the first or second service.

This difference between the procedures is also reflected in Table 38, where the frequency of cystic cows in different age classes is shown in each of the four years.

The average frequency for the year 1959 is only 1.56 %, while the respective figure according to VARO (1960) was 7.32 %. In this latter figure are also included the cows found to be cystic only at the repeat services. It is evident that most of the cysts do not appear until later, since out of the 370 cows found cystic at later services 239 had already been studied at the first service but declared normal at that time (VARO 1960). It is further difficult to compare the figures of VARO and those in Table 38 because of the fact that this table includes only Ayrshire cows which had a known sire. In addition, data of another society were included in the average presented by VARO.

The occurrence of ovarian cysts was less frequent in 1960 than in the preceding year. The figures from 1961 and 1962 are more comparable with

Table 38. Average incidence of cystic ovaries in different age classes of Ayrshire cows in the Uusimaa A. I. unit in 1959—62.

Age yrs.	Recorded herds										Unrecord. herds			
	No. of cows studied				% cystic						No. of cows studied		% cystic	
	1959	1960	1961	1962	1959	1960	1961	1962	1959 -60	1961 -62	1959 -60	1961 -62	1959 -60	1961 -62
≧10	96	223	245	350	0.00	2.24	11.02	6.29	1.57	8.24	26	55	0.38	3.64
9	162	237	237	272	3.09	1.27	7.17	6.25	2.01	6.68	37	71	0.00	1.41
8	224	355	418	456	0.89	3.38	5.98	6.36	2.42	6.18	54	123	3.70	0.81
7	369	579	644	630	2.17	1.55	8.54	4.60	1.79	6.59	106	223	0.94	3.14
6	504	793	871	791	1.98	2.27	6.77	4.05	2.16	5.48	200	321	1.00	2.49
5	779	1 058	1 029	1 093	1.54	1.61	5.54	4.21	1.58	4.85	210	553	2.26	2.89
4	970	1 210	1 369	1 571	2.99	1.40	4.89	2.93	2.11	3.84	468	945	1.92	1.69
3	1 093	1 533	1 822	1 785	1.46	1.24	3.24	2.30	1.33	2.77	833	1 215	0.72	1.40
2	664	1 175	1 160	1 295	1.36	0.34	1.21	1.54	0.71	1.38	685	943	0.29	0.64
2 h	893	957	912	1 097	1.57	0.52	1.86	1.00	1.03	1.39	633	776	0.16	1.16
1 h	1 120	1 720	1 783	1 886	0.63	0.29	0.90	0.64	0.42	0.76	1 146	1 613	0.44	0.31
?	1 115	583	1 535	1 889	1.17	1.72	2.15	2.49	1.35	2.34	708	1 163	0.99	1.29
Rec.	7 989	10 423	12 025	13 115	1.56	1.19	3.71	2.68	1.35	4.33	—	—	—	—
Unrec.	2 240	2 966	3 683	4 318	1.03	0.67	1.19	1.37	0.83	1.29	5 206	8 001	0.83	1.29

those of VARO. They show that the year 1959 was marked by an exceptionally high frequency of cystic ovaries. The difference may partly be due to the fact that the values of Table 38 are based only on cows with known sires. It is also possible that the recording of cysts was not so complete in the later years as in the first year.

Especially the results of the two last years show that the occurrence of cysts is considerably dependent on the age of the cows. Only about 1 % of the heifers had a cyst, while more than 6 % of the 7-yr. old or older cows were diagnosed as cystic during a service period. This tendency can also be seen in some degree in the statistics from the years 1959—60, but obviously the difference between older and younger cows is based mainly on the cysts

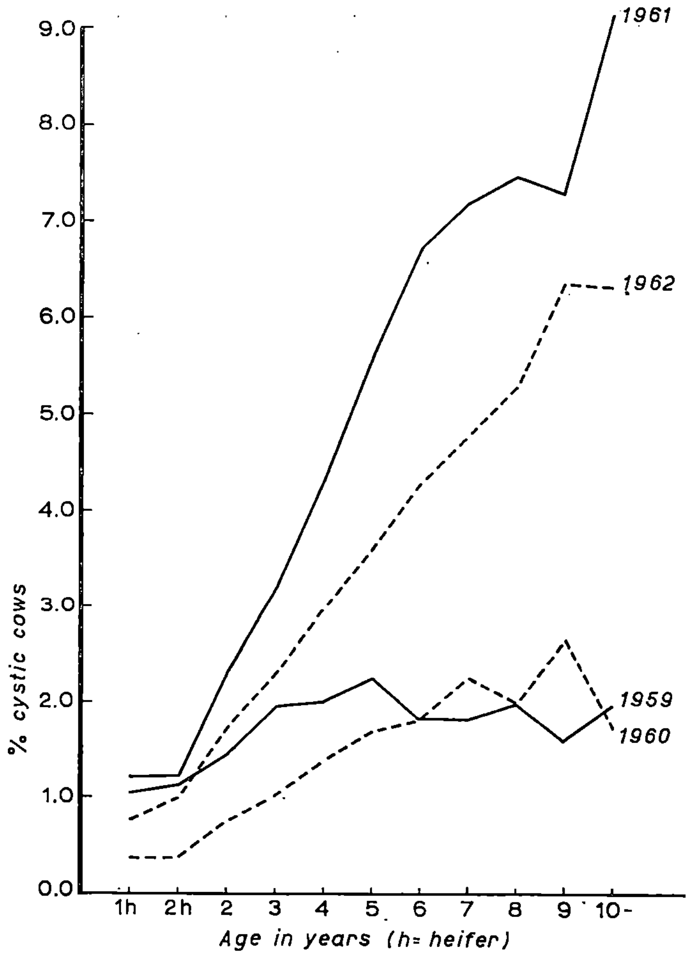

Fig. 4. The average incidence of cystic cows among daughters of Ayrshire bulls in different age classes in the Uusimaa A. I. unit in 1959—62. (In the years 1959—60 only cysts found at the first service were considered.)

occurring after the first service. Fewer cystic cows were observed in the unrecorded herds than in the recorded ones.

The effect of age on the frequency of cystic ovaries is shown graphically in Fig. 4. To see the trends more clearly, the curves are based on 3-year moving averages.

The high statistical significance of the age effects can be seen in Table 39, where results of variance analyses on the occurrence of ovarian cysts are presented. Again, yearly age classes have been used.

In the rows where the 8 cow classes and 2 heifer classes are included in the same analysis, the age effect was highly significant in all years except 1959.

Table 39. Components of variance in the incidence of cystic ovaries in Ayrshire cows of the Uusimaa A. I. unit in 1959—1962.

Data			Numbers		% of total variance			Error variance	$h^2 \pm$ S.E.
Min. no. of cows /sire	Age classes in years	Year of insemin.	Sires	Cows per sire	Between years	Between age classes	Between sires		%
A. I., recorded cows:									
10	Cows 5—9	1959	44	24.1	—	0.00	3.09**	0.0206819	12.36±6.17
10	» 5—9	1960	61	27.9	—	0.26(*)	0.09	0.0184251	0.36±2.66
10	» 5—9	1961	74	26.8	—	0.00	3.52***	0.0584518	14.08±4.77
10	» 5—9	1962	79	26.5	—	0.06	—0.26	0.0443260	—1.04±2.57
10	» 5—9	1959—62	258	26.5	1.10***	0.00	2.33***	0.0383045	9.32±2.15
10	Cows 2—4	1959	68	28.9	—	0.20(*)	0.96(*)	0.0183023	3.84±3.03
10	» 2—4	1960	86	33.8	—	0.14(*)	—0.10	0.0088675	—0.40±1.87
10	» 2—4	1961	104	33.1	—	0.45**	0.03	0.0294923	0.12±1.69
10	» 2—4	1962	124	29.4	—	0.18*	—0.28	0.0212708	—1.12±1.87
10	» 2—4	1959—62	382	31.3	0.28(*)	0.29***	0.07	0.0201315	0.28±0.95
10	Heif. 1—2	1959	56	29.3	—	0.69*	1.49*	0.0088876	5.96±3.71
10	» 1—2	1960	75	29.1	—	0.00	0.39	0.0036357	1.56±2.50
10	» 1—2	1961	76	28.0	—	0.35*	—0.23	0.0120859	—0.92±2.47
10	» 1—2	1962	83	28.7	—	0.00	—1.04	0.0063209	—4.16±2.81
10	» 1—2	1959—62	290	28.8	0.00	0.31**	0.08	0.0075922	0.32±1.18
10	C&H 1—9	1959	168	27.8	—	0.09	1.77***	0.0155204	7.08±2.34
10	» 1—9	1960	222	30.6	—	0.55***	0.05	0.0095716	0.20±1.26
10	» 1—9	1961	254	29.7	—	1.44***	1.65***	0.0321652	6.60±1.78
10	» 1—9	1962	286	28.4	—	1.17***	—0.29	0.0228068	—1.16±1.27
10	» 1—9	1959—62	930	29.2	0.42**	1.07***	0.87***	0.0208412	3.48±0.80
3	Cows 5—9	1959—62	481	16.8	1.05***	0.01	4.10***	0.0401796	16.40±2.59
3	» 2—4	1959—62	604	21.9	0.26(*)	0.39***	0.68**	0.0206450	2.72±1.21
3	Heif. 1—2	1959—62	446	20.7	0.08	0.11(*)	0.70*	0.0078841	2.80±1.48
3	C&H 1—9	1959—62	1 533	19.9	0.40*	1.23***	2.54***	0.0218979	10.16±1.09
A. I., unrecorded cows:									
3	C&H 1—9	1959—62	987	9.4	0.11(*)	0.32**	2.09***	0.0104134	8.36±2.29
N. S., recorded cows:									
3	C&H 1—11	1959—62	617	4.6	0.56*	0.00	12.42***	0.0158874	49.68±7.77

It did not change much when progeny groups of less than 10 daughters were included in the analysis. However, in the unrecorded herds the part played by age was already smaller, and in the N. S. data there were no age effects which could not be explained by differences between sires. The differences due to age were not significant when only 5- to 9-yr. old cows were considered, but they were significant in comparisons of 2- to 4-year old cows. The differences between the two heifer classes were insignificant.

The annual variation was highly significant in the oldest group. This is explained mainly by the different procedures applied with regard to the cysts found at the repeat services in the years 1959 and 1960 on the one hand and in the years 1961 and 1962 on the other. In the group of 2- to 4-yr. old cows this effect was less important, and no effect at all was observed in the heifer group.

