A STUDY OF SOME ASPECTS OF SELECTION FOR THE FERTILITY OF NEW ZEALAND ROMNEY EWES

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J. N. CLARKE

MASSEY UNIVERSITY COLLEGE OF MANAWATU

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"Ewes yearly by lambing rich
masters do make,
The lambs of such twinners,
for breeders go take."

- from Youatt (1837), as quoted by
Wentworth and Sweet (1917).

I INTRODUCTION

The majority of present day animal breeding methods have their origin in pre-scientific times. They have largely evolved from the empirical evidence of husbandrymen who have been keen and critical observers of the performance of their stock, and it is only relatively recently that the genetic basis of the various procedures has been determined. This in turn has led to the realisation that any permanent improvement in the inherent ability of animals to produce more, rests upon the successful manipulation of these genetic factors.

In the genetic improvement of sheep, the breeder is concerned with replacing the existing population of genotypes with another which is superior in some particular feature of merit. Selection is generally conceded to be the main force at the breeder's command for accomplishing this purpose. Broadly, selection may be defined as choice based on information. It takes place at many phases of any livestock industry, beginning with the selection of the type of production, and passing through the selection of a breed or a strain to the selection of an individual animal. In particular, the within-flock selection of individuals may be simply defined as the non-random designation of animals to be parents of the next generation. Such designation is intended to change the mean of the population by increasing the frequency of the desired genes. It is therefore, largely dependent upon the ability to classify individuals in terms of their genetic work. For this reason, it is perhaps best defined in terms of its observable consequences, as, "the non-random differential reproduction of genotypes" (Lerner 1958).

Genetic improvement is in this way intimately associated with a number of diverse reproductive phenomena which include differential viability, differences in mating tendencies, fecundity and duration of reproductive capacity (Wright 1955). Indeed, the fertility of individuals directs the improvement possible in a breed or flock, largely determining the proportion of available animals that must be retained for breeding, and hence the margin of selection that is possible.

The present trend of emphasis in the research and practice of all livestock breeding, appears to hinge around an increasing awareness of economic merit. In order to apportion the importance of each character in terms of its contribution to the net financial return of a flock, the concept of relative economic values has been employed (Hazel 1943). This concept allows breeding objectives to be rationalised and placed on a sound economic basis, with the result that the financial progress to be expected from selective breeding can be considerably greater than when the breeder's ideals are confused, fluctuating or erroneous (Hazel and Lush 1942).

Although the economic importance of an adequate level of flock reproductive performance has always been recognised in a general way, the efforts of New Zealand Romney ram breeders have largely been directed towards increasing individual productivity in fleece weight, fleece style, carcass conformation and breed type. Rae (1954) has shown that this situation is completely out of step with the relative economic importance of the various characters in this breed. The expected financial return from one generation of single character selection indicates a higher economic importance for fertility than for any other character. Further realisation of the importance of fertility has come from recent breed cross comparisons involving Romney sheep under New Zealand conditions.

Despite the importance of the Romney breed in the sheep industry of this country, few attempts have been made to assemble the information required to define the problems involved in breeding for the improvement of productivity.

Rae (1946, 1950, 1958) has reviewed many of the pertinent studies and concludes that they merely serve to outline the general structure of the breeding industry, and to indicate where information of a more specific nature is lacking. In view of the wide geographical distribution of the breed, together with the fact that it is expected to produce both meat and wool, it is not surprising that breeders' opinions vary as to what constitutes an ideal sheep. This situation lays further stress on the importance of carefully defined selection objectives and techniques, which are considered in relation to the broad economic and physical environment in which the sheep are required to produce. To this end, further work is needed to guide breeders in their choice of efficient breeding techniques for the improvement of the economically important character, fertility.

II REVIEW OF LITERATURE

A. INTRODUCTION

The difficulty of classifying individuals in terms of their genetic worth lies in the fact that the observed phenotype of an animal is the result of environmental influences as well as of inherent potential. Thus, the variation that exists between animals in their expression of the desired qualities, which is the material available to the breeder in directing the population towards his goals, can be subdivided into genetic and environmental sources. The approach of present day genetics to this problem is from the standpoint of assessing the value of different indicators of an animal's breeding merit, in the sense of its ability to leave superior offspring. This approach, which is essentially statistical in nature, has led to the modern theory of population genetics. The main integrating concept is the additive genetic variance between individuals and its related parameter, the heritability.

The merit of this approach lies not so much in suggesting new ways of improvement, but rather in providing a rational method of integrating several rather diverse phenomena. For example, the prediction of genetic gain from selection procedures, the use of different bases ~~for~~ and aids to selection, and the construction of selection indices can all be couched in terms of basic variation and its genetic components. The theory has, in this way, extremely useful applications in the designing of breeding schemes.

In this section literature on the application of modern genetic theory to fertility of sheep, will be briefly reviewed in relation to the accuracy of assessing phenotype, and the value of phenotype as an indication of genotype.

Before these aspects can be adequately dealt with, however, it is necessary to define reproductive efficiency more precisely and to consider the ways in which it may be measured.

B. DEFINITION AND MEASUREMENT OF FERTILITY

Reproduction is the biological phenomenon largely responsible for the continuity of life. Fertility, being an inseparable part of this general field, has been the subject of a large number of investigations in which the problem has been tackled from many different angles. In popular usage in the animal husbandry sense, fertility denotes the ability of an animal to produce large numbers of living young. It is the end product - the number of young produced - which is the criterion by which the fertility of a flock of sheep is judged.

In technical writings there exists a general lack of uniformity in the use of the terms fertility, fecundity and prolificacy. Jones and Rouse (1920) and Lush (1943) point out the precise meanings of these terms. Briefly, fertility strictly refers to the total actual reproductive capacity of a female and a male, as expressed by their ability, when mated together, to produce individual off-spring. Expressed in this way fertility denotes a qualitative aspect of reproduction, while fecundity represents its quantitative equivalent.

As Goot (1950) and Sharafeldin (1960) remark, the main reason for the implied equivalence of these terms in the literature, probably lies in the difficulty of procuring suitable information which would make their separation possible. On this ground, it therefore seems justifiable when dealing with mammals to use the term fertility to represent both qualitative and quantitative aspects of reproductive efficiency. In this connection the term, lamb production, is gaining popularity in current scientific writings.

In the present state of physiological knowledge and techniques, the practical measurement of fertility is limited to those stages of the reproductive cycle where visible expression is possible in terms of the number of offspring produced. Goot (1950) has discussed many of the common methods used for estimating fertility in sheep, and suggests seven indices for its calculation. All of these assess fertility at lambing or at some subsequent date.

In any study of fertility in mammals it is important to realise that the efficiency of reproduction depends on chains of events, each of which determines the upper limit of the succeeding one. Workers have variously considered aspects by the following three major stages:

1. The number of ova shed
2. The number of ova fertilized
3. The number of zygotes carried to term.

The first of these is largely a character of the dam, while the second may conceivably be influenced by either the sire or the dam. While it may be tempting to regard the third component as a function of the viability of the young, the potential influence of the dam, quite apart from her contribution to the genotype of the litter, cannot be ignored. In addition, each of these separate processes is capable of modification by a whole host of internal and external factors. While the majority of the crucial reproductive events are governed by several interacting hormones or by overlapping series of hormones, it is also known that the nervous system is frequently equally important, (Nalbandov 1958, 1963).

The complexity of fertility, however, does not end with its multiple determination. The number of young born in many species of mammals has been shown to be subject to a strong maternal effect, dependent upon the weight of the dam. A larger mother tends to produce a larger litter in which individual weights are consequently depressed. Should this effect carry over to the time when the daughters' reproduce, there may result a negative daughter-dam relationship which, in mice, has been found to mask the positive genetic pathway expected for a heritable character (Falconer 1955).

This discussion has been presented to illustrate that fertility may be regarded as a quantitative character, but that it is one of considerable complexity. Furthermore, it is to be expected that fertility is capable of being affected throughout all stages of an animal's life in that any period of unfavourable conditions may upset the function of the mechanism controlling it. For the same reasons, a complete description of the genetics of fertility must be regarded as a goal for the future rather than a present achievement, requiring a detailed analysis of the character into its components and a separate but integrated investigation of each of these.

So far as individual variations in quantitative fertility measurements have a hereditary basis, they are subject to selection, and the average of the flock is expected to be changed by the same breeding methods used for improving other characters. The extent to which any character can be influenced by selective breeding depends upon the degree to which the various environmental influences can be discounted and the true genetic ranking of the animals exposed.

C. THE EFFECTS OF NON-GENETIC FACTORS ON EWE FERTILITY

As far back as the last century Heape (1899), in a study of a large number of breeding ewes in several hundred English flocks, suggested five physiological factors which may affect the hereditary expression of fertility. In order of importance he considered these to be the physical condition of the ewe, the nutrition of the ewe, the district, the age of the ewe and the season of the year at which mating occurred. Since this time, the effects of a large number of environmental factors on ewe fertility have been investigated for many different breeds run under a wide range of environmental conditions. These have recently been reviewed in connection with breeding problems by Reeve and Robertson (1953), Ch'ang (1955) and Sharafeldin (1960). As a result of this work there has been a considerable increase in the understanding of the underlying physiological mechanisms, and, more important as far as selective breeding is concerned, a large amount of information has accumulated on the quantitative measurement of these effects under many conditions. Since a given set of estimates is strictly applicable only to the particular populations for which they were derived, there exists some justification for such a wide range. In addition, knowledge of their underlying biological bases provides useful information for a preliminary assessment of the possible magnitude of these effects, and may also prove of considerable value in suggesting new approaches and techniques for their accurate and efficient estimation.

In this review particular attention will be paid to those effects having a useful application in selective breeding schemes, and especially those pertaining to the Romney breed of this country.

1. AGE OF EWE

The age fertility relationship in sheep, as well as in other species of domestic animals, has been the subject of many investigations. From this work it may be concluded that during her breeding life, the fertility of a ewe increases with age and then decreases, often after a plateaued level lasting a number of lambings (Heape 1899, Jones and Rouse 1920, Nichols 1926, Johansson and Hansson 1943, Barton 1947, Desai and Winters 1951a, Goot 1952a, Hart and Stevens 1952, Wright and Stevens 1953, Ragab and Asker 1954, Karam 1957, Hickey 1960, Sharafeldin 1960). Differences in the shape of the age-fertility relationships found, could be attributed to several important factors. In the first place breed differences have been demonstrated (Reeve and Robertson 1953). Secondly, age and year effects are commonly confounded in many of the studies carried out. Thirdly, the higher level of fertility demonstrated by mature ewes, could in part be due to the selective elimination of lowly fertile young animals. Fourthly, different environmental conditions may result in a differential fertility response in ewes of different ages. These possibilities emphasise the necessity of considering age-fertility associations that are directly applicable to the population of animals for which the information is desired.

Table 1 summarises a number of age-fertility associations found in New Zealand Romney ewes.

Table 1

The Effect of Age on the Fertility of Ewes

Reference	Barton(1947)	Goot (1950)		Hickey(1960)
Age at Mating	Total Lambs Born per Ewe Lambing (%)	Total Lambs Born per Ewe put to Ram (%)	Lambs Docked per Ewe put to Ram (%)	Lambs Docked per Ewe put to Ram (%)
Two-tooth	126.5	101.1	84.1	78.2
Four-tooth	143.0	120.9	108.5	94.4
Six-tooth	150.7	132.0	118.3	96.8
Full-mouth	148.6	137.4	120.4	109.2
5½ years	151.0	137.0[a]	120.0[a]	108.6
Average of all ewes[a]	141.8	124.8	109.3	93.9

a includes ewes aged 5½ years and older.

Barton's (1947) report also dealt with the incidence of barrenness and the level of lamb deaths in a stud flock of New Zealand Romney ewes. The incidence of barrenness over 13 seasons averaged 15.8% for all ewes, with a striking reduction from 25.2% for two-tooth ewes to 13.5% for four-tooths.

Goot's studies refer to two flocks of New Zealand Romney stud ewes and also demonstrated a high incidence of barrenness in two-tooth ewes. Approximately 43% of the total variation in barrenness was found to be attributable to age (Goot 1952a). Goot (1950, 1952b) also found that variations due to age accounted for between half and three-quarters of the total variance in six other fertility measurements.

The material analysed by Hickey (1960) was collected from a group of co-operating commercial farms over a period of six successive years. Breed averages were not specified.

Hart and Stevens (1952), and Wright and Stevens (1953) have also discussed age-fertility associations, while Ch'ang's (1955) analysis detected significant effects due to age and year on the incidence of barrenness, single births and twin births in New Zealand Romney ewes.

It is of some interest to consider the biological basis of age-fertility relationships. Coop (1962) has suggested that the lower breeding performance of two-tooth ewes in comparison with their older contemporaries, can be explained almost entirely in terms of liveweight at mating. This perhaps suggests that physiological maturity might be an important factor influencing fertility, and that environmental variation in fertility might be effectively allowed for in terms of some function of liveweight. Donald (1962) has also put forward this possibility, although the efficiency of such a method must await further detailed investigation of the relationships involved. Parity, or the number of previous pregnancies, is also likely to be a component of the age effect, and is in fact suggested by Sharafeldin's (1960) work on the effect of the age of the ewe at her first lambing.

The survival of lambs is a further aspect of reproductive efficiency that has been considered in relation to the age of the ewe. In general, it appears to show a similar trend to the age-lambing relationship, (Rae 1946, Barton 1947, Goot 1951, Purser and Young 1959, Sharafeldin 1960). In this case, the underlying biological basis would appear to involve effects associated with the lamb's birthweight (Purser and Young 1959), the ewe's milk yield (Barnicoat et al 1956), the number of lambs born (Wallace 1949) and suckled (Mason and Dassa 1954, Alexander and Davies 1959), and the behaviour of the ewe (Alexander 1960).

2. YEAR EFFECT ON THE FERTILITY OF EWES

Yearly variations in the lambing ability of ewes have been reported by Goot (1950, 1952a, 1952b), Desai and Winters (1951a), Ragab and Asker (1954), Ch'ang (1955), Sidwell (1956) and Sharafeldin (1960).

The effect of different years on the fertility of ewes is a subject which includes the influence of many factors which are difficult to isolate and measure separately. They embrace both meteorological and managemental changes such as temperature, rainfall, light, soil characteristics and husbandry practices. In addition, genetic changes in the average merit of the animals may also contribute to yearly variations.

Goot (1952a) reported that approximately 11% of the total variance in barrenness was due to differences between years, and yearly differences also proved to be a significant source of variation in the number of lambs docked per ewe mated. (Goot 1952b).

3. THE INFLUENCE OF OTHER NON-GENETIC EFFECTS

Reeve and Robertson (1953) have reviewed the effects of the body weight of the ewe, the time of mating in relation to the normal breeding season and the practice of "flushing", in connection with their influence on the incidence of multiple births in sheep. They conclude that these factors may have an important effect.

With grazing animals, the quantities of feed eaten are not easily measured, though changes in the liveweight of the animals are readily determined, and probably form the best and most convenient measure of the level of nutrition to which animals are subjected. However, with respect to the effects of nutrition on fertility, there is clearly a very real need to establish, both for the rearing phase and for different times of the year throughout the breeding life of the flock, the average liveweight growth curves which will lead to optimum reproductive efficiency. Until such information becomes available, there is little in the way of precise criteria which will help the breeder allow for nutritionally induced variations in the fertility of different animals. Some recently reported investigations suggest that useful information is coming to hand. For example, recent work by Tribe and Seebeck (1962), Coop (1962), Coop and Hayman (1962) and Wallace (1963) has been concerned with differentiating between the effects of liveweight and liveweight change around mating, on the lambing performance of ewes. Work of this nature should help elucidate more precisely the classical concept of "flushing" that has arisen over the years. As Moule (1962) points out,

> "the majority of the experiments to investigate "flushing" have not been properly isolated, have not been analytical, and both confirmatory and negatory results have been obtained because of bad design and failure to control variables"

The effects of the other environmental factors known to influence fertility are not considered within the scope of this review, due, primarily, to the difficulties involved in their isolation and precise measurement in the present state of knowledge on their underlying biological mechanisms.

D. EVIDENCE OF GENETIC VARIATION IN FERTILITY

Historically the approach of studies on the inheritance of fertility in sheep has been similar to those on other characters. Following early attempts at simple Mendelian analysis, the total phenotypic correlations between relatives were investigated Rae (1956). It was not until the statistical methods derived from the theory of population genetics were developed by Wright, Fisher, Haldane and Lush, that real progress was made in estimating the genetic variation in reproductive efficiency. Much of the earlier work has been reviewed by Reeve and Robertson (1953), Ch'ang (1955), Rae (1956) and Sharafeldin (1960), and will only be briefly considered in conjunction with more recent pertinent studies.

1. BETWEEN BREED GENETIC VARIATION

Despite the remarkable fertility differences that have been found, there exists little in the way of critical information as to how far the observed differences between breeds may be of genetic origin (Reeve and Robertson 1953, Rae 1956). Nevertheless, the work of Terrill and Stoehr (1939), Rasmussen (1941) and Johansson and Hansson (1943) leaves little doubt that genetic factors are involved.

2. WITHIN BREED GENETIC VARIATION

A number of studies have succeeded in producing evidence that the variance which exists between individuals in their lambing abilities, is partly due to genetic differences. Much of the earlier work, however, led to a number of contradictory opinions and provided little in the way of quantitative conclusions in terms of precise heritability estimates. In retrospect such a situation is understandable in view of the disadvantages of a low reproductive rate, the long interval between generations, and the high cost of each individual, which are difficulties in using the sheep as an experimental animal. These, together with the many environmental and physiological factors which are involved in the expression of fertility, have meant that large experimental flocks are required for the accurate estimation of effects and variance components. Due to such difficulties, many early estimates were based on data from commercial breeders' flocks and breed registry records, where adequate control and estimation of environmental components of variation was often neither economically feasible nor statistically possible.

Reeve and Robertson (1953) have commented on cases of outstanding performance shown by individual animals, and sometimes by their descendants. The question of attributing such remarkable differences to hereditary and environmental factors is the problem emphasised by these workers. In any case, population genetics and selection theory deals essentially with differences between groups of animals, the recognition of a few champion performers being of lesser importance.

(a) Type of Birth Effect:

Indications of the inheritance of reproductive rate have been obtained by comparing the fertility of ewes born as twins with ewes born as singles. The effect of the type of birth of the dam and the sire on the subsequent lambing performance of the ewe, has also been studied.

Rietz and Roberts (1915) analysed extensive data from the American Shropshire Sheep Record with a view to testing Heape's (1899) statement that

> "there is some reason to believe that twin lambs produce more twins than single lambs and that the influence of heredity is brought to bear".

These workers demonstrated small positive associations between the type of birth of the sire, the dam, the maternal grandam and the type of birth of the offspring. Wentworth and Sweet (1917) also studied breed registry records and reached much the same conclusions.

Marshall and Potts (1921) found that the highest lambing performance was exhibited by single-born ewes whose parents were both twins. Twin-born ewes were found to be 4.7% more prolific on average, than single-born ewes.

Reeve and Robertson (1953) and Rae (1956) have reviewed some Russian work which has resulted in conflicting opinions as to the importance of an animal's birth rank. Nikoljskii (1933) and Smirnov (1935) could demonstrate no definite relationship between prolificacy and birth rank in the Karakul and Romanov breeds respectively. Nordracev (1939) on the other hand, demonstrated a positive association in Rambouillets and Belogradskii's (1940) results for

Romanov sheep indicated a daughter-dam regression of the order of 0.29 (Reeve and Robertson 1953). Logyrin's (1938) work on the Romanov, however, gave a daughter-dam regression of 0.046.