The picture shown by the heritability estimates differs in some respects from that concerning NR-%. Firstly, the pronounced annual variation of the estimates is noteworthy. Considering the pooled estimates on all ten age classes, it is seen that in 1959 and 1961 the heritability was 6—7 % and highly significant, while in 1960 and 1962 the estimates were close to zero. The pooled estimate from all four years and all ten age classes is only 3.48 %. The difference between the years 1959 and 1961 on the one hand and the years 1960 and 1962 on the other is due mainly to the oldest group of cows, where the estimates from the years 1959 and 1961 exceed 12 %. In 1959, moderately high estimates were also obtained for the young cows and heifers. The declining trend in the heritability estimates may partly be due to the fact that in the later years no special attention was given to the cysts by the A. I. technicians and that new, inexperienced personnel had to be employed each year. The exceptionally poor results of 1962 can obviously be partly explained by the changes in punching personnel, mentioned in connection with the NR-%.

Secondly, it is noteworthy that the heritability of the cystic condition is so very closely dependent on the age of the cows. At the age of 5 years or more the heritability is essentially higher than that of the other fertility traits, but at the younger ages there is no such difference.

Thirdly, the inclusion of progeny groups of less than 10 daughters increased the heritability estimates, thus showing that data concerning the cystic condition are more liable to systematic errors than the NR-%. Obviously, this is due to differences between technicians in observing and recording the cysts. This situation is also seen in the results of variance analysis based on the N. S. data, where an estimate as high as 49 % was obtained. This can also be partly explained by herd differences in the incidence of cysts. The similarity of the heritability estimates from the years 1959 and 1961 indicates that data concerning only the first services are quite as valuable as statistics based on all services in judging progeny groups with regard to "cystic tendency".

a) Numbers and means

Data from 16 Swedish A. I. societies were used in this part of the study. The proportion of animals with a known sire in these societies is shown in Fig. 5.

It is seen that the situation is far from ideal in some of the societies which have recently started the punch-card system but that it has gradually improved in most units.

In the data available, there were only two classes of animals: heifers and cows. With regard to the heifers, this may not hinder the analysis, but it is to be expected that some results, especially those concerning ovarian cysts and multiple births of cows, will be seriously complicated by age effects. To eliminate at least a part of the age effects and to see their relative magnitudes

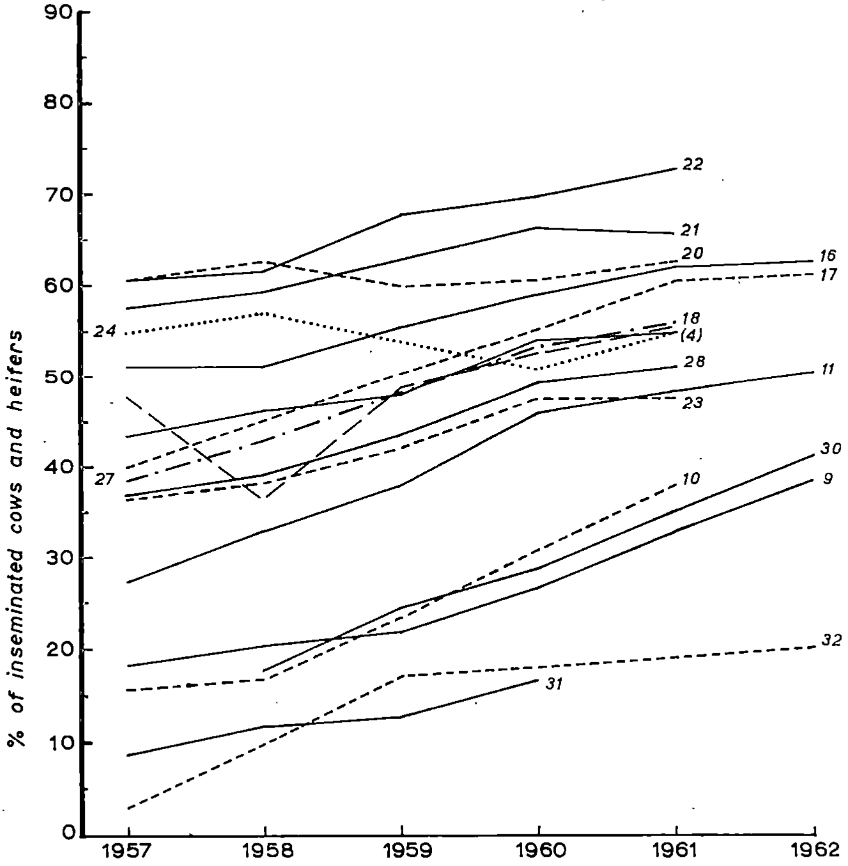

Fig. 5. The percentage of animals with known sire of the cows and heifers inseminated in certain Swedish A. I. societies in the years 1957—62. (The numbers at the ends of the lines are society code numbers.)

in the different traits, two groups of different ages were taken from the cow data according to the years in which the sires had been in service. The group of "old" cows consisted of cows whose sires had been removed from service at least 7 years before the insemination year in question, i.e. in 1953 for cows inseminated in 1960, and in 1954 for cows inseminated in 1961. The "young" group consisted of cows whose sires had entered the service 6 years or less before the year of insemination. Analyses were also performed on all the combined data available without regard to the years of service of the sires.

Progeny groups comprising at least 10 heifers or cows were first accepted for the analyses. The numbers of such groups in different A. I. units and the numbers of heifers and cows are shown in Table 40. At the bottom of the table are shown the total numbers in each particular part of the data to be analyzed separately.

In the heifer material, exclusion of progeny groups of less than 20 heifers meant a loss of only 30 groups and 434 heifers, and 90 % of the cows were left after exclusion of groups smaller than 100 cows.

The society averages of the different fertility traits are shown in Table 41.

It is seen that the averages of both heifers and cows vary considerably from unit to unit with regard to each trait. Thus, the range in "cystic tendency" is from 0 to 2 % in the heifers and from 2 to 8 % in the cows. The respective limits in need for sterility treatments are 5—15 % and 10—24 %, in final conception rate 89—94 % and 88—94 %, in NR-% 51—61 % and 48—61 %,

Table 40. Numbers of Swedish Red and White (SRB) bulls and their daughters used in the analyses.

A. I. unit no.	No. of years	Heifers				Cows			
		No. of sires			Total no. of daughters	No. of sires			Total no. of daughters
		1960	1961	Total		1960	1961	Total	
9	2	12	11	23	2 582	13	16	29	5 431
10	2	23	26	49	3 271	28	36	64	6 832
11	2	42	45	87	8 492	49	60	109	19 988
16	2	15	13	28	4 127	18	19	37	12 680
17	2	35	39	74	10 232	40	57	97	26 310
18	2	8	8	16	1 828	15	17	32	4 196
20	2	14	14	28	4 768	28	29	57	15 053
21	2	10	13	23	2 342	16	21	37	8 212
22	2	20	21	41	5 244	31	35	66	17 194
23	2	12	12	24	2 452	18	20	38	7 001
24	2	18	20	38	5 623	29	35	64	17 649
27	2	37	35	72	6 718	52	56	108	19 823
28	2	22	25	47	5 154	26	30	56	13 903
30	2	15	19	34	3 065	21	26	47	6 490
31	1	13	—	13	642	14	—	14	1 003
32	2	5	6	11	845	4	6	10	1 462
≧ 10 daught., total	31	301	307	608	67 385	402	463	865	183 227
» 10 daught., old	—	—	—	—	—	103	147	250	47 656
» 10 daught., young	—	—	—	—	—	175	189	364	43 673
≧ 20 daught., total	31	282	296	578	66 951	—	—	—	—
≧ 100 daught., total	30	—	—	—	—	246	294	540	164 915

Table 41. Averages of the fertility traits (%) of SRB heifers and cows in different A. I. units according to the Swedish A. I. statistics 1960—1961.

A. I. unit no.	Cystic ovaries		Sterility treatments		Final concep. rate		NR-%		Sterility cullings		Mult. births	Still-births	Abor-tions
	Heifers	Cows	Heifers	Cows	Heifers	Cows	Heifers	Cows	Heifers	Cows	Cows	Cows	Cows
9	0.23	2.43	12.01	17.64	90.20	93.41	57.59	56.67	2.21	1.09	0.57	0.53	0.75
10	0.24	2.56	15.13	19.04	90.34	93.81	54.20	57.71	4.62	2.17	0.25	0.54	1.13
11	0.72	5.91	12.02	20.30	88.78	91.29	51.32	51.81	5.25	4.10	0.62	1.02	1.28
16	0.53	2.82	7.61	13.11	89.97	90.86	54.93	47.85	3.13	2.57	0.95	0.82	1.28
17	1.99	8.00	9.65	20.52	91.59	91.20	57.50	53.38	3.36	3.44	0.70	1.13	1.47
18	0.16	5.98	10.72	21.33	90.04	87.99	55.58	47.62	3.50	4.86	0.91	0.86	1.17
20	0.17	3.89	9.23	18.15	92.37	90.76	56.50	55.52	2.96	3.59	0.78	1.10	0.92
21	0.13	3.15	12.72	18.00	92.02	92.06	57.94	55.64	3.93	3.37	0.73	0.71	1.21
22	0.65	6.21	13.69	23.65	92.89	90.23	59.97	56.21	1.95	2.83	0.59	0.98	1.46
23	0.53	4.49	6.61	15.61	93.72	92.26	55.95	53.09	2.53	3.09	0.59	1.11	1.60
24	0.02	2.34	5.30	10.19	92.55	93.59	56.68	59.03	3.29	2.73	0.48	0.90	1.18
27	0.94	4.12	8.96	14.08	91.68	91.82	60.81	60.53	3.16	3.02	0.39	0.60	1.00
28	0.16	3.85	12.07	17.92	92.32	93.35	60.34	60.97	3.92	2.78	0.74	0.91	1.47
30	0.03	2.17	11.81	15.75	92.63	92.79	53.18	55.45	3.49	2.99	0.28	1.17	1.59
31	0.93	2.49	8.57	14.86	90.81	92.72	55.61	52.34	1.87	1.40	0.30	1.10	1.69
32	0.24	1.98	5.09	10.88	94.20	93.71	50.77	51.64	2.84	2.80	0.21	0.55	1.03
Mean	0.66	4.58	10.28	17.49	91.44	91.77	56.61	55.43	3.46	3.11	0.61	0.91	1.27
Old	—	6.18	—	18.69	—	89.76	—	54.10	—	4.09	0.85	0.80	1.10
Young	—	3.05	—	16.05	—	93.25	—	56.59	—	2.38	0.27	1.00	1.41
≧ 20 d.	0.65	—	10.21	—	91.51	—	56.72	—	3.44	—	—	—	—
≧ 100 d.		4.69		17.65		91.78		55.52		3.10			

and in sterility cullings 2—5 % and 1—5 %. Almost similar ranges can be seen in the frequency of multiple births, stillbirths and abortions of cows. These ranges show that a comparison of progeny groups from different A. I. units presupposes an adjustment to the unit means.