Conflicting results were also reported by Castle (1924), while Desai and Winters (1951a) found that twin-born ewes gave birth, on average, to 0.12 more lambs, and showed a higher frequency of triplet production, than single-born ewes.

Ragab and Asker (1954) working with the Egyptian Ossimi breed, and Karam (1957) with Rahmani ewes, both concluded that the type of birth of the ewe had no effect on her twinning performance, although their results indicated a small lambing percentage advantage in favour of twin-born females.

Sharafeldin's (1960) analysis of Texel sheep demonstrated differences in the intensity of type of birth effects, the birth rank of the ewe herself tending to have a more consistently pronounced effect than either the birth rank of her sire or her dam.

In the New Zealand Romney Barton (1947), Wright and Stevens (1953), Rae and Ch'ang (1955) and Wallace (1958) have reported fertility differences between twin- and single-born ewes. Barton's (1947) analysis indicated a difference of 4.9lambs per 100 ewes at lambing, although when only those ewes breeding for the first time as two-tooths were considered, the lambing performance of the twin-born ewes was slightly inferior. He also found that single-born animals failing to breed as two-tooths showed a particularly inferior performance at their four-tooth and later lambings.

In a South Island Romney stud flock, Wright and Stevens (1953) concluded that up to their third lambing single-born ewes are less fertile than twin-born ewes. Over four lambings twin-born animals averaged 36 more lambs per 100 ewes, than ewes born as singles. Rae and Ch'ang (1955) demonstrated a similar difference in the annual lambing percentage of single- and twin-born ewes.

Wallace (1958) found that the proportion of dry ewes was approximately twice as great, and the incidence of twinning half as large, for twin-born ewes in comparison with those of single birth rank. This observation was made on the lambing performance of two-tooth ewes born in a flock selected for high twinning rate. At the four-tooth and six-tooth ages, however, the percentage of dry ewes and the twinning rate were much the same for both birth rank classes.

(b) Estimates of the Repeatability of Reproductive Performance:

The repeatability of fertility refers to the consistency of the reproductive performance of the same ewe at different lambings. Repeatability is usually estimated as a correlation coefficient which expresses the variation in the performance of the same ewe at different lambings as a proportion of the total variation in the character. In genetic terms repeatability measures the degree to which the character is free from temporary influence of diverse origin (Lerner 1958). In this way it serves to indicate an upper limit to the heritability of the character, although if environmental conditions have permanent effects on a ewe's ability to produce, the coefficient of repeatability will also be partly a measure of these. Repeatability also serves to indicate the extent of future gains in lifetime performance from culling based on prior records, and the relative value of repeated records in a selection programme. These aspects have been considered in some detail by Lush (1943 and 1948).

Reeve and Robertson (1953) and Ch'ang (1955), who have reviewed the literature, note a paucity of information on the repeatability of the number of lambs born per lambing. Johansson and Hansson (1943) made a detailed genetic analysis of extensive Swedish farm records, calculating a within-breed repeatability coefficient of the order of 0.180 to 0.185, using both intra-class correlation and linear regression methods. Using two binomial methods of analysis on the same body of data, Rendel (1956) obtained average repeatability coefficients of 0.11 and 0.09 for the incidence of multiple births.

Using the intra-class correlation method Desai and Winters (1951b) reported a repeatability estimate of 0.05 ± 0.03. Similar estimates were obtained by Karam (1957) for the Egyptian Rhmani breed (0.06 ± 0.04) and by Mason and Dassat (1954) for Italian Langhe sheep (0.08). Felts *et al.* (1957) however, obtained an estimate of 0.24 for the repeatability of the number of lambs born.

In New Zealand Romneys Ch'ang (1955) obtained reasonably consistent results using two techniques for measuring the amount of association in discrete data. The estimates for the number of lambs at birth ranged from 0.12 to 0.25 (Rae and Ch'ang 1955).

In Australian Merinos Turner *et al.* (1958) report an intra-ewe correlation of 0.30 for the number of lambs per birth, while more recently Young *et al.* (1963) found the repeatability of the number of lambs born and the number weaned, to be of the order of 0.05 and 0.08, respectively.

Some earlier work not covered by the previously mentioned reviewers, also indicates that fertility is a repeatable character. For example, Biegert (1938) concluded from studies on twin pregnancy in Wurttemburg sheep, that ewes which bore twins at their first or second lambings, tended to have a higher subsequent lambing rate than other ewes of the same year. A similar tendency has been found by Nikoljskii (1933) in Karakuls, by Smirnov (1935) in Romanovs, and by Kurdrasov (1939 and 1951) in Rambouillets.

(c) Estimates of Heritability of Reproductive Performance:

Heritability has been defined by Lush (1940, 1949) as the fraction of the observed or phenotypic variance which is due to differences between the genes or genotypes of individuals. More precisely, the definition of heritability in the narrow sense is the fraction of the observed phenotypic variance of a character which is caused by additively genetic differences between individuals. It is thus a measure of the additive genetic variance within a population.

Many techniques and methods of estimating the heritability of different traits have been developed (Lush 1940 and 1949 , Lerner 1950 and 1958, Falconer 1960, Johansson 1961). These methods all depend upon the measurement of the similarity between individuals related by lineal or collateral descent, as compared with unrelated individuals, often after various amounts of the recognisable environmental contributions to such similarity have been eliminated. Depending upon the method used, the estimate obtained usually lies somewhere between the narrow and broad definitions. The estimate almost always includes a little of the epistatic variance and sometimes a portion of the dominance variance. These sources of variation depend upon inter and intra-allelic gene combinations respectively. Due to Mendelian segregation and recombination each generation, the effects of these combinations gradually diminish in a large random mating population. For this reason, it is the heritability in the narrow sense that is of interest to selection studies.

Much of the earlier work on the inheritance of fertility in sheep has been reviewed by Reeve and Robertson (1953), Ch'ang (1955) and Rae (1956), and will not be repeated here. The general conclusion reached from this work, is that inheritance accounts for, at the most, only 10-15% of the total variation in one lambing record, this being based largely on the detailed analysis made by Johansson and Hansson (1943).

Further work also substantiates this general conclusion, although much of it is based on limited amounts of data. Thus, for the number of lambs at birth Broenbreck (1952) reported an estimate of 0.17 for the Columbia and Targhee breeds; Ragab and Askar (1954) an estimate of 0.036 for the Ossimi breed; Karam (1957) an estimate of 0.08 for the Rahmani breed; and Felts et al.(1957) an estimate of 0.068. Sidwell (1956) estimated the heritability of birth rank as 0.22 and 0.12 for mature crossbred and Navajo ewes respectively, and also calculated an estimate of 0.18 from Wentworth and Sweet's (1917) data for Southdowns. In the Texel breed Sharafeldin's (1960) analysis gave estimates of 0.172 ± 0.188 and 0.048 ± 0.104 for the number of lambs born at the first lambing of ewes. Karam and Ragab's (1958) estimates for the same breed were 0.266 ± 0.108, 0.538 ± 0.143 and 0.298 ± 0.330, as obtained by three different methods of analyses. In Australian Merinos Young et al.(1963) have recently reported heritability estimates of 0.09 ± 0.09 for the number of lambs weaned, and 0.19 ± 0.10 for the number of lambs born. These estimates were based on the sum of two year old and three year old lambing records.

In the New Zealand Romney breed, Ch'ang (1955) employed several different statistical procedures to calculate the heritability of the number of lambs born, the incidence of barrenness and the incidence of twinning. In general, the results showed the heritability of these measures of reproductive performance to be low, the estimates ranging from zero to 0.15 (Rae and Ch'ang 1955).

(a) The Effect of Sires on the Fertility of their Daughters:

The existence of significant differences between sires in the fertility of their female offspring serves to demonstrate the importance of the sire in transmitting this character to his daughters. Such an effect must be clearly distinguished from the physiological and psychological influence of the sire on the fertility of ewes to which he is mated, even though this effect may also have a genetic basis.

Although some early workers (Marshall and Potts 1921, Nordrucev 1939 and 1951) have considered possible sire effects, it is often not clear from their statements whether they were referring to male or female fertility. Both Johansson and Hansson (1943) and Desai and Winters (1951a) failed to demonstrate significant fertility differences between groups of daughters from different sires. Nevertheless, the latter workers noted that the sire contributed 4.66% of the within-line sums of squares. Ragab and Asker (1954) and Mendel (1956) found significant differences between sires in the incidence of twinning in their offspring, while Ch'ang (1955) and Sharafeldin (1960) also found significant sire differences with respect to the number of lambs born.

(c) Selection Experiments for Fertility in Sheep:

Given the necessary estimates of genetic parameters, population genetics theory allows certain inferences to be made concerning the rate of genetic improvement possible under specified selection procedures. Conversely, heritability estimates can be checked by examining the actual changes induced in a population, following the application of a measured selection intensity. This may be considered as a dynamic application of population genetics theory, and heritability estimated in this way has been termed the realised heritability by Falconer (1960). This method is perhaps the most effective way of estimating the proportionate amount of additive genetic variance, and in addition is no doubt the best way of assessing the practical utility of proposed breeding schemes. However, when one or more generations of selection have been made, the precise measurement of the genetic response actually obtained introduces several problems. There are matters of procedure rather than principle and have been discussed in detail by Falconer (1953, 1954, 1955, 1960), Dickerson (1958, 1961), Henderson et al. (1958) and Smith (1962).

Unfortunately selection experiments in larger domestic animals are beset with practical and economic difficulties. These limitations have severely restricted the scope of many experiments and have tended to result in the use of laboratory animals for checking the response of populations to selection. This would appear to be especially true for lowly heritable characters which require large numbers of animals for an adequate analysis of selection response. In spite of the difficulties, a few experiments have been carried out and confirm that lamb production is a character that can be improved by selective breeding (Kiser and Christgau 1940, Wallace 1958, Turner et al. 1962).