The averages of heifers and cows differ from each other, especially with regard to cystic ovaries and need for sterility treatments. The difference in the NR-% is about 1 % or the same as in the Uusimaa A. I. statistics. The means of the "old" and "young" cows are also different. In the final conception rate, the young cows are even better than the heifers. The same applies to cullings due to sterility. In the NR-% they seem to be equal.

The correlations of the unit means between heifers and cows were 0.65 for ovarian cysts, 0.78 for need for sterility treatment, 0.30 for final conception rate, 0.58 for NR-%, and 0.48 for sterility cullings.

The average frequency of multiple births in the Swedish data is surprisingly low as compared with that in the Finnish milk-recording statistics or Uusimaa A. I. statistics. Because the means reported by Korkman (1948) from the SRB breed are also at a higher level, it appears that it has been difficult for the Swedish A. I. technicians and veterinarians to obtain information on multiple births. The difference between the recorded und unrecorded herds in the Uusimaa statistics (Table 34) indicates that the difficulties obviously have been mainly concentrated in the unrecorded herds included in the Swedish statistics. In any case, the effect of age on the frequency of multiple births

Table 42. Components of variance in some fertility traits of SRB heifers according to the Swedish A. I. statistics 1960—61.

Fertility trait	Min. no. of cows per sire	Numbers: Sir-es	Cows per sire	% of total variance: Between A. I. units	Between years	Between sires	Error variance	Heritability (%): h^2 + S. E. W&C	h^2 K&H
Cyst. ovar.	10	608	110.8	0.61***	0.04*	0.25***	0.0064749	1.00±0.26	1.04
Ster. treatm. ...	10	608	110.8	0.71***	0.05(*)	0.60***	0.0910073	2.40±0.34	2.44
Fin. conc. rate .	10	608	110.8	0.21***	0.00	1.06***	0.0772621	4.24±0.45	4.32
NR-% I serv. .	10	608	110.8	0.31**	0.05(*)	1.06***	0.242192	4.24±0.45	4.32
Cull. steril.	10	608	110.8	0.22***	0.01	0.67***	0.0330862	2.68±0.36	2.72
Cyst. ovar.	20	578	115.8	0.59***	0.05**	—0.02	0.0063743	—0.08±0.21	
Ster. treatm. ...	20	578	115.8	0.74***	0.04(*)	0.41***	0.0906212	1.64±0.30	
Fin. conc. rate .	20	578	115.8	0.22***	0.00	0.86***	0.0768775	3.44±0.41	
NR-% I serv. .	20	578	115.8	0.31**	0.06(*)	0.96***	0.242287	3.84±0.43	
Cull. steril.	20	578	115.8	0.23***	0.01	0.58***	0.0329208	2.32±0.34	

(W & C = components of variance computed according to WINSOR & CLARKE 1940)
(K & H = components of variance computed according to KING & HENDERSON 1954)

becomes apparent in these statistics also. Stillbirths seem to be more common in the young than the old cows, possibly owing to difficulties at the first calving.

b) Heifer fertility

The results of variance analyses on fertility of heifers are shown in Table 42. A comparison of the upper and lower parts of the table shows that the exclusion of the smallest groups has decreased the heritability estimates in some degree. In fact, this change has been considerably greater than the effect of the method of KING and HENDERSON (1954) as compared with the method of WINSOR and CLARKE (1940) in computing the coefficients of variance components.

Assuming that the results for the progeny groups of at lest 20 daughters are the most reliable, one can observe that all the heritability estimates are significant with the exception of that concerning cystic ovaries. The highest estimate (3.8 %) was obtained for the NR-% after the first service. This is more than twice the corresponding estimate obtained from the Uusimaa A. I. statistics (Table 30). The estimate concerning the final conception rate is almost as high, while the heritability of cullings due to sterility and that of the need for sterility treatments are significantly lower. The very low estimate for cystic ovaries is in agreement with the results obtained from the Ayrshire heifers in the Uusimaa A. I. unit.

The annual differences within A. I. units seem to be at the borderline of significance in some cases, but on the whole their importance is comparatively small, as was also the case in the Uusimaa statistic. On the other hand, the differences between A. I. units are highly significant, their variance components being almost as large as those of sire differences.

Table 43. Heritability of some fertility traits of SRB heifers in eight Swedish A. I. units in 1960—61.

A. I. unit code no.	Numbers		Heritability ± standard error (%) in different traits					
	Sires	Cows per sire	Cystic ovaries	Sterility treatments	Final conc. rate	NR-% I serv.	Sterility cullings	Average
11	79	106.1	—0.76±0.72	2.96±1.07	6.24±1.59	4.60±1.33	4.12±1.26	3.43±1.17
16	27	152.1	0.60±0.88	1.28±1.06	1.64±1.16	3.20±1.59	1.88±1.23	1.72±0.34
17	68	149.1	0.16±0.49	0.76±0.59	8.32±1.89	3.92±1.13	4.96±1.31	3.62±1.49
20	27	176.1	—0.52±0.76	0.80±0.84	0.80±0.84	3.20±1.49	—0.28±0.69	0.80±0.66
22	40	130.8	—0.72±0.85	1.60±1.04	2.16±1.17	0.36±0.76	0.20±0.73	0.72±0.52
24	37	151.6	—0.92±0.83	1.00±0.85	—0.24±0.67	2.96±1.30	0.40±0.71	0.64±0.66
27	69	96.8	0.96±0.87	0.52±0.79	1.52±0.96	4.36±1.44	1.52±0.96	1.78±0.67
28	45	113.8	—0.64±0.88	0.20±0.78	1.24±1.00	1.84±1.13	1.72±1.10	0.87±0.48
Mean h^2			—0.23±0.25	1.14±0.30	2.71±1.05	3.06±0.49	1.82±0.66	1.70±0.32
S. D. h^2 %			0.71	0.85	2.96	1.40	1.86	
C. V. h^2 %			308.7	74.6	109.2	45.8	102.2	

Table 43 has been constructed to see whether there are differences between the A. I. units with regard to the heritability of different measures of fertility. At least 20 daughters were required in each progeny group in these analyses and at least 4 000 heifers in each A. I. unit.

The standard errors in each trait × unit square have been computed according to the formula of ROBERTSON (1959 a), but the standard errors of the averages at the right and bottom are conventional standard errors based on variations in the heritability estimates.

The average estimates of the different traits are a little lower than the pooled estimates of the 16 A. I. units in Table 42, but the rank order of the traits is the same. However, the differences in the variance of the estimates are noteworthy. The coefficient of variation is lowest with regard to the NR-% and second lowest with regard to sterility treatments. There are no negative values in these columns. The relative variability of the estimates concerning the final conception rate and the cullings due to sterility are at the same level. It thus appears that the NR-% is the most suitable measure of heifer fertility in general, but that the final conception rate or cullings due to sterility are most suitable in certain societies.

The averages at the right reveal that the heritability of heifer fertility in general may be different in various A. I. units. It is not possible to conclude whether these divergences are due to differences in the accuracy of data recording and observations or in the preselection of bulls for A. I. service with regard to heifer fertility. Some of the differences are reflections of the variations among the mean incidences of the all-or-none traits.

c) Cow fertility

The use of 10 daughters as a minimum group size gives a relatively lower standard in the cows than in the heifers, since there is a wider range of age

Table 44. Components of variance in some fertility traits of SRB cows according to the Swedish A. I. statistics 1960—61.

Fertility trait	Data		Numbers		% of total variance			Error variance	$h^2 \pm$ S. E.
	Age class	Min. no. of cows/sire	Sires	Cows per sire	Betw. A. I. units	Betw.. years	Betw. sires		%
Cyst. ovaries .	Young	10	364	120.0	0.89***	0.10*	0.45***	0.0291877	1.80±0.38
Ster. treatm. .	»	10	364	120.0	0.85***	0.00	0.47***	0.133059	1.88±0.39
Fin. conc. rate	»	10	364	120.0	0.14*	0.04(*)	0.57***	0.0624798	2.28±0.42
NR-% I serv.	»	10	364	120.0	0.40***	0.03(*)	0.42***	0.243629	1.68±0.37
Cull. steril. . . .	»	10	364	120.0	0.15**	0.01	0.07	0.0231736	0.28±0.27
Mult. births .	»	10	364	120.0	0.03(*)	0.00	—0.10	0.0027139	—0.40±0.28
Stillbirths	»	10	364	120.0	0.04(*)	0.02	0.19**	0.0099059	0.76±0.30
Abortions	»	10	364	120.0	0.03	0.02	0.25***	0.0138366	1.00±0.32
Cyst. ovaries .	Old	10	250	190.6	0.85***	0.00	0.67***	0.0571192	2.68±0.43
Ster. treatm. .	»	10	250	190.6	1.22***	0.04(*)	0.32***	0.149696	1.28±0.30
Fin. conc. rate	»	10	250	190.6	0.36***	0.00	0.53***	0.0911672	2.16±0.38
NR-% I serv. .	»	10	250	190.6	0.70***	0.08*	0.32***	0.245734	1.28±0.30
Cull. steril. . . .	»	10	250	190.6	0.19***	0.00	0.57***	0.0389138	2.28±0.39
Mult. births .	»	10	250	190.6	0.00	0.08*	0.20***	0.0083933	0.80±0.25
Stillbirths	»	10	250	190.6	0.04**	0.00	0.00	0.0079112	0.00±0.18
Abortions	»	10	250	190.6	0.04(*)	0.00	0.01	0.0109111	0.04±0.19
Cyst. ovaries .	All	10	865	211.8	0.87***	0.00	0.76***	0.0429979	3.04±0.24
Ster. treatm. .	»	10	865	211.8	1.05***	0.02(*)	0,43***	0.142276	1.72±0.17
Fin. conc. rate	»	10	865	211.8	0.19***	0.02(*)	0.67***	0.0748542	2.68±0.22
NR-% I serv. .	»	10	865	211.8	0.57***	0.09***	0.32***	0.244733	1.28±0.15
Cull. steril. . . .	»	10	865	211.8	0.14***	0.00	0.41***	0.0299567	1.64±0.17
Mult. births .	»	10	865	211.8	0.04*	0.01(*)	0.15***	0.0060802	0.60±0.12
Stillbirths	»	10	865	211.8	0.04***	0.00	0.05*	0.0090531	0.20±0.10
Abortions	»	10	865	211.8	0.03***	0.00	0.09***	0.0124976	0.36±0.11
Cyst. ovaries .	All	100	540	305.4	0.83***	0.00	0.70***	0.0440271	2.80±0.25
Ster. treatm. .	»	100	540	305.4	1.08***	0.02(*)	0.38***	0.143288	1.52±0.17
Fin. conc. rate	»	100	540	305.4	0.16***	0.02(*)	0.59***	0.0748669	2.36±0.22
NR-% I serv. .	»	100	540	305.4	0.57***	0.08***	0.27***	0.244783	1.08±0.15
Cull. steril. . . .	»	100	540	305.4	0.12***	0.01	0.37***	0.0299341	1.48±0.17
Mult. births .	»	100	540	305.4	0.03*	0.00	0.22***	0.0063331	0.88±0.13
Stillbirths	»	100	540	305.4	0.03**	0.00	—0.01	0.0090263	—0.04±0.08
Abortions	»	100	540	305.4	0.03**	0.00	0.02	0.0123976	0.08±0.08

classes among the cows. It is hoped, however, that the division into "old" and "young" cows will eliminate part of the age effects and that the calculations performed on progeny groups of at least 100 daughters will give an idea of the effect of minimum group size. The results of the variance analyses are presented in Table 44.

Numerous comparisons can be made in this table. Firstly, there are significant differences between unit means in the fertility traits. The relative importance of the unit differences is greatest with regard to the cystic ovaries, sterility treatments and NR-%. This applies equally well to both young and old cows. However, the importance of differences between unit means in the NR-% and the final conception rate increases in the older age classes. The general picture of the unit differences is about the same as with regard to heifers in Table 42.

The differences between yearly averages within the A. I. units are much less important than variations in the unit means. Here again the results for heifers and cows are rather similar. The yearly variation seems to be highest in the NR-%.

The heritability estimates proved to be at a slightly lower level than those concerning heifers in Table 42. It is most surprising that even the old cows did not give a higher value for cystic ovaries than 2.68 %, and it is equally surprising that intermingling the old and young cows only increased the heritability estimate of cystic ovaries very little. The effect of blending was still smaller in the other traits. Further, it can be observed that the estimates were independent of the minimum group size. It is difficult to believe that mere blending of the data from recorded and non-recorded herds in the Swedish A. I. statistics could have made the results so very different from those obtained from the Uusimaa A. I. statistics.

In any case, the fact that the above-mentioned factors did not appreciably influence the estimates indicates that the results for both young and old cows make it possible to compare the heritabilities of the different traits with each other and with the estimates obtained for heifers. It is noteworthy that the final conception rate had a higher heritability than the NR-% in both old and young cows, although the latter measure seemed to be slightly better than the former in the heifers. Among the young cows the final conception rate even gave the highest estimate, while in the old cows it was exceeded by cystic ovaries and cullings due to sterility. If the estimates of heifers, young cows and old cows are averaged, the highest mean is obtained for the final conception rate (2.6 %). The rank order of the remaining traits is as follows: NR-% 2.3 %, culling due to sterility 1.63 %, sterility treatments 1.60 %, and cystic ovaries 1.47 %. The heritability of multiple births in these statistics was unexpectedly low, but it is still in agreement with that obtained from the Uusimaa A. I. statistics (Table 37). The heritability of stillbirths and abortions was also low, especially among the older cows.

While considering the rank order of the different measures in the Swedish A. I. statistics it should be remembered that the final conception rate in cows is not a pure fertility trait. It only shows the proportion of cows which are declared fertile among those served at least once during a service period. The cows which are culled for other reasons than sterility also affect this figure, which could also be called the culling percentage. Culling of young cows because of poor production is rather common in Sweden: more than 10 % of I-calvers of the SRB breed are culled before completing their first lactation (305 days). A certain part of this culling may take place after the cows have been inseminated at least once. This applies especially to cows culled for poor persistency in milk production. Because both persistency and the whole lactation yield are inheritable traits, this culling may erroneously increase the differences between sire progeny groups as regards the final conception rate. However, this may also influence the NR-%, sterility treatments, frequency of cysts and cullings due to sterility, so it is difficult to tell whether and to what extent the rank order really changes for this reason.

In Table 45, heritabilities are estimated separately for the eight largest populations, each of which comprised at least 10 000 cows.

The significances of the estimates are based on standard errors computed according to the formula of ROBERTSON (1959 a), while the standard errors of the means at the bottom are conventional standard errors.

As in the case of the heifers in Table 43, the rank order of the different traits seems to vary from unit to unit. In half of the units, the highest heritability has been obtained for the cystic ovaries, but because old and young cows were intermingled in the data, this apparent superiority cannot be taken too seriously.

The variability of the estimates from unit to unit does not differ so much from trait to trait as in heifers. There appears to be no correspondence in the rank order of the estimates between heifers and cows. This dissimilarity of the results for the two groups of data indicates again that the genetic correlation between heifer fertility and cow fertility may be very weak. The decision as to the best measure of fertility thus depends on the importance to be attached to heifer fertility as compared with cow fertility.

6. *The theoretical heritability of all-or-none fertility traits*

Part of the variability of heritability estimates obtained for different traits from different data is obviously due to variation in the mean level of incidence

Table 45. Heritability of some fertility traits of SRB cows in eight Swedish A. I. units in 1960—61. At least 100 daughters/sire. (Bold face type = at least 95 % significance.)

A. I. unit no.	Numbers		Heritability ± standard error (%) in different traits							
	Sires	Cows per sire	Cystic ovaries	Ster. treatments	Fin. conc. rate	NR-% I serv.	Cull. ster.	Mult. births	Still-births	Abor-tions
11	66	273.2	3.40	1.72	1.60	1.36	0.92	0.20	0.08	0.04
16	24	455.6	1.12	0.36	1.84	1.68	0.44	1.92	0.04	—0.36
17	67	371.1	2.36	2.36	1.76	1.00	2.04	1.12	—0.12	0.08
20	40	351.2	1.72	0.88	5.96	0.64	2.84	0.32	0.20	0.40
22	44	393.3	3.72	1.80	3.60	1.92	1.40	1.36	0,04	—0.12
24	45	347.7	2.92	1.16	1.44	0.84	0.20	1.84	—0.24	—0.24
27	68	258.0	0.96	0.76	2.00	0.80	2.12	0.76	—0.32	0.04
28	46	289.7	4.20	2.28	0.44	0.36	0.44	—0.12	0.00	0.52
Mean h^2			2.55	1.42	2.33	1.08	1.30	0.93	—0.04	0.05
S. E. h^2			±0.43	±0.26	±0.60	±0.19	±0.34	±0.27	±0.06	±0.11
S. D. h^2, %			1.21	0.73	1.71	0.53	0.96	0.76	0.17	0.30
C. V. h^2, %			47.4	51.4	73.4	49.1	73.8	81.7	425.0	600.0

Table 46. The theoretical heritabilities of some all-or-none fertility traits as compared to the actual heritability estimates in the present study.

Fertility trait	Data	Actual heritability, % II calv.	III calv.	IV calv.		II-IV calv. (4-6 y.)	Theoretical h², % II calv.	III calv.	IV calv.		II-IV calv. (4-6 y.)
	Rec.										
Overtimedness	56/57	6.0***	1.0			3.2***	19.9	3.6			11.3
» (cumulat.)	62/63	2.0***	4.2***								
S/C	56/57	3.6***	—0.7			2.0**					
» (cumulat.)	62/63	4.0***	6.1***								
Concep. aft. 1 s.	56/57					1.7*					2.9
Concep. aft. 2 s.	56/57					1.6*					4.3
Concep. aft. 3 s.	56/57					0.5					2.6
Fert. disturb.	56/57					1.0**					22.6
Cull. steril. (3–10 y.)	61/62					2.1*					12.2
Mult. births	56/57					2.1*					23.2
—»—	62/63	3.6***	2.8***	3.2***		3.1***	40.7	21.7	22.6		26.2
		Heifers	Young cows 2-4 y.	Older cows 4-5 y.	Oldest cows ≥ 6 y.	All cows+heifers	Heifers	Young cows	Older cows	Oldest cows	All C+H
	A. I.										
—»—	Uus.					0.3					3.6
—»—	Swed.		—0.4		0.8***	0.6***		—15.3		12.6	12.2
Stillbirths	»		0.8***		0.0	0.2*		10.6		0.0	3.0
Abortions	»		1.0***		0.0	0.4***		10.8		0.5	4.3
Ster. treatments	»	1.6***	1.9***		1.3***	1.5***	4.7	4.3		2.7	3.3
Cull. steril.	»	2.3***	0.3		2.3***	1.5***	13.3	2.1		11.6	9.0
Cystic ovar.	»	—0.1	1.8***		2.7***	2.8***	—1.6	11.2		10.5	13.3
—»—	Uus.	0.3	0.3		9.3***	3.5***	5.1	2.2		46.9	24.4
NR-⁰/₀ I serv.	Swed.	3.8***	1.7***		1.3***	1.1***	6.1	2.7		2.0	1.7
—»—	Uus.	1.8**	1.7**	1.0(*)	0.1	1.3***	3.0	2.8	1.8	0.1	2.2
Fin. concep. rate	Swed.	3.4***	2.3***		2.1***	2.4***	11.1	8.4		6.1	7.8
Heat symptoms	Uus.	2.2(*)	2.6*		7.6**	3.5***	5.1	5.7		18.3	8.4
Retain. plac.	»					0.8					7.1

of the traits. To make the estimates more comparable, some estimates have been corrected to a common incidence level in Table 46, according to the method of LUSH *et al.* (1948). These corrected estimates are called "theoretical heritabilities" in the present study.

Relatively high values were obtained for the theoretical heritability in some cases, e.g. with regard to multiple births in several age classes, cystic ovaries in the oldest age class, and overtimedness before the second calving. This latter figure is almost as high as the heritability of milk yield and thus suggests that overtimedness and milk yield are only different expressions of the same thing. This possibility has been discussed by HENRICSON (1957) and CASIDA (1961) among others. The information available in the present study does not make possible far-reaching inferences, but it indicates that the relations of fertility and milk-producing ability deserve serious consideration in studying the usefulness of heifer lactation yield as a measure of production ability.