In each of these three experiments the plan has involved the formation of single- and twin-producing flocks of sheep on the basis of the ewes' birth rank, her own tendency to produce singles or twins, and her ancestral disposition towards singles and twins. Attempts have been made to avoid undue effects of inbreeding through the choice of the sires.

Kiser and Christgau's (1940) experiment, involving purebred Shropshire sheep, ran over a period of six years, but group sizes were small, varying between 18 and 25 ewes each year. The first lambing records of the ewes bred in the two groups indicated that the twin group exhibited a higher fertility, although the differences decreased in later years.

Wallace's (1958) selection experiment with New Zealand Romneys also employed a control flock in which no direct attention was paid to the lambing history of the ewes or their ancestors. Each flock was run on a strictly self-contained basis, with the annual selection of ewe and ram replacements, and the culling of about one half of the ewes after their third lambing season. Results over a ten year period demonstrated fertility differences between the high and low twinning flocks, especially at the four-tooth and subsequent lambings of the ewes. At six years of age the mean percentage of lambs born per ewe lambing was 162 for the high and 122 for the low fertility flocks.

In the Merino experiment of Turner et al.(1962), all surviving progeny entered the group into which they were born, no culling of ewes being practised. As with Wallace's (1958) flocks, care was taken to ensure that the selection groups received as near identical environmental conditions as possible. The unselected daughters of the base ewes showed a difference in lamb drop between the two groups which averaged 21 more lambs born per 100 ewes mated at two to six years of age. As was also found by Wallace, this difference tended to increase with the age of the daughter ewes, reaching 31 lambs per 100 ewes mated at six years of age.

Rae (1958) has described a selection experiment for lamb production as measured by the total weight of lamb weaned by each ewe. Although the experiment is still in its initial stages, selection has resulted in an annual increase of approximately 2 lb. of lamb weaned per ewe.

Very little in the way of adequately documented evidence pertaining to the effectiveness of practical selection in the field, has been reported in the literature. Turner *et al.*(1962) briefly commented on a small group of ewes from a property where selection for multiple births has led to the formation of a multiple birth flock producing 160 lambs per ewe mated at two and three years of age.

Colburn (1960) has outlined some of the methods he has used in an endeavour to improve prolificacy, milking capacity, and growth rate in a self-contained flock of Clun Forest sheep. He makes no attempt, however, to assess the merits of his scheme, nor the progress that has been obtained over the few years in which it has been in operation.

E. CONCLUSIONS

As Reeve and Robertson (1953) conclude,

> "there is ample evidence that a number of non-genetic factors such as age of dam, earliness of lambing, body weight of the ewe, and both the level of nutrition and changes in this level at time of mating, may have a profound effect" on the incidence

of multiple births.

Combined with the low heritability exhibited by fertility characters, this suggests that non-genetic sources of variation would have to be eliminated as far as possible before much genetic progress could be expected to result from selection. Desai and Winters (1951a) have discussed the expected increase in selection efficiency, through the adjustment for known and measurable environmental influences on fertility in sheep. As they point out, environmental factors should account for a substantial portion of the total variation before their elimination can be expected to increase the genetic gain. In this connection the effect of dam's age may be relatively easily, and frequently usefully allowed for.

The range of estimates obtained with regard to the importance of genetic influences may represent genuine differences among the populations studied, although allowance must be made for sampling variation and the possibility of bias arising from the inclusion of un-measured non-genetic effects. In addition different amounts of non-additive genetic influences may have become incorporated according to the method of estimation used.

There is a suggestion from the effects of crossbreeding on the fertility of sheep (Rae 1952b), that non-additive genetic effects may be an important source of variation in this character. Dickerson (1951, 1952 and 1955) and Dickerson et al (1954) have discussed evidence bearing on the hypothesis that non-additive genetic variation may be important in many fertility characters, on the assumption that they will have always possessed positive selective value. Robertson (1955) has made essentially the same generalisations.

Despite low estimates of heritability, it is generally agreed that some improvement in the fertility of the progeny may be accomplished through the selection of female parents. This would tend to be confirmed by the few selection experiments reported, although precise measurement of their effectiveness is difficult due to uncertainties concerning the magnitude of the genetic response obtained and the measurement of the intensity of selection applied. In addition, the small size of the majority of these selection groups, and the short periods for which selection has been applied, further limit the interpretation of results.

Where the heritability of a character is low and hence the accuracy of ranking individuals according to their genetic worth also low, greater emphasis needs to be placed on aids to selection such as the use of progeny tests, sib tests, and information on ancestors and collateral relatives, (Lush 1943).

For example, Rae (1955, 1958b and 1963b) has suggested that the selection of both ewes and rams for lamb production may be usefully aided by information pertaining to half-sisters' performance. No specific assessment of the efficiency or practical utility of such methods of improving sheep fertility, appears to have been reported in the literature.

III NATURE AND SCOPE OF THE STUDY

A. OBJECTS OF THE INVESTIGATION

The review of work which has been reported suggests a number of criteria and methods which may be applied to the improvement of lamb production. The general conclusion to be reached, however, is that further critical work is necessary on the importance and inter-relationships of the factors affecting lamb production, before any accurate assessment can be undertaken of the most profitable way of breeding for this character. This is especially true in view of the variable and often conflicting results that have been reported. Furthermore it seems that certain methods may be more efficient and easier to apply than other methods, and that these characteristics are likely to be related to the particular conditions of environment, husbandry and industry organisation under which the flocks are run.

Broadly the purpose of this study is to further consider some aspects of the problems and methods of within-flock selective breeding for the improvement of the ability of New Zealand Romney ewes to produce lambs. Aspects which have received particular attention are:

1. Problems involved in selecting for increased lamb production utilising information on the number of lambs born per ewe. This section covers -

   (a) peculiarities of the scale of measurement

   (b) the use of birth rank information

   (c) the use of repeated measurements

   (d) the problem of broad categories

2. The value of the selection index approach, whereby pertinent information on the performance of relatives is combined into an overall estimate of an animal's breeding value.

B. THE MEASUREMENT OF FERTILITY

From the point of view of increasing financial returns, the sheep breeder is interested in producing large numbers of living young up to the time at which they form a commercially saleable product. This will generally occur at weaning time or some subsequent date, depending upon the patterns of husbandry and farm management undertaken. In this thesis, however, female fertility has been assessed on the basis of the total number of lambs born (dead or alive) per ewe mated and present at lambing time. This measure has been chosen for the following reasons:

1. The measure has considerable practical advantages in that ewes can be readily sorted immediately following lambing, into comparable fertility groups.

2. Due to the sequential nature of reproductive events, the number of ova produced is the first expression of a ewe's potential fertility. Ovulation rate would possible be an ideal measurement from the point of view of selective breeding. This is suggested because it is largely a character of the dam, and is unconfounded with effects associated with the viability of the young and with other factors which are possibly not associated with an animal's potential reproductive capacity. This falls in line with an hypothesis put forward by Cockrem (1962) that,

> "in general, the nearer to the initial gene action a character can be measured the higher will be the heritability".

Although the results of Falconer's (1960) analysis on the components of litter size in mice do suggest that ovulation rate is more influenced by genes with predominantly additive effects, and shows a higher heritability relative to the other components studied, Cockrem's hypothesis might not always be strictly correct. This is because heritability is a ratio and may alter with changes in either its numerator or denominator.

Despite these exhortations, the presently available techniques limit the earliest practical large scale measurement of female fertility to the number of lambs present at birth. It is interesting to note that in Australian Merinos, Young et al.(1963) have reported a considerably higher heritability for this measure, in comparison with a measurement based on the number of offspring weaned.

IV SOURCE OF DATA

The data studied in the present investigation have been obtained from a flock of New Zealand Romney sheep established at Massey Agricultural College in 1944 to investigate methods of genetic improvement in this breed. Information pertaining to aspects of the reproductive performance of the ewes of this flock was gathered as part of such investigations. This study makes use of data collected over 14 consecutive years and includes approximately 800 daughter-dam pairs.

Details of the flock concerned and the area on which it has been run have been described by Rae (1950, 1958c) and Ch'ang (1955). Only features of its maintenance and management which are pertinent to the present study will be dealt with here.

The flock was initially run on the Pahiatua Block of the Massey College sheep farm, being transferred early in 1949 to the fertile flat areas of the Tuapaka Block. This signifies that the flock has, in general, been maintained in an environment which may be considered to be similar to that of a large proportion of the commercial sheep units in the Manawatu area.

The mixed age ewe flock, which was initially established from local hill-country sheep, was run with Romney rams from mid-March in each year for a period of up to eight weeks. The Romney rams were then withdrawn and Cheviot rams introduced for a short period (of about 2 weeks). From 1946 onwards seven Romney rams were used over the entire flock in each of the years. These rams were in most cases used for three consecutive seasons, being followed in the fourth year by a fresh batch of two-tooth rams. Young rams were procured from widely different sources involving several Romney stud flocks in the Manawatu-Wairarapa area. These features favour the assumption that inbreeding has not been an important source of variation in this data, and that, genetically, the flock may be regarded as a fairly representative sample of local sheep.

Ewes were randomly allocated each year to approximately equal-sized mating groups, with the restriction that the age composition of the ewes in each mating group was kept as uniform as possible. One Romney ram randomly allocated to each mating group, this being a system of mating common in commercial stud practice and is one which allows the identification of an individual's pedigree. This feature of the mating management is compatible with the contention that the flock is essentially a random bred population.

Young replacement ewes were selected at random from those available each year, and were mated to lamb for the first time as two-tooths. Mature ewes were, as a general rule, cast for age at approximately five and a half years. No deliberate selection for any character was practised throughout the history of the flock.