The high theoretical heritability of multiple births in the recording statistics is noteworthy. Can this be interpreted as meaning that the birth of twins is a relatively sure sign of a genetic tendency for multiple births, but that the birth of a single calf does not tell much of the genetic quality of a cow? The answer depends partly on the validity of the assumption that the underlying causes of multiple births are normally distributed. Testing this is not possible on the basis of the available data, but it can be mentioned that some authors consider the mode of inheritance as probably monogenic and recessive (LÖWE 1939, KARWETZKI 1941, WEBER 1944, PFAU *et al.* 1948).

Transforming the heritability estimates into the probit scale also made the heritability of conception after two services higher than that after a single service.

Although there was no essential difference between the actual heritabilities of "cullings due to sterility" on the one hand and of the need for sterility treatments on the other, the theoretical heritability of the "cullings" seems to be higher than that of the need for treatments, especially in heifers and old cows. A similar differentiation was obtained between the final conception rate and the NR-% in the Swedish A. I. statistics. The heritability of the NR-% proved to be one of the lowest in the probit scale.

The general level of the estimates in the probit scale seems to indicate that the genetic variability in reproductive fitness has not been exhausted by natural selection and that studies aimed at finding good measures for this trait should be continued.

C. Discussion

1. Heritability of fertility

A survey of the numerous tables presented in the present study reveals that, with very few exceptions, the heritability estimates are generally positive.

Most estimates lie between 1 and 2 %, which is about 1/3 of the estimates obtained from individual experimental farms in the literature review. However, it was also possible in this study to measure the ordinary breeding efficiency in such a way that even higher heritabilities could be obtained, especially in some special stages of a cow's life. The pooled estimates on overtimedness and on the number of services per conception during the first three lactations in the recording statistics were 3.2 % and 2.0 %, respectively, which agree reasonably well with the average estimates of the calving interval and the S/C in Tables 1 and 2. There is not such close agreement with the estimates of LEGATES (1954) and DUNBAR and HENDERSON (1953) concerning the heritability of the C. I. in A. I. populations. The volume of data in these studies was considerably smaller than in the present one, but the method of analysis was more highly developed. DUNBAR and HENDERSON, for example, eliminated the effects of herd differences and sire-herd interactions from the results. However, they did not take the age of the cows into account as was done in the present study, where the heritability of breeding efficiency during the first lactation proved to be exceptionally high.

The discrepancy becomes still more apparent when the heritability of overtimedness obtained in this study is transformed into the probit scale, which should better correspond to the heritability of the continuously variable calving interval. The high heritability of breeding efficiency during the first lactation — if real — is probably a consequence of the radical change in the hormone balance and other physiological processes taking place when the cow's first lactation starts. It is also possible that this pronounced change is related to the level of milk production. Unfortunately, however, it was not possible to study how much of the heritability remains when variations in the milk-producing ability are eliminated.

A somewhat conflicting picture was obtained of the heritability of breeding efficiency at the later lactations. The recording statistics from the years 1956/57 — 57/58 indicated that the heritability of the C. I. or S/C during the later lactations is questionable, but the cumulative numbers of services from the recording statistics 1961/62 and 1962/63 suggested the opposite. The heritability of the cumulative number of services increased from 4 % to 6 % when the services required for the third conception were added to those required for the first two calvings. The corresponding increase in the heritability of cumulative overtimedness was from 2 % to 4 %. The results given by the recording statistics 1961/62 (Tampere + Uusimaa) seem to confirm the impression that the accuracy of assessment of fertility tends to improve when increasingly more service periods are taken into account. Further confirmation is given by KOORT (1948), who obtained a heritability of ca. 20 % for the average number of services required during several (2—12, ave. 4.3) service periods. In the case where age was determined by the year of birth, there was no decline in the heritability estimates with age even in the recording statistics 1956/57 — 57/58.

From the A. I. statistics it can be seen that the heritability of breeding efficiency as a heifer is at least at the same level as that as a cow. Because conception in heifers is not complicated by lactation, heifer fertility can be considered as "pure" fertility and is obviously influenced by certain anatomical and physiological defects causing absolute sterility. The fact that heifer fertility can be measured earlier than cow fertility also makes it interesting from the viewpoint of progeny-testing bulls for fertility. Table 28 showed, however, that heifer fertility and cow fertility may be genetically unrelated. Similar results were obtained by INSKEEP *et al.* (1961) and from the intensity of heat symptoms in the present study, and therefore this problem will be investigated more closely in later parts of this series of studies.

The heritability of multiple births on the basis of recording statistics was about 3 %, which again is about 1/3 of the average estimate of previous studies. However, no previous estimates are available from A. I. populations for comparison. The age of the cow did not have much influence on the heritability, except at the first calving, when multiple births are relatively rare.

With regard to the occurrence of cystic ovaries, it appeared that the hereditary differences are especially evident in the older age classes. This agrees with the studies of HENRICSON (1957) who, assuming a recessive mode of inheritance, found the penetrance of the trait to increase with age. The heritability estimate on cows 5 years old or older ($h^2 = 9$ %) in the Uusimaa A. I. statistics was also in reasonable agreement with the results of HENRICSON, but the pooled estimate on all age classes was only 3.5 %. In the Swedish material available, the estimates were still lower. Worthy of note is the considerable variation of the heritability estimates from year to year, a feature which was not observed in the other fertility traits studied. This annual variation of the heritabilities is partly associated with annual variations in the average incidence of cystic ovaries. A possible explanation for these fluctuations in the frequency are the variations in the quality of basic feeds from year to year. This may concern not only the protein, vitamin and mineral contents of the feeds, but possibly also estrogenic substances (STRÖM 1954, KALLELA 1964).

With regard to the other fertility traits, especially in the A. I. statistics, the heritability estimates varied much more between the A. I. units than between the years. This variation is not necessarily due entirely to differences in the management of different A. I. units, but possibly also to differences between the agricultural societies supervising the work of milk recorders.

The heritability of the frequency of stillbirths and abortions in the Swedish A. I. statistics was low, but taking into account the low frequency of the cases reported, the results do not seriously disagree with those obtained by ERB *et al.* (1959). His figures for both traits were 5 %, the average incidencies being 26 % for abortions and 16 % for stillbirths. The theoretical heritability of both stillbirths and abortions among the young cows in the Swedish data was about 10 %, while the respective figures computed from the estimates of ERB *et al.* are 11 % for stillbirths and 9 % for abortions. It is also noteworthy that the heritability in the Swedish data was entirely limited to the young cows and not to the old cows.

The fact that the heritability of fertility seemed to vary according to the measure of fertility adopted, the age of the cow, the way the age was measured, the years and the A. I. units makes it easy to understand why such different results have been obtained by different authors with regard to the heritability of fertility and why such different standpoints have been taken concerning the necessity for selecting for fertility in dairy cattle breeding.

2. *Applicability of the results under different conditions*

The question also arises whether the heritability estimates obtained apply only to the conditions from which the data were collected or whether they have a wider applicability. The indoor feeding period in Finland is about 8 months long, and it is a common experience that cows calving at the beginning of this period attain better annual yields than cows calving in the late spring or in summer. Because of the great economic importance of milk production in Finnish farming more and more concentrated feed is being used to increase the farmer's monthly income. During the long winter period it is easier to provide uniform and adequate feeding for the cows. Sometimes the temperature in the barns is also well adjusted, and the cows are protected from draught. It is probable that this tendency towards intensive milk production places too high demands on the physiological balance of the cows, especially since knowledge of correct rations has not increased at the same tempo as the desire to obtain high yields. The health and fertility of the cows are therefore often disturbed, but the affected animals are not culled without first trying medicines and veterinary treatments. Natural selection is thus not allowed to exert its full power, a fact which tends to conserve the additive genetic variability in fertility.

On the other hand, a high production level may be considered a means for revealing those animals which do not have a sufficiently strong physiological and hormonal constitution. The expressivity of a weak constitution should be increased by this stress. The importance of this fact becomes understandable when one takes into account the relationship between the incidence level and heritability estimates of all-or-none traits.

Finland is not alone, however, in the above-mentioned respects; conditions are rather similar in the other Scandinavian countries. The fact that the heritability estimates in the literature are, on the whole, similar to those of the present study, indicates that the heritability of fertility is about the same in most countries and breeds. The negative estimates of heritability obtained in some American studies may be due to the peculiarities and inaccuracies of the data used. However, it is possible that the high labor costs prevailing in the United States allow natural selection to work more efficiently than in the Scandinavian countries, or that cows may become "sterile" through no fault of their own, thus lowering the heritability estimates. The fact that positive estimates have been obtained from experimental farms in the U.S.A. seems to show that the problem of sterility itself is similar in Scandinavia and North America.

It is not at all certain that genes causing fertility disturbances in modern dairy cattle are the same as those which were subject to natural selection before the present century. However, the fact that there have been so few generations of cattle since the end of the last century obviously means that the genetic situation has not yet changed very much. Thus the theories which claim that the additively genetic variability of fitness characters has disappeared as a result of natural selection — only nonadditive variability being left — may hold reasonably true at present. If this is really so, then the most effective genetic means for maintaining fertility would be a planned crossbreeding and utilization of heterosis. However, the crossbreeding experiments between Holstein and Guernsey breeds carried out at the Illinois Agricultural Experimental Station have not shown the nonadditive gene actions to be of any great importance concerning fertility traits (VERLEY and TOUCHBERRY 1961), although they were important with regard to general viability (DICKINSON and TOUCHBERRY 1961).

The applicability of the results can also be considered from another angle. Because the estimates were derived from hundreds or thousands of herds, they should reflect the influence of just those particular causes of fertility which are common among most herds. On this basis, the applicability is wider than that of the estimates from individual experimental herds. Selective measures undertaken on the basis of the present results should tend to lower the frequency of those sterility genes which are most frequent in the whole breed and whose effect is most pronounced.

Of course, the results apply only to conditions where recording of sires, ages and fertility traits is at least as accurate as in the statistics used in the present study.