Except during the mating period, ewes were rotationally grazed throughout the year in mobs that were quite independent of the mating groups. Lambs were born in August and September and remained with their dams until weaning took place in early January. The lambs were then shorn, the shearing of hoggets taking place in October, while ewe shearing occurred approximately one month later. This system of management may be considered to be typical of the way in which commercial flocks are handled in the Manawatu district with the exceptions of the mating management followed, which necessitated the separation of mating groups. One further exception is that no effort was made to give preferential treatment to individual animals. Such a plan was adopted with the intention of avoiding, as far as possible, the existence of environmentally induced correlations between parents and offspring and between members of half-sister groups.

V SELECTING FOR FERTILITY BASED ON THE NUMBER OF LAMBS AT BIRTH

A. INTRODUCTION

A ewe that has been mated to a fertile ram may be classified at lambing as having produced either zero lambs, one lamb, or two lambs. All ewes, except the relatively small proportion which produce three or more lambs, will fall into one or other of these mutually exclusive classes at any given lambing.

At first sight this character appears to fall outside the realm of quantitative genetics, in that its phenotypic distribution does not exhibit continuous variation. This discontinuity of phenotypic values is similar to the discontinuous variation produced by genes possessing major effects and has probably been one of the reasons why much of the earlier work was aimed at investigating whether simple Mendelism is involved in the inheritance of fertility in farm animals. Such studies, however, have revealed that most fertility traits are complexly determined and are, in general, inherited in a multifactorial manner and, at the same time, are often subjected to substantial modification by the environment (Reeve and Robertson 1953, Rae 1956).

On this basis it seems reasonable to regard the character, number of lambs at birth, as dependent on one or several continuous underlying variates, the value of each of which in a particular individual is the result of both genetic and non-genetic factors. This view has been proposed by Lush (1948, 1956) and Ch'ang (1955) and is based on a comparable situation which exists for characters involving resistance to death (Lush et al. 1948, Robertson and Lerner 1949, Dempster and Lerner 1950, Falconer 1960). The value of the character as it appears on the phenotypic scale of measurement, according to this view, depends upon whether or not some threshold level on the underlying scale is exceeded. That is, it is postulated that the character has an underlying continuity, but owing to the nature of the character its phenotypic expression can be measured only on a discrete scale. As a consequence of this model there will exist no visible phenotypic difference between two genetically distinct individuals which are both on the same sides of the pertinent thresholds. For the same reason, a genetic change will produce no phenotypic effect unless it moves the individual across a threshold. If this occurs even a small genetic change may have a relatively large phenotypic effect.

An important question is whether or not population genetics theory can adequately cope with characters exhibiting this discreteness of phenotypic values. That is, in what way is this phenomenon likely to influence genetic gains from selective breeding, and what effect is it likely to have upon their prediction? The latter question will be dealt with first, while the absolute and relative effectiveness of various methods of selection will be discussed later.

The effective amount of selection pressure in all cases where selection is applied for or against any trait depends upon the degree to which phenotypic variation, on which selection is based, is reflected by genetic variation. The heritability parameter would appear to be equally important, regardless of the nature of the phenotypic distribution shown by the character. Discontinuity of the phenotypic distribution does, however, appear to present several problems in the statistical estimation and interpretation of basic selection parameters.

B. ESTIMATION OF GENETIC PARAMETERS

The presently available statistical techniques for the estimation of repeatability and heritability depend on the analysis of variation and the estimation of covariances and correlations between related individuals. Since these techniques were developed in the main for characters distributed in a continuous manner, it may be expected that their use on discretely distributed data is likely to present some difficulties. Such difficulties are to be expected particularly in connection with the calculation of sampling errors and with tests of significance.

For these reasons, the greater the number of different statistical methods which are found to give comparable results for the same data, the greater the reliance which can be placed on the estimates obtained, and on the biological interpretations made. The methods of analysis employed in this thesis also permit consideration to be given to other aspects of the estimation of genetic parameters in discretely distributed fertility data. The results obtained will be discussed in relation to the comparable estimates calculated by Ch'ang (1955) for the same experimental flock.

1. REPEATABILITY

There exists a number of theoretical requirements which must be satisfied in order to compute repeatability as the intra-class correlation - its usual method of calculation. Firstly, it is required that the variance of the character remain the same at each occasion on which it is measured. Failure to satisfy this will result in some under-estimation of the correlation compared with the result from the inter-class correlation method (Lush and Molln 1942, Lush 1956). In addition, since the repeated measurements are likely to be made on the animals at different ages, age effects should be corrected for, in order to obtain a coefficient that is applicable over all the ages considered.

The second assumption implicit in the concept of repeatability is that the repeated measurements on the same individual are indeed measurements of the same genetic character. In the case of lamb production this implies that the same underlying variate may be held to represent the situation at each lambing. If this assumption is not valid, then the variance between the means of individuals will be augmented by additional variance arising from what may be formally regarded as interaction between genotype and the environment pertaining to the time or location of a measurement (Falconer 1960).

A further question to be considered in relation to the repeatability of lamb production is the interpretation of the visual scale of measurement. The scale of measurement involving zero, one or two lambs has been chosen for its convenience. However, it can be readily imagined that the difference between zero and one lamb may not be the same in size on the postulated underlying scale of potential reproducing capacity, as the difference between one lamb and two. If this is so it means that, with respect to an animal's future probable lamb production, the differences between a dry ewe, a single-bearing ewe and a twin-bearing ewe cannot all be adequately represented by a constant arithmetic unit on the phenotypic scale. If present to any marked degree, this situation would seriously impair the usefulness and interpretation of repeatability estimates obtained from intra-class correlation coefficients where the differences between zero, one and two lambs are represented as unit increments. The same is true for the inter-class correlation method and for the methods of measuring association in discrete data used by Ch'ang (1955).

In this connection a further point arises. Even if the differences in the probable lambing abilities of dry, single-bearing and twin-bearing ewes do justify measurement on a linear scale of visible expression with reference to one particular future lambing (say as a four-tooth), this need not necessarily be the case with respect to some other subsequent lambing (as a six-tooth say). Such a situation could perhaps be imagined to arise where the number of lambs born to a young animal could have a differential effect on her growth and maturation, or influence her recovery following parturition and lactation, and thereby affect her reproductive performance at her subsequent lambing. Such an effect is in fact suggested by the repeatability coefficients presented by Ch'ang (1955), and would seem to require negation before average inter-correlations can be validly combined into a single intra-class coefficient.

Another possibility is that the smaller variation in lamb production at the first lambing of a ewe may make the difference of one lamb at the first lambing mean more in genetic terms, than difference of one lamb at the second or third lambing.

(a) Methods of Analysis:

A method of attack to the problem of estimating the repeatability of coarsely grouped fertility data suggested by Lush (1956), has been adapted in relation to the above mentioned problems, and used in this study. Lush's method, which will be referred to as the regression method, involves the computation of the regression of the average number of lambs born at a consecutive series of lambings, on the number of lambs born at the first lambing or some other prior lambing. For example, in the calculation of the repeatability of first lambing records, ewes are merely sorted into those which gave birth to no lamb, to one lamb and to two lambs at two years of age. Within each of these three groups the mean number of lambs born per lambing by the same ewes in subsequent years, is then calculated for each ewe, and averaged over all the ewes in a group. The differences between group averages (i.e. between groups zero and one, and between group one and two), may then be pooled to obtain a single estimate of the regression coefficient. That this coefficient is the desired repeatability estimate has been demonstrated by Lush (1956). In the case of the two-tooth example presented, the coefficient obtained indicates the value of the first lambing record as an indication of the animal's future annual lamb production. The coefficient obtained is independent of the number of subsequent lambings averaged, as Lush points out. The repeatability of later lambings is calculated in a similar manner, although it will naturally involve the averaging of fewer subsequent records.

The modifications made to this basic regression approach involved an attempt to find out, firstly, whether repeatability can be considered to be the same between different lambings, and secondly, whether the repeatability of barrenness is of a similar order to the repeatability of twinning, when both are considered in relation to the subsequent lamb production of single-bearing ewes.

Method I: The Least Squares Fitting of Constants.

(i) Method of analysis:

As with the regression method of Lush's, ewes were classified on the basis of some initial lambing performance into three lambing status classes according to whether they produced zero, one or two lambs at birth. The small number of ewes producing three or more lambs at this initial lambing have been excluded from the analyses. The average number of lambs produced per ewe at each of her subsequent lambings was considered separately for each status classification. For example, the effect of a ewe's two-tooth lambing status classification on her lamb production when she became a four-tooth, a six-tooth and a full-mouth ewe, were estimated by means of three separate analyses. Three further analyses were involved in estimating the effect of the four-tooth and six-tooth status classifications.

Since the lamb production of a ewe has been shown to vary with effects associated with the yearly environment and age of the ewe, it was considered desirable to eliminate these influences as far as possible. This was done by the simultaneous fitting of constants to represent the effects of the year of birth of the ewe. Since all ewes in this study were mated to lamb for their first time as two-tooths, and since only those animals with records over consecutive years were included in this analysis, all ewes made their two-tooth and subsequent lambing records in the same years within this year of birth classification.

This is illustrated in the following example of the way in which the data was distributed, the a_i classifications representing the different birth years. Thus a_1 records were all made by animals born in the year 1944, and a_2 records by animals born in 1945.

Lambing years / Age	1946	1947	1948	1949	1950	1951	1952
2-tooth	a_1	a_2	a_3	a_4	a_5	a_6	a_7
4-tooth		a_1	a_2	a_3	a_4	a_5	a_6
6-tooth			a_1	a_2	a_3	a_4	a_5
8-tooth				a_1	a_2	a_3	a_4

The linear mathematical model chosen to represent the data, is:

$$y_{ijk} = \mu + a_i + t_j + e_{ijk} \qquad \begin{array}{l} i = 1.........p; \\ j = 1.........q; \\ k = 1.........n_{ij}. \end{array}$$

where - y_{ijk} denotes the lamb production of the kth sheep born in the ith year and belonging to the jth lambing status group

μ is the general mean value common to all ewes.

a_i is the effect of the ith year of birth.

t_j is the effect of the jth lambing status.

e_{ijk} is a residual random deviation associated with y_{ijk}.

The e_{ijk} were assumed to have an expectation of zero, to be uncorrelated, and to have the same variance (σ_e^2). These assumptions are sufficient to apply to the least squares method of estimation (Kempthorne 1952, Harvey 1960). For testing the differential effects amongst the classifications, the e_{ijk} must, in addition, be assumed to be normally distributed.

The least squares method takes as its estimates of the population parameters μ, a_i and t_j, those particular values which minimise the sum of squares of deviations, $F = \sum_{ijk} (y_{ijk} - \mu - a_i - t_j)^2$.

The values are given by the solution of the least squares normal equations which result from the use of differential calculus, whereby, $\frac{\delta F}{\delta \mu}$, $\frac{\delta F}{\delta a_i}$ and $\frac{\delta F}{\delta t_j}$ are set equal to zero.

$$\begin{array}{llcl}
\text{Equation for } \mu & : & N_{..}\hat{\mu} + \sum_i N_i \hat{a}_i + \sum_j N_{.j} \hat{t}_j = & Y_{..} \\
a_i & : & N_{i.}\hat{\mu} + N_{i.}\hat{a}_i + \sum_j n_{ij} \hat{t}_j = & Y_{i.} \\
t_j & : & N_{.j}\mu + \sum_i n_{ij}\hat{a}_i + N_{.j} \hat{t}_j = & Y_{.j} \\
\text{Where} & & Y_{..} = \sum_{ijk} y_{ijk}, \quad N_{..} = \sum_{ij} n_{ij} &
\end{array}$$

The equations as they stand have no unique solution as the matrix of coefficients is not of full rank. To obtain a solution, some restriction must be imposed on the parameters, and that commonly used is $\sum_i \hat{a}_i = \sum_j \hat{t}_j = 0$. Under this particular constraint the resulting estimate of μ is the mean of a hypothetical population in which all sub-class numbers are equal. However, the condition imposed has no effects on the estimatable quantities, these being the sub-class means and functions of them. When the appropriate subtractions to the coefficients in the least squares equations have been made (Harvey 1960), the reduced set of equations may be solved for $\hat{\mu}$, $\hat{a}_j$, and $\hat{t}_j$.

From the estimates, the reduction in sums of squares due to the fitting of all constants R (μ, a_i, t_j) was obtained. The quantity R (μ, a_i, t_j) is equal to $\sum_i \widehat{(\mu + a_i)}\ Y_{i.} + \sum_j \hat{t}_j\ Y_{.j}$. The reduction in sums of squares due to fitting a_i in the one-way classification model $y_{ij} = \mu + a_i + e_{ij}$, was obtained from the relation. R $(\mu, a_i) = \sum_i \frac{Y_{i.}^2}{n_{i.}}$. The reduction in sums of squares due to fitting t_j was calculated in a similar manner. The least squares sums of squares for testing the significance of the differences amongst the classifications was obtained by difference. Thus, for testing the significance of differences among the lambing status classes, the sums of squares was obtained from R (μ, a_i, t_j) - R (μ, a_i). The mean squares for effects were each tested against the mean square for error + interaction.

If the assumption of additivity implicit in the model is to hold, interactions between the two classes of effects must be shown to be non-significant. The sum of squares attributable to interaction was computed as the difference,

$$R\ (\mu,\ a_i,\ t_j\ (at)\ ij) - R\ (\mu,\ a_i,\ t_j)\ \text{where}\ R\ (\mu,\ a_i,\ t_j\ (at)\ ij) = \sum_{ij} \frac{Y_{ij}^2}{n_{ij}}\ ,$$

the uncorrected sum of squares between the AT sub-classes. The interaction mean square was tested against the within sub-class sum of squares, or error, which is given by the relation $\sum_{ijk} Y^2_{ijk} - \sum_{ij} \frac{Y^2_{ij}}{n_{ij}}$

From the inverse matrix of the reduced set of equations for the t_j, augmented to include the elements for t_3 by requiring that each row and column sum to zero, the standard errors of the t_j can be obtained. If C^{ij} is the element for the i-th row and j-th column of the matrix inverse so obtained, the standard error of a difference between two constant estimates is -

$$\hat{S}_{(ti-tj)} = \sqrt{(C^{ii} + C^{jj} - 2C^{ij})\sigma^2_e}$$

Pairwise comparisons among the t_j were made by the adaptation of Duncan's (1955) multiple range test suggested by Kramer (1957) for use when the standard error of each mean is different and the estimates are correlated. In this case a conservative test to find differences among adjusted means is obtained by requiring that $(\bar{y}_i - \bar{y}_j) \cdot \sqrt{2/c^{ii} - 2c^{ij} + c^{jj})}$ exceed $\hat{\sigma}e.Z_{p,n_2}$ to be judged significant, where $\bar{y}_i$ and $\bar{y}_j$ are the two means. The significant studentised range (Z_{p,n_2}) can be obtained from Duncan's (1955) tables for either the 5% or 1% levels of probability.

When the analysis of variance demonstrates a significant interaction effect, estimates of the main effects as given by the above model are biased. When interaction effects exist in the two-way classification, and all sub-classes are filled, Harvey (1960) has demonstrated that the weighted squares of means analysis is equivalent to the complete least squares analysis with constants fitted for all main effects and the interaction. The former method has been used in this study, and since the procedure has been described in many statistical books (Snedecor 1946, Goulden 1952) it will not be repeated here.

(ii) Results:

The following example has been chosen to illustrate the computational processes involved in this method of analysis. The example represents the analysis of the effect of the two-tooth lambing status of a ewe, on the number of lambs produced by the same animal as a four-tooth.

The least squares equations are shown in Table 2.

TABLE 2. The Least Squares Equations for the Effect of Two-tooth Lambing Status on Four-tooth Lamb Production.

	Mean	Birth Years										Lambing Status			Lamb Prod
	μ	a_I	a_2	a_3	a_4	a_5	a_6	a_7	a_8	a_9	a_{10}	t_1	t_2	t_3	$\sum y$
μ	954	119	168	18	67	102	200	20	83	118	59	127	606	221	1187
a_1	119	119										7	73	39	158
a_2	168		168									26	91	51	187
a_3	18			18								0	16	2	27
a_4	67				67							6	42	19	107
a_5	102					102						15	63	24	127
a_6	200						200					23	142	36	239
a_7	20							20				3	16	1	27
a_8	83								83			7	51	25	104
a_9	118									118		28	75	15	143
a_{10}	59										59	13	37	9	68
t_1	127	7	26	0	6	15	22	3	7	28	13	127			135
t_2	606	73	91	16	42	63	142	16	51	75	37		606		755
t_3	221	39	51	2	19	24	36	1	25	15	9			221	297

The a_i equations were solved for $(\widehat{\mu + a_i})$ in terms of the t's and these expressions were substituted into the t_i equations to give the following relation:

$$\begin{array}{ccc}
\begin{pmatrix} 106.852396 & -79.675709 & -27.178684 \\ -79.673698 & 216.634241 & -136.960530 \\ -27.178681 & -136.960539 & 164.139225 \end{pmatrix} & \begin{pmatrix} t_1 \\ t_2 \\ t_3 \end{pmatrix} = & \begin{pmatrix} -19.519491 \\ -1.459344 \\ 20.978849 \end{pmatrix} \\
A & \hat{t} \quad = & r
\end{array}$$

These equations were rounded to four decimal places and solved. The inverse of the A matrix is given below:

$$A^{-1} = \begin{pmatrix} 0.00432939 & -0.00164421 & -0.00268578 \\ -0.00164421 & 0.00215178 & -0.00050757 \\ -0.00268578 & -0.00050757 & 0.00319335 \end{pmatrix}$$

The t_j estimates obtained and the comparisons amongst them are as follows:

$$\hat{t}_1 = -0.13846 \qquad \hat{t}_2 - \hat{t}_1 = +0.15677$$

$$\hat{t}_2 = +0.01831 \qquad \hat{t}_3 - \hat{t}_2 = +0.10184$$

$$\hat{t}_3 = +0.12015 \qquad \hat{t}_3 - \hat{t}_1 = +0.25861$$

The analysis of variance to test the significance of interactions is shown in Table 3.

TABLE 3. Analysis of Variance for Interaction

Source		d.f.	S.S.	MS	F	P
Total	A	954	1823.00			
$R(\mu, a_i, t_j)$	B	12	1496.67			
$R(\mu, a_i, t_j(at)_{ij})$	C	29[b]	1504.14			
Interaction	C-B	17	7.47	0.44	1.29	n.s.[a]
Error	A-C	925	318.86	0.34		

a F value for 20 and 1000 d.f., P = .05 is 1.58

b In the case of empty sub-classes, the d.f. for the S.S. between sub-classes is equal to the number of fitted sub-classes, i.e. is given by:

(pq) - number of empty sub-classes.

⁂

As the interaction mean square proved to be non-significant the analysis was continued on the assumption that the sub-classification effects were additive.

The estimates of effects and their sums of squares gave the analysis of variance shown in Table 4.

TABLE 4. Analysis of Variance of Effects.

Source		d.f.	S. S.	M.S.	F.	P.
Total	A	954	1823.0000			
$R(\mu, a_i, t_j)$	B	12	1496.6708			
Error and interaction	A-B	942	326.3292	0.346		
$R(\mu, a_i)$	C	10	1491.4762			
Lambing status	B-C	2	5.1946	2.597	7.51	**a
$R(\mu, t_j)$	D	3	1483.2749			
Birth years	B-D	9	13.3959	1.488	4.30	**b

a $P < .01$ F values: d.f. 2 and 400, $P = .01$ is 4.66
$P = .05$ is 3.02
Effects statistically significant at the 1% level of probability
b $P < .01$ F values: d.f. 9 and 400, $P = .01$ is 2.46
Effects statistically significant at the 1% level of probability

....