3. Systematic nongenetic causes of variation in fertility

The systematic environmental factors considered in the present study were the age of the cow, the year of calving or insemination, and the A. I. unit. The importance of age varied according to the trait and according to the way in which age itself was measured. In measures of the ordinary breeding efficiency, such as overtimedness, number of services per conception and nonreturn percentage, the effect of age on the means was rather slight, especially among the younger age classes. When age was measured according to the parity, however, there was a considerable effect on the heritability estimates. The first lactation appeared to be exceptional in this respect. Unfortunately it was not possible to measure age according to the parity in the A. I. statistics. The results obtained from the recording statistics indicate that the calving number should also be recorded in the A. I. statistics.

In some special traits, such as cystic ovaries and multiple births, the effect of age on the mean incidence was highly significant. This is in complete agreement with results obtained by other workers (p. 29). The cullings due to sterility, intensity of heat symptoms and the need for sterility treatments appeared to be significantly dependent on age, too. It can thus be concluded that consideration of the age is necessary in evaluating progeny of bulls with regard to fertility. Especially in the case of cystic ovaries, age also affected the heritability estimates, so that estimates giving possibilities for phenotypic selection were obtained only for the older cows. With regard to multiple births, only the first calving had an essentially lower heritability than the other calvings.

A n n u a l variations occurred in several fertility traits both in the recording statistics and in the A. I. statistics. Special attention was paid to the variation in the average incidence of cystic ovaries which also considerably affected the heritability of the trait. Although the annual variations in the NR-% in the Uusimaa A. I. statistics were rather small as compared with other causes of variation, they were sufficiently important that they should be alertly watched for. This is also necessary on account of possible developments in the semen-handling techniques. In the Swedish A. I. statistics the NR-% appeared to be the trait most subject to annual variations. This indicates that it is not only female fertility that may vary from year to year, but that variations in male fertility may also affect the NR-%.

Significant differences between the A. I. u n i t s were obtained especially in the recording statistics of 1962/63 and in the Swedish A. I. statistics. In the former, this applied only to the ordinary breeding efficiency but not to multiple births. In the Swedish A. I. statistics, the most sensitive traits in this respect were cystic ovaries and the need for sterility treatments. This is readily understandable, since both measures are dependent on decisions made by the board of an A. I. society with regard to the extent and costs of diagnoses and treatments. The NR-% also appeared to be considerably dependent on the A. I. unit. The reasons are partly the same as those for the yearly variations within the units, but there are also additional causes, e.g. different distances from the bull station to the technicians, different soil, climate, feeding, etc., in different areas of a country.

The month of calving or insemination is a definite cause of variation in most fertility traits according to both practical experience and investigations (ALIM 1957, BRANTON *et al.* 1956, CARMAN 1955, HILDER *et al.* 1944, JOHANSSON 1942, KOORT 1948, MERCIER and SALISBURY 1947, POU *et al.* 1953, TRIM-

BERGER and DAVIS 1945). Because in most cases it is not systematically distributed among the daughters of different bulls, this trait was not included in the present study. But inferences can be drawn about the existence of some other systematic factors on the basis of heritability estimates derived from different material. For example, the exceptionally high estimates obtained from naturally bred cows indicate that there are considerable differences between different herds or bull associations. It is difficult to be certain whether these differences are reflections of real differences in "herd sterility" or whether they are only due to differences in book-keeping accuracy. Most likely both reasons are important. Their effects vary slightly from trait to trait. Neither of them had an influence on the analyses of multiple births and intensity of heat symptoms, but their influence was considerable regarding the ordinary breeding efficiency in the recording statistics.

4. *Comparison of the sources of information*

This study was also aimed at determining the value of the data obtained through the A. I. technicians as compared with information given by the milk recorders. The heritability estimates on the NR-% after the first service in recorded herds show that the A. I. statistics may be seriously considered as an alternative to the recording statistics as far as ordinary breeding effeciency is concerned. With regard to cystic ovaries, it is almost the only source of information. The low heritability of multiple births, stillbirths and abortions showed, however, that the A. I. technicians may have difficulty in collecting data other than those directly observed by themselves on the cows. This doubt was confirmed by the relatively low heritability of retained placenta in the Uusimaa A. I. statistics. The estimate was namely 0.80 %, while the estimate of ERB *et al.* (1959) was as high as 16 %. The heritability of the intensity of heat symptoms was also lower than that obtained by ROTTENSTEN and TOUCHBERRY (1957), but because the latter study was based on data from experimental conditions, it is not very suitable for comparison.

Attention should be paid, however, to the fact that the data collected by the A. I. technicians from non-recorded herds seemed to be rather unsuitable for use. For instance, the sire was known in too few cases, and the heritability estimates were also lower than those based on data from recorded herds. In addition, since the means of different fertility traits, including the NR-%, deviated from the means of recorded cows, the data from the two classes of herds should be handled separately. Although the situation seems to be gradually improving, it will obviously take a long time before the non-recorded herds can become a useful and important source of information. At the moment, the useful data to be obtained through A. I. technicians and milk recorders come from the same herds, and it is justifiable to ask whether data other than those concerning the NR-% and cystic ovaries can profitably and reliably be collected through the A. I. statistics.

The collection of fertility records of the cow's lifetime obviously can be more reliably done in the recording statistics than in the A. I. statistics. In regard to cullings due to sterility, the two statistics seem to be about equally valuable.

One encouraging experience was also obtained in favour of the A. I. technicians. A comparison of the heritability estimates on cystic ovaries between the Uusimaa A. I. statistics and the Swedish A. I. statistics shows that the heritabilities are about the same, even though the diagnoses in the Uusimaa unit are made exclusively by technicians.

The A. I. statistics are of special value in recording heifer fertility.

5. *Comparison of different measures of fertility*

The best measure of a trait cannot be definitely determined on the basis of heritability estimates, but these are valuable means for a preliminary elimination of alternatives.

Of the traits studied on the basis of the recording statistics, the overtimedness and the number of services were rather similarly affected by several factors, such as the age of the cow, the method of measuring age, and the inclusion in the data of cows born in natural service. For example, both of these measures had the highest heritability before the second calving. The heritability of overtimedness was higher than that of the S/C in the recording statistics of 1956/57, while the reverse was the case in 1962/63. Consequently, it is difficult to determine the mutual superiority of these two measures. The latter statistics showed that the overtimedness was less liable than the S/C to faults caused by carelessness in recording. The theoretical heritability of overtimedness in the former statistics was over 10 %, indicating that the actual calving interval might be a suitable measure of fertility in A. I. populations. On the other hand, the available heritability estimates of the C. I. in the literature did not exceed those of the S/C. It is possible that only the right-hand tail of the distribution of the C. I. has any sense from the standpoint of assessing fertility. Unfortunately, no estimates for the C. I. could be computed in the present study.

Expression of the fertility as the percentage of cows conceiving after one, two or three services led to slightly higher theoretical heritabilities than the S/C. Since, however, the actual heritability estimates were lower, the former methods cannot be utilized in practical assessments of fertility.

The different fertility disturbances and treatments are so seldom noted in the milk-recording reports that their value is questionable. Because their heritability — even in the Swedish A. I. statistics, where almost every treatment may have been reported — could hardly compete with that of other measures, efforts to improve their reporting in connection with milk recording may be pointless. However, a more detailed classification of the treatments according to their nature might perhaps give some valuable information.

The frequency of cullings due to sterility seems to be equally possible to ascertain from both statistics. One of the disadvantages of this trait is the fact that it can be measured only once in a cow's lifetime, so that repeated measurements are not possible. Since the heritability was not higher than that of an individual measurement in breeding efficiency, it appears that registration of this trait is hardly worth while except for scientific studies. Its value is further lessened by the fact that its heritability was lowest in the young cows, which in the progeny testing of bulls are most important. On the other hand, the use of cullings may be seriously considered as an alternative for measuring heifer fertility.

The frequency of multiple births seemed to respond to most factors so very differently from overtimedness, S/C or NR-%, that it can hardly be closely related to these measures, although conception is usually impaired after twinning. Because milk production and the general health of a cow are also often seriously depressed by the birth of twins, the finding that the heritability of multiple births is significantly about 3 % is still of importance. In the registration of this trait it is best to rely on milk recorders.

The effect of systematic factors on the frequency of cystic ovaries also differed considerably from their effect on breeding efficiency. Thus, as a measure of fertility it hardly can replace the NR-%, for instance. Because of its relatively high heritability at the older ages, it can be considered a special hereditary weakness which should be taken into account in selecting dams for young A. I. bulls.

The intensity of heat symptoms seems, as a whole, to have about as high a heritability as cystic ovaries, but the heritability is not so concentrated in the older age classes. There were some indications that this trait is more closely related to breeding efficiency than are multiple births or cystic ovaries. It would be desirable to obtain more data on this trait, but because it can only be measured subjectively, it would hardly be of value if this feature were routinely included in the A. I. statistics.

The heritability of the NR-% after the first insemination proved to have approximately the same heritability as the final conception rate in the younger age classes. A selection between these two measures can thus be made on other than genetical grounds. Because of the feasibility of the determination of NR-% in practice, it appears that there is no strong reason to register the final conception rate.

It is more difficult to decide whether it is better to register the breeding efficiency by using overtimedness, calving interval os S/C from the milk-recording reports or by utilizing the NR-% from the A. I. statistics. In the basic heritability there is obviously no essential difference, but the collection of cumulative records may be easier for the milk recorder than for the A. I. technician. The same applies to a still greater extent to the recording of sires and ages of the cows. The A. I. statistics could be recorded more simply if registration of the sire and age could be omitted. On the other hand, the milk recorder would not have to record fertility traits if this is done in any case by the A. I. technicians. Because the main use of the fertility records is in progeny-testing bulls and not in judging individual cows, the A. I. statistics seem to be more practical, since in them the basic data can be collected as a by-product. The milk recorder could then concentrate on the recording of production traits. If the production ability is measured on an operational year basis, and averages of several records are used for evaluating individual animals, cows with poor fertility will obviously be penalized to approximately the same degree as poor fertility has economic importance.

For a final choice between the different measures of fertility, it is necessary to determine their relationships to each other and to production traits, a problem which will be studied in a future paper.

6. Progeny-testing bulls for fertility

On the basis of the heritability estimates obtained, a preliminary discussion can be made on the possibilities of progeny-testing A. I. bulls for female fertility. According to ROBERTSON and RENDEL (1950), the accuracy of a progeny test increases with the number of daughters according to the formula $b = \frac{n\,0.25\,h^2}{1 + (n\text{-}1)\,0.25\,h^2}$, where b = regression of future daughters on present daughters, n = the number of present daugters, and h^2 = heritability of the trait in question. In Fig. 6 this formula has been applied to three different levels of h^2 to determine the accuracy obtainable with different numbers of daughters in regard to the cumulative number of services required for 3 conceptions ($h^2 = 6$ %), the frequency of multiple births ($h^2 = 3$ %) and the NR-% of young cows ($h^2 = 1.5$ %).