The results obtained by the use of this method of analysis have been summarised in Table 5. Details of the analysis of variance and the effects of different birth years have not been presented since the study was primarily concerned with the estimation of lambing status effects and their interpretation in relation to selective breeding practice.

TABLE 5. Estimates of the Effects of Lambing Status on Subsequent Lamb Production.

(t_1 = barren ewes, t_2 = single-bearing ewes, t_3 = twin-bearing ewes)

Age		Estimates			Levels of Significance[a]			
At Status Classification	At Lamb Prod. Assess.	t_1	t_2	t_3	d.f. for Error + Interaction	Interaction	Lambing Status	Birth Year
2th	4th	-0.138	+0.018	+0.120	942	n.s.	P<.01	P<0.01
2th	6th	-0.138	-0.057	+0.194	843	n.s.	P<0.01	P<0.01
2th	8th	-0.037	-0.061	+0.098	582	P<0.01	-[b]	-[b]
4th	6th	-0.191	-0.018	+0.209	835	n.s.	P<0.01	P<0.01
4th	8th	-0.144	+0.046	+0.098	579	n.s.	n.s.[c]	P<0.01
6th	8th	-0.123	+0.006	+0.117	571	n.s.	n.s.[c]	P<0.01

a Denotes the level of significance demonstrated by the analysis of variance. Thus, n.s. indicates effects are not statistically significant at the 5% level; P<0.05 indicates effects are statistically significant at the 5% level; and P<0.01 indicates a 1% level of significance.

b Analysis of variance of effects not carried out.

c Status effects just below significance at the 5% level.

....

Comparisons amongst these estimates gave the regressions of subsequent lamb production on an initial difference of one lamb reported in Tables 6 and 7. The standard errors of the comparisons are also given together with the levels of significance demonstrated by the multiple range test.

TABLE 6. Regression of Subsequent Lamb Production on the Initial Difference between Barren and Single-Bearing Ewes.

Age of Initial Difference Classification	Age of Subsequent Lamb Production		
	4th	6th	8th
2th	0.157 ± 0.058**	0.081 ± 0.062 n.s.	⌿ a.
4th		0.173 ± 0.077*	0.190 ± 0.095*
6th			0.129 ± 0.122 n.s.

TABLE 7. Regression of Subsequent Lamb Production on the Initial Difference between Single-Bearing and Twin-Bearing Ewes.

Age of Initial Difference Classification	Age of Subsequent Lamb Production Assessment		
	4th	6th	8th
2th	0.102 ± 0.047*	0.251 ± 0.050**	⌿ b.
4th		0.227 ± 0.047**	0.052 ± 0.060 n.s.
6th			0.111 ± 0.057 n.s.

** and * denote significance at the 1% and 5% levels of probability respectively, while n.s. denotes a non-significant estimate at the 5% level.

⌿ The analysis of variance showed the presence of a significant interaction between lambing status and years of birth. Ignoring this interaction the least squares estimates obtained were: a. $t_2 - t_1 = -0.024$

b. $t_3 - t_2 = +0.159$

Inspection of the sub-class means indicated that the above interaction arose due to a variable difference between the t_1 and t_2 classifications with years of birth. The difference $(t_2 - t_1)$ was positive for five of the birth years but showed relatively large negative values for the remaining three. The method of analysis involving the weighted squares of means gave the following estimates:

a. $t_2 - t_1 = +0.079$; b. $t_3 - t_2 = +0.269$

(iii) Discussion:

The method of fitting constants by least squares represents a general method of analysis which is applicable to multiple classifications. The method allows the separation of confounded effects resulting from the non-orthogonality induced by missing sub-classes and disproportionate subclass numbers (Yates 1933). The estimates obtained are linear, unbiased minimum variance estimates of the unknown parameters.

The effects of the lambing status classes obtained above, may be looked upon as the average differences between individuals of different classes, after the contributions of effects associated with year of birth have been eliminated. In this light the method of analysis is compatible with the regression method of repeatability estimation proposed by Lush (1956).

Discussion of the results obtained by this method will be withheld until the second method of estimation has been considered.

<u>Method II.</u> Weighted Mean Differences.

The general method of fitting constants by least squares involves considerable computational work and frequently simpler methods are available. The general least squares approach, however, is one which allows the investigation of the likely importance of interactions between classifications, and prior appraisal of this possibility is theoretically necessary before efficient and unbiased methods of estimation can be decided upon. When interactions between main effects are negligible the most efficient estimates of these main effects are obtained by fitting constants to represent these main effects only (Yates 1933). If interactions cannot be ignored, the efficient estimates of the main effects are the means of the subclass means (assuming the multiple classification to be complete), rather than the class means. This arises due to a partial confounding of the interaction and main effects as a result of unequal subclass numbers.

The general statistical approach to this problem is to let the test of significance of interaction effects be a guide to methods of estimating main effects. As has been pointed out the test requires the assumption that the residual errors in the linear model are normally distributed. This may seem to be inconsistent with the likely distributional properties of coarsely grouped lamb production data, although Cochran (1947) shows that departure from normality does not appear to introduce any serious errors in the significance level of the F test. Nevertheless, one should perhaps not take the evidence of significant interaction too literally. Even if interaction is significant in the sample, but there is good reason to believe that the interaction in the population is negligible, the least squares constants estimated in a 2-way model without an interaction term, are still efficient ✓ estimates of the main effects (Coulden 1952). The converse is also true, although as Kempthorne (1952) has emphasised it is necessary to be more specific about what is meant by main effects when interactions are present.

In the particular case under consideration the interest lies in estimating the difference in the lamb producing abilities of animals classified into three classes on the basis of some prior reproductive performance. If yearly environmental influences have an important effect on the magnitude of these differences, then the estimates of the effects obtained will be expected to vary according to the years in which lambing performances are assessed. In statistical terms this means that an interaction between lambing status and year of birth can be expected to occur, and its insignificance in the majority of the above cases considered, may well be related to its small magnitude in relation to other sources of variation.

For predictive purposes the ideal for such a situation would be to endeavour to relate the differences in lambing status to some recognisable and measurable environmental component. To the extent that this cannot be efficiently carried out, however, the animal breeder is interested in the situation as it exists for a population of possible years rather than with what is the case for the particular years for which data is available. Thus if the subclasses are regarded as a series of individual samples from the population of animals of different birth years, the subclass means are efficient estimates of the hypothetical subclass means of the population sampled, regardless of disproportion. On the basis of this reasoning the method of weighted mean differences has been employed.

In this method the average lamb production of groups of ewes classified into lambing status categories has been once again calculated at each of their subsequent lambings. For each pair of lambings the differences between the status classifications of one lamb and no lambs, two lambs and one lamb, were pooled over birth years. This pooling was accomplished by weighting each of the within-year differences according to the number of animals in each status class.

Suppose X_i represents the average lamb production of animals in the t_1 (Barren ewe) status class which were born in the ith year, and Y_i the average lamb production of animals in the t_2 (single-bearing ewe) status class which were born in same year. Since X_i and Y_i are each the means of unpaired variates based on different numbers of ewes, the variance of the difference $(Y_i - X_i)$ will be given by the formula $S^2_{md} = S^2_d \dfrac{n_{x_i} + n_{y_i}}{n_{x_i} n_{y_i}}$,

where S^2_{md} is the variance of $(Y_i - X_i)$, S^2_d represents the variance of a difference, n_{x_i} represents the number of animals averaged in X_i, and n_{y_i} the number averaged in Y_i. This shows that the weights required should be:

$$W_i = \frac{n_{x_i} \quad n_{y_i}}{n_{x_i} + n_{y_i}}$$

The pooled weighted mean difference $(\bar{D})$, representing the regression estimate of repeatability $(\hat{R})$, has been calculated as, $\hat{R} = \bar{D} = \dfrac{\sum_{i=1}^{N} W_i D_i}{\sum_{i=1}^{N} W_i}$

Where $D_i = (Y_i - X_i)$ and N is the number of birth years over which the mean differences were pooled.

The sampling variance of the pooled estimates $(\hat{S}^2_{\bar{D}})$ have been calculated as that of a weighted mean:

$$\hat{S}^2_{\bar{D}} = \frac{\sum_i W_i (D_i - \bar{D})^2}{(N-1) \sum_i W_i} = \frac{\sum_i W_i D_i^2 - \frac{(\sum W_i D_i)^2}{\sum W_i}}{(N-1) \sum_i W_i}$$

(ii) **Results:**

The results obtained by this method for the particular cominations of lambings for which data were available are shown in Tables 8 and 9.

TABLE 8. Regression of Subsequent Lamb Production on the Initial Difference between Barren and Single-Bearing Ewes.

Age of Initial Difference Classification	Age of Subsequent Lamb Production Assessment		
	4th	6th	8th
2th	0.159± 0.069	0.085± 0.045	-0.040± 0.146
4th		0.168± 0.115	0.207± 0.103
6th			0.153± 0.081

TABLE 9. Regression of Subsequent Lamb Production on the Initial Difference between Single-Bearing and Twin-Bearing Ewes

Age of Initial Difference Classification	Age of Subsequent Lamb Production Assessment		
	4th	6th	8th
2th	0.108± 0.044	0.251± 0.046	0.153± 0.074
4th		0.228± 0.047	0.050± 0.093
6th			0.110± 0.065

(iii) Discussion:

The results obtained by this method are strikingly similar to those obtained by the more sophisticated least squares method of analysis, and for this reason they will be discussed together.

In general it can be seen that the repeatability of lamb production is low, the estimates presented being in line with those reported by other workers using different statistical techniques. A more appropriate comparison with the results of previous workers is obtained when the estimates of Tables 8 and 9 are pooled. These are presented in Table 10.

TABLE 10. Regression of Subsequent Lamb Production on an Initial Difference of one Lamb.