This figure shows that an accuracy of 70 % should be attained with about 150 daughters in progeny testing for the cumulative number of services up to the third calving, while the corresponding number for multiple births is slightly over 300, and for the NR-% more than 600. The difference in the required number of daughters becomes smaller when one takes into account that several records per cow are also available for the multiple births and NR-% at the time when the cumulative number of services required for 3 conceptions is known. According to the studies of KORKMAN (1948), the repeatability of multiple births is not higher than the heritability. It can thus be assumed that information obtained from 600 calvings of 300 cows is equally valuable as that from 600 cows with one calving each. With regard to the NR-%, the repeatability seems to differ more from the heritability (DUNDAR and HENDERSON

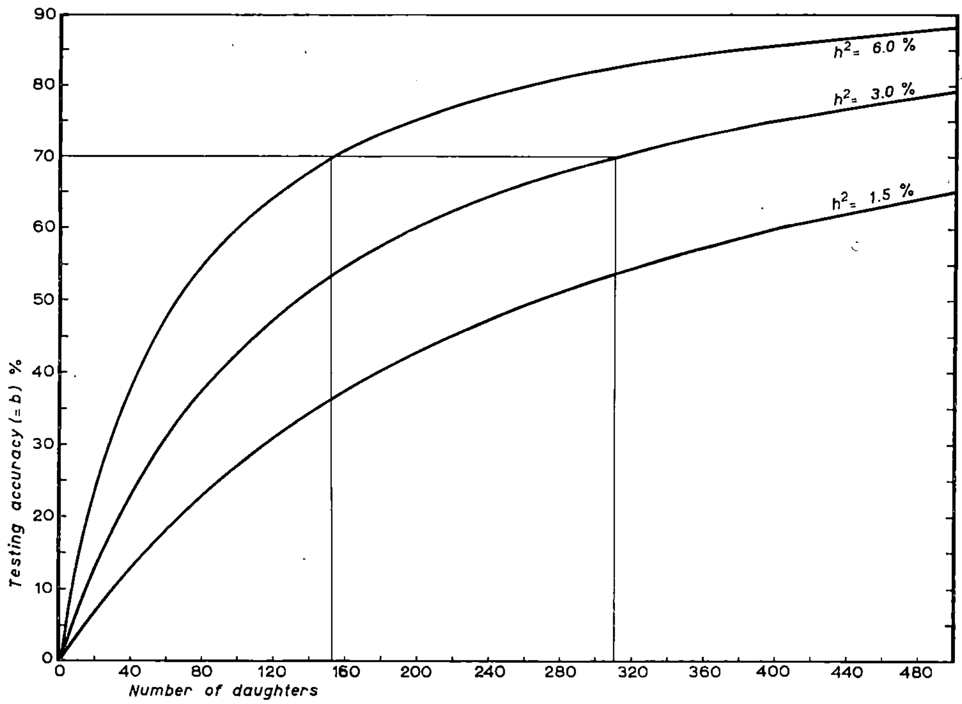

Fig. 6. The dependence of progeny-testing accuracy on the number of daughters with regard to some fertility traits (h^2 = 6 % = S/C as an average of 3 first service periods; h^2 = 3 % = multiple births; h^2 = 1.5 % = NR-%).

1953), but replacing the number of daughters by the number of records in Fig. 6 hardly causes any appreciable errors even in this trait.

In the progeny tests made on the basis of data from the recording year 1962/63, utilizing daughters with 1—3 complete annual milk records, there were a total of 75 Ayrshire bulls which had at least 600 daughter records included in the test. The number of bulls with at least 300 records was 133. In the Uusimaa A. I. statistics of the years 1958/62 there were 35 bulls with at least 600 records and 58 bulls with at least 300 records from recorded herds. Thus it appears that if the most important environmental causes of variation are properly eliminated, it is possible to progeny-test A. I. bulls for female fertility with reasonable accuracy. The requirements with regard to the number of progeny are so large that the principal application of the results will be in selection of sires for young bulls. However, bearing in mind the relatively high heritability of overtimedness and S/C during the first lactation, there seems to be some hope that the whole progeny-testing for fertility could be based on a single measure such as the length of the first calving interval. Before a final conclusion can be reached, the genetic correlation of this measure to the later fertility has to be determined.

Several other aspects of the fertility problem should be studied before an answer can be obtained to the question of whether selection against sterility or for fertility by progeny testing of bulls really pays. For example, if the whole additive genetic variance of the cow's fertility is only reflection of the heritability of milk-producing ability, it may be more economical to remedy such fertility disturbances by nutritional and medical means than by selection. However, a thorough understanding of the interrelationships of fertility and production is necessary in any case.

Summary

The present study is the first of a series intended to throw additional light on the question of proper weighting of fertility traits in dairy cattle breeding and to find the most effective methods of assessing the fertility of individual animals. As an introduction to the series, the importance of fertility from the viewpoint of both immediate economy and selection possibilities was discussed and the problems involved were presented.

The main objectives of this first study were (1) to determine whether there is any additive genetic variability in the female fertility when measured on a large practical scale, (2) to find the best measure of fertility under these circumstances and (3) to compare the relative value of two possible sources of information (milk recording and A. I. statistics) for collecting the data needed in progeny-testing A. I. bulls for female fertility.

Causes of variation in several fertility traits were studied. The data comprised ca. 200 000 service periods of nearly 80 000 cows from the Finnish recording statistics, nearly 120 000 service periods of over 50 000 cows from Finnish A. I. statistics, and about 180 000 service periods of 160 000 cows from Swedish A. I. statistics. Heritability estimates were obtained by multiplying the paternal half-sib correlation by four. For comparing heritability estimates of all-or-none traits at varying incidence levels, estimates were transformed to correspond to the probit scale. The results are presented in Table 46, which also shows the most important actual heritability estimates.

The principal findings and conclusions are as follows:

1. The heritability of female fertility varied according to the measure of fertility, the age at which fertility was measured, the A. I. units (areas), the year of calving or insemination, and the source of information.

2. The general level of the heritability estimates was positive, the most frequent value being between 1 and 2 %, or about 1/3 of the level obtained in individual experimental herds in the literature.

3. The heritability of heifer fertility was generally at the same level as that of cow fertility, except with regard to cystic ovaries, where no heritability was found in heifers.

4. In cow fertility, breeding efficiency as measured by overtimedness of the calving interval or by the number of services per conception, appeared to have an exceptionally high heritability during the first lactation as compared with other lactations.

5. There were some indications that heifer fertility and cow fertility may be genetically unrelated.

6. In the Finnish recording statistics, the frequency of overtimed calving intervals and the number of services per conception appeared to be the best measures of breeding efficiency. It was not possible to definitely decide which method was superior. By utilizing repeated measurements, it is possible to judge individual cows with an accuracy of 6 % at the time of the third calving. The heritability of overtimedness during the first lactation alone was at the same level.

7. The actual heritability of conception after one, two or three services was lower than that of the S/C.

8. The noting of fertility disturbances and treatments in the milk-recording reports was too incomplete to be of value in judging animals for fertility.

9. The frequency of cullings due to sterility gave similar heritability estimates to those given by the other measures of fertility, but because repeated measurements are not possible in this trait, it hardly can replace overtimedness or the S/C as a measure of fertility.

10. The heritability of multiple births in the recording statistics was 3 %, but this trait responded to most factors so very differently from the ordinary measures of breeding efficiency that it cannot be used in their place.

11. In the A. I. statistics, the NR-% after the first service and the final conception rate proved to be about equally valuable as measures of genetically determined fertility. The NR-% is to be preferred because of its practicability. Both of these measures showed a heritability of 1.5 %.

12. The occurrence of cystic ovaries proved to be a heritable trait, especially in the older age classes. It is obvious, however, that this trait cannot replace the NR-% as a measure of fertility. The same applies to the intensity of heat symptoms.

13. The heritability of stillbirths and abortions was very low in the Swedish A. I. statistics, and there was no heritability in the older age classes. Very little heritability was obtained for retained placenta either, according to the Finnish A. I. statistics.

14. The frequencies of need for sterility treatments and cullings due to sterility had about the same heritability (1.5 %) in the Swedish A. I. statistics. In the probit scale, the cullings seemed to be more strongly heritable.

15. The A. I. statistics appeared to be a suitable alternative to the recording statistics for collecting information on the ordinary breeding efficiency of cows. On the other hand, the A. I. technicians seem to find difficulty in collecting data other than those directly observed by themselves on the cows

(multiple births, stillbirths, abortions, retained placenta). The information they obtained on cystic ovaries and heat symptoms was more usable.

16. It appeared that the A. I. statistics do not help as much as expected in obtaining data from non-recorded herds for progeny-testing bulls for fertility. The sire and age of non-recorded cows was known in too few cases, and the data containing this information led to very low heritability estimates. Even the sires and ages of recorded cows were less frequently known in the A. I. statistics than in the recording statistics.

17. The diagnoses concerning cystic ovaries seemed to be equally reliable in both the Finnish and the Swedish A. I. statistics, although the former were made exclusively by technicians.

18. The importance of age of the cows as a cause of variation in fertility varied according to the trait and to the way age itself was measured. The effect on the ordinary breeding efficiency was not very large at young ages, but the frequency of cystic ovaries, multiple births, distinct heat symptoms, cullings due to sterility, and need for sterility treatment appeared to be significantly dependent on age. It is to be noted that even in cases where the means did not vary with age, the heritability might be dependent on this factor.

19. The annual variations were of minor importance, except in cystic ovaries, where they also affected the heritability estimates. Some annual effects were also found in the ordinary breeding efficiency.

20. Significant differences between A. I. units were obtained, especially in the number of services in the recording statistics and cystic ovaries and sterility treatments in the A. I. statistics. Almost all measures were sensitive to the unit differences, but in multiple births, stillbirths and abortions their effect was not significant. In some degree, the heritability estimates, too, varied according to the A. I. units.

21. It was concluded that if the most important environmental causes of variation are properly eliminated it is possible with reasonable accuracy to progeny-test A. I. bulls for female fertility.

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SELOSTUS

Hedelmällisyys jalostuskysymyksenä lypsykarjan keinosiemennyspopulaatioissa I. Naaraspuolisen hedelmällisyyden rekisteröinti ja heritabiliteetti

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Tämä tutkimus on ensimmäinen sarjassa, jonka tarkoituksena on luoda lisävalaistusta kysymykseen hedelmällisyyspiirteiden tarkoituksenmukaisimmasta painottamisesta lypsykarjan jalostuksessa sekä löytää menetelmät yksityisten eläinten hedelmällisyyden arvostelemiseksi. Johdantona koko tutkimussarjaan tarkasteltiin aluksi hedelmällisyyden alhaisuuden välittömiä taloudellisia vaikutuksia ja sen merkitystä valintamahdollisuuksien kannalta sekä esiteltiin lähemmin aiheeseen liittyvät tutkittavat kysymykset.

Tutkimussarjan nyt esillä olevan ensimmäisen osan päätavoitteina oli (1) selvittää, onko naaraspuolisessa hedelmällisyydessä — sellaisena kuin se voidaan käytännössä mitata — lainkaan additiivista perinnöllistä muuntelua, (2) löytää näissä oloissa parhaat hedelmällisyyden mitat sekä (3) selvittää, mikä merkitys keinosiemennyssonnien jälkeläisarvostelussa tarvittavien hedelmällisyystietojen hankinnassa on ns. keinosiemennystilastolla karjantarkkailuun verrattuna.

Useiden erilaisten hedelmällisyyspiirteiden muuntelun syitä tutkittiin aineistossa, joka käsitti lähes 80 000 lehmän n. 200 000 astutuskautta suomalaisesta karjantarkkailutilastosta, yli 50 000 lehmän lähes 120 000 astutuskautta suomalaisesta keinosiemennystilastosta ja n. 160 000 lehmän 180 000 astutuskautta ruotsalaisesta keinosiemennystilastosta. Erilaisten hedelmällisyyden mittojen samoin kuin eri tietolähteidenkin käyttökelpoisuuden kriteereinä käytettiin heritabiliteettiarvioita, jotka saatiin kertomalla isänpuoleisten puolisisarusten välinen luokansisäinen korrelaatio neljällä. Eräitä "kaikki-tai-ei-mitään"-luonteisia hedelmällisyyspiirteitä koskevia heritabiliteettiarvioita muunnettiin probit-asteikkoon, jotta voitaisiin vertailla sellaisten piirteiden heritabiliteetteja, joiden esiintymistiheys on erilainen. Näitä muunnettuja heritabiliteetteja on esitetty taulukossa 46, johon myös on kerätty tärkeimmät todelliset heritabiliteettiarviot.

Tärkeimmät tulokset ja johtopäätökset olivat seuraavat:

1. Naaraspuolisen hedelmällisyyden heritabiliteetti vaihteli sen mukaan, millä tavalla ja missä iässä hedelmällisyys oli mitattu, sekä keinosiemennysyhdistyksen (alueen), siemennys- tai poikimisvuoden ja tietolähteen mukaan.

2. Saatujen heritabiliteettiarvioiden yleistaso oli positiivinen; yleisin arvio oli 1 ja 2 %:n välillä, mikä on noin 1/3 koeolosuhteissa saaduista arvioista.

3. Hiehojen hedelmällisyyden heritabiliteetti oli yleensä vähintään samalla tasolla kuin lehmienkin, mutta ns. munasarjarakkuloiden esiintymiseen nähden ei hiehoilla havaittu juuri mitään heritabiliteettia.

4. Yliaikaisuutena tai tiinehtymiseen tarvittujen astutusten lukuna mitatulla tiinehtymistaipumuksella näytti olevan poikkeuksellisen korkea heritabiliteetti ensimmäisellä lypsykaudella.

5. Hiehojen ja lehmien hedelmällisyys eivät näyttäneet olevan periytymisen puolesta sukua toisilleen.

6. Suomalaisessa karjantarkkailutilastossa yliaikaisuus ja astutusten luku tiineyttä kohti näyttivät olevan parhaita tiinehtymistaipumuksen mittoja. Näiden kahden mitan keskinäistä paremmuusjärjestystä ei voitu lopullisesti ratkaista. Käyttämällä hyväksi toistuvia mittauksia näyttää olevan mahdollista arvostella yksityisten lehmien hedelmällisyyttä 6 %:n varmuudella, kun lehmä on poikinut kolme kertaa. Ensimmäisen poikimisvälin yliaikaisuus yksistäänkin antoi näin suuren heritabiliteettiarvion.

7. Yhdestä, kahdesta tai kolmesta siemennyksestä tiinehtymisten todelliset heritabiliteetit olivat alhaisempia kuin tiinehtymiseen tarvittujen siemennysten kokonaisluvun.

8. Hedelmällisyyshäiriöiden ja mahoushoitojen merkitseminen karjantarkkailussa osoittautui siksi puutteelliseksi, ettei näitä merkintöjä voi käyttää hedelmällisyyden arvostelussa.

9. Mahoudesta johtuneiden poistojen lukuisuus antoi samanlaisia heritabiliteettiarvioita kuin muutkin hedelmällisyyden mitat, mutta koska tämä piirre voidaan mitata vain kerran kultakin lehmältä, se tuskin pystyy korvaamaan yliaikaisuutta tai astutusten lukua hedelmällisyyden mittana.

10. Kaksossynnytysten heritabiliteetti tarkkailutilastossa oli 3 %, mutta tämä piirre reagoi useimpiin tekijöihin nähden siinä määrin tiinehtymistaipumuksen mitoista poikkeavasti, että sitä ei voida käyttää näiden asemesta.

11. Keinosiemennystilastossa tiinehtymis-% 1. siemennyksestä ja lopullinen tiinehtymis-% osoittautuivat suunnilleen yhtä arvokkaiksi perinnöllisen hedelmällisyyden mitoiksi. Tiinehty-

mis-% 1. siemennyksestä voidaan siten asettaa etusijalle sen käytännöllisyyden vuoksi. Kummankin mitan heritabiliteetti lehmillä oli noin 1.5 %.

12. Munasarjarakkuloiden esiintyminen näytti olevan perinnöllinen ominaisuus varsinkin vanhemmissa ikäluokissa. Monet seikat viittasivat siihen, että tämä piirre ei voi korvata tiinehtymis-%:a hedelmällisyyden mittana. Sama koskee kiiman voimakkuutta.

13. Kuolleiden vasikoiden synnytysten ja luomistapausten heritabiliteetit olivat varsin alhaisia ruotsalaisessa keinosiemennystilastossa, eikä vanhemmissa ikäluokissa voitu havaita lainkaan heritabiliteettia. Myös jälkeisten jäämisen heritabiliteetti oli varsin alhainen suomalaisen keinosiemennystilaston mukaan laskettuna.

14. Ruotsalaisen keinosiemennystilaston mukaan olivat mahoushoitojen ja mahoudesta johtuvien poistojen yleisyyksien heritabiliteetit suunnilleen samansuuruisia. Probit-asteikossa kuitenkin poistojen heritabiliteetti näytti olevan suurempi.

15. Keinosiemennystilasto näytti olevan karjantarkkailutilaston kanssa samanveroinen, kun kyse oli lehmien tiinehtymistaipumusta koskevien tietojen keruusta. Sen sijaan ilmeni, että keinosiementäjillä on vaikeuksia sellaisten tietojen keräämisessä, joita he eivät itse ole olleet toteamassa, kuten esim. tiedot kaksossynnytyksistä, kuolleina syntyneistä tai luoduista vasikoista tahi jälkeisten jäämisestä. Heidän keräämänsä tiedot munasarjarakkuloista ja kiiman voimakkuudesta olivat sitä vastoin käyttökelpoisia.

16. Tutkimuksista ilmeni, että keinosiemennystilastosta ei ole odotetun suuruista apua, kun on saatava hedelmällisyystietoja sonnien jälkeläisarvostelua varten karjantarkkailuun kuulumattomista karjoista. Tarkkailuun kuulumattomien lehmien isä ja ikä tunnettiin nimittäin liian harvoissa tapauksissa, ja ne aineiston osat, joissa nämä tiedot oli merkitty, johtivat varsin alhaisiin heritabiliteettiarvioihin. Myös tarkkailuun kuuluvien lehmien isän ja iän merkitseminen oli keinosiemennystilastossa harvinaisempaa kuin karjantarkkailutilastossa.

17. Munasarjarakkuloita koskevat diagnoosit näyttivät olevan yhtä luotettavia sekä suomalaisessa että ruotsalaisessa keinosiemennystilastossa, vaikka ne edellisessä tilastossa ovat yksinomaan keinosiementäjien tekemiä.

18. Lehmän iän merkitys hedelmällisyyden muuntelun syynä vaihteli sen mukaan, mistä hedelmällisyyden piirteestä oli kysymys ja millä tavalla itse ikä oli mitattu. Iän vaikutus ei ollut kovin suuri varsinaisessa tiinehtymistaipumuksessa nuorella iällä, mutta munasarjarakkuloiden, kaksossynnytysten, mahoudesta johtuvien poistojen, mahoushoitojen ja selvien kiiman oireiden yleisyydet näyttivät olevan merkitsevästi riippuvaisia iästä. Merkillepantavaa on, että sellaisillakin mitoilla, joiden keskiarvot eivät vaihdelleet iän mukaan, saattoi heritabiliteetti olla riippuvainen iästä.

19. Vuotuisten vaihteluiden merkitys oli verraten vähäinen, paitsi munasarjarakkuloiden ollessa kyseessä; tässä tapauksessa vaihtelut vaikuttivat myös heritabiliteettiarvioihin. Jonkin verran vuosittaisia vaihteluita oli havaittavissa myös tiinehtymistaipumuksessa.

20. Keinosiemennysyhdistysten välillä oli merkitseviä eroja; varsinkin vaihtelivat siemennysten luku karjantarkkailutilastossa sekä munasarjarakkuloiden ja mahoushoitojen yleisyys keinosiemennystilastossa. Lähes kaikki piirteet olivat jossakin määrin alttiita yhdistysten välisille eroille, mutta kaksossynnytyksissä, luomistapauksissa ja kuolleiden vasikoiden synnytyksissä niiden vaikutus ei ollut tilastollisesti merkitsevä. Jossakin määrin myös heritabiliteettiarviot vaihtelivat yhdistysten mukaan.

21. Tutkimuksen mukaan näyttää olevan mahdollista saavuttaa kohtalainen varmuus keinosiemennyssonnien jälkeläisarvostelussa naaraspuoliseen hedelmällisyyteen nähden, jos tärkeimmät ulkonaiset muuntelun syyt sopivasti eliminoidaan.

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