Age of Initial Difference Classification	Age of Subsequent Lamb Production Assessment		
	4th	6th	8th
2th	0.128	0.187	0.074
4th		0.212	0.097
6th			0.118

The general ranking of the repeatability coefficients reported in Table 10 is similar to the comparable estimates obtained by Ch'ang (1955) for the same flock of sheep, using methods of analysis considered appropriate for measuring the amount of association in discretely distributed data. The one inconsistency in this comparison is the lower value obtained in this study for the relationship between two and eight-tooth records. This is possibly related to the significant interaction with year of birth demonstrated by the least-squares method for this case. Further confirmation of this hypothesis is provided by the within year of birth differences for the 1952 and 1953 birth years. Data for these years were not included in Ch'ang's study, but in the present study these years contributed large negative values to the pooled regression of subsequent performance on the initial difference between barren and single-bearing ewes.

Interpretation of trends in the regression values of Tables 6, 7, 8 and 9 is rendered imprecise in light of the standard errors of the estimates. It does appear, however, that the values for the regression on an initial difference of one lamb are similar, regardless of whether this difference is between zero and one lamb or between one lamb and two, only in the case where two consecutive lambing ages are considered. The estimates obtained between non-consecutive lambing ages tend to be lower for barrenness than for twinning, in comparison with single births, when the initial lamb production classification is based on two-tooth records, while the reverse is evident for the relationship between four-tooth and five year old lambing records. The standard errors of the estimates indicate that relatively large departures from this general trend may be expected to occur in different years.

Working with Australian Merinos, Young *et al.* (1963) have recently reported coefficients for the regression of subsequent lamb production records on an initial difference of one lamb. Their calculations are based more directly on Lush's (1956) regression approach, in that the subsequent lamb production considered involves the average number of lambs per lambing, for ewes with between two and six lambing records. The regressions reported represent pooled values over two-year-old to four-year-old initial ages, and indicate that the difference between one and two lambs born is twice as repeatable as the difference between zero and one lamb at birth.

These Australian workers have also considered the influence of age on repeatability by means of their regression approach. The results presented by them indicate that the character, number of lambs born, is more repeatable when assessed on the performance of three year old ewes, in comparison with records made at two and four years of age.

This trend is not evident to any marked extent in the present data, as is indicated by the pooled row values of Tables 8, 9 and 10. These are presented in Tables 11.

TABLE 11. Repeatability of Lamb Production Records at Different Ages.
(Pooled values of Tables 8, 9 and 10)

Age of Initial Classification	Initial Difference Bet. Zero & 1 Lamb	Initial Difference Between 1 Lamb & 2	Average Value for an Initial Diff. of 1 Lamb
2th	0.08	0.17	0.14
4th	0.19	0.15	0.16
6th	0.15	0.11	0.12
	Pooled over the 3 initial ages		0.14

Young et al.(1963) also state that the regression values for both the initial differences between zero and one lamb and between one lamb and two, were larger for an initial age of three years than for an initial age of two years. These workers, however, did not correct for age effects on fertility records, and the results would therefore be expected to very according to the way the relevant estimates are calculated and combined. This is demonstrated by the following results (Table 12), in which subsequent lamb production has been calculated as the average number of lambs born per ewe per lambing, over all consecutive lambings for which records were available. That is, the average subsequent lamb production of all ewes has been averaged regardless of the number of lambings for which records were available. Differences were again weighted and pooled over the different birth years.

TABLE 12. Regression of Average Subsequent Lamb Production on an Initial Difference of One Lamb (Number of Subsequent records averaged from 1 to 3)

Age	Between Barren & Single Births	Between Single & Twin Births
2th	0.12	0.15
4th	0.17	0.15
6th	0.16	0.11

When, however, the appropriate weights and weighted differences were pooled over different birth years and also over groups of ewes whose subsequent lamb production was assessed from averages based on records made at comparable lambing ages, the results presented in Table 13 were found.

TABLE 13. Regression Estimates for Pooled Weighted Differences of Groups of Ewes with Comparable Numbers of Lambings.

Age	Between Barren & Single Births	Between Single & Twin Births
2th	0.05	0.20
4th	0.18	0.14
6th	0.16	0.11

The tendency for a lower repeatability of barrenness than of twinning (in comparison to the production of single bearing ewes) is once again demonstrated in Table 13 for the case of the two-tooth performance of an animal, and this effect was presumably masked in the results reported in Table 12, by the influence of age on lamb production, and on repeatability associations.

(b) Discussion:

As Ch'ang (1955) has noted, techniques for measuring the amount of association occurring in discretely distributed data are few. Rae (1946) has reviewed a number of methods that are available and Ch'ang (1955) has applied two of these to the problem of estimating the repeatability of the number of lambs at birth. These methods gave estimates which fell in line with the estimates obtained by other workers on other breeds by means of analyses involving intra and inter-class correlations. A method of analysis applicable to data distributed in an all-or- none manner into two categories has been used by Rendel (1956) to estimate the repeatability of multiple births, and gave results comparable with the inter-class correlations and regressions obtained by Johansson and Hansson (1943) for the same body of data.

As part of an attempt to develop satisfactory methods of analysing discrete data, Tallis (1962) has recently published a method of estimating the degree of correlation, with particular reference to the genetic analysis of sheep fertility data. The method is based on maximum likelihood estimation from 2 x 2 or 3 x 3 contingency tables, on the assumption that an animal's potential to produce offspring is normally distributed. The method has not been used in the present instance, mainly because of the apparent inaccessibility of tables of ordinates of the bivariate normal distribution. In addition, it is not evident whether the positions of the threshold levels obtained by this method can be easily interpreted in relation to the underlying scale postulated. Young *et al.* (1963) gave details of the application of this method to 2 x 2 contingency tables in an appendix to their paper.

The advantages of Lush's (1956) basic regression approach to repeatability estimation will have already become obvious. Firstly, the method provides a means of answering the question of whether the difference between zero lambs and one lamb is of the same size, in terms of future lamb production, as the difference between one lamb and two. Secondly, regression coefficients measure the amount of association from the point of view of predicting future performance on the basis of some previous record and are therefore directly applicable to the problem of assessing future performance. Thirdly, the method is easily applied to fertility data and results from different groups of sheep are easily pooled.

The results of this study, in conjunction with those of Young et al. (1963), would seem to indicate that twinning and barrenness may not always represent a similar underlying genetic phenomenon, and that in some circumstances selection for twins might be more effective than selecting against barrenness in increasing the lifetime lamb production of a flock.

With particular reference to the results obtained above, it is the predictive value of two-tooth barrenness that seems to require particular consideration. The repeatability of barrenness at the two-tooth age is important in selective breeding practice for two reasons. In the first place a high proportion of ewes is likely to be dry as two-tooths and the breeder must decide what to do with these animals. Secondly, the two-tooth record is the first direct item of information the breeder has on a ewe's reproductive performance, and any advantage that may be had from culling based on this information may be immediately utilised without the consequent delay of waiting for subsequent records. Some pertinent information concerning the subsequent performance of dry two-tooth ewes will now be considered.

Investigations on Romneys made at the Whatawhata Hill Country Research Station have shown that over a period of six years only about 3% of the ewes have been dry for two successive lambing seasons. Of the dry two-tooth ewes, 81% lambed the following year as four-tooths; of the ewes which lambed as two-tooths, 82% lambed the following year as four-tooths. From these observations Edgar (1958) concluded that ewes which were dry as two-tooths were just as likely to lamb as four-tooths as those which had lambed the previous year. At Whatawhata, ewes which failed to lamb in two successive years have been retained, for detailed study. 65 of 114 twice dry ewes lambed in their third season. Of the remaining 40 thrice-barren ewes, slaughter studies showed that 19 had blocked fallopian tubes, 11 had an interrupted pregnancy and 5 had an infantile reproductive tract. In the remaining 5 no cause of barrenness could be ascertained. These observations, together with a separate examination of dry ewes slaughtered at a freezing works led to the conclusion that permanent sterility in ewes is relatively unimportant. Only 1.2% of the Whatawhata ewes were dry for three successive seasons.

On the other hand, Barton's (1947) analysis of the records of a New Zealand Romney stud flock in which there had been no direct selection against barrenness, indicated a different situation. Data collected over 13 lambing seasons indicated that two-tooth ewes which failed to lamb showed a higher proportion of dry ewes at their four-tooth and subsequent lambings than ewes lambing as two-tooths. The average differences in subsequent lambing percentage between the two groups was 17.8 lambs per 100 ewes lambing.

In the flocks involved in his twinning selection experiment, Wallace (1958) found that ewes dry as two-tooths were more prone to be dry again later in life than ewes lambing as two-tooths, and that the average subsequent lamb production of the dry two-tooths was also inferior.

An understanding of the complexity of reproductive physiology allows the conclusion that a ewe may be dry for many different reasons, and in an attempt to reconcile these variable results Wallace (1958) has suggested that dry two-tooth ewes should be regarded as being of three main kinds:

1. those which are completely infertile due to a permanent sterility of the type caused by blocked fallopian tubes (Edgar 1958).

2. those which are inherently poorly fertile. Ewes of this group would tend to show a poorer subsequent reproductive performance than those which lambed as two-tooths.

3. those which are temporarily infertile as the result of environmental or managemental effects. The sequential nature of the reproductive processes, means that partial or complete failure of any of the many factors involved is potentially capable of completely disrupting the chain of events and may thereby result in an animal being recorded as dry. It is Wallace's contention that under certain conditions the young ewe is particularly susceptible to these influences, but that they are mainly of a temporary nature only and are relatively less important at older ages. On this basis it is expected that flocks kept in a more favourable environment in terms of nutritional and other husbandry practices (e.g. the flocks studied by Barton 1947, Coot 1952 and Wallace 1958), would have a smaller proportion of animals in this category than flocks run under hill country conditions. In this case it is also expected that a higher repeatability of barrenness would be evident.

The flock concerned in the present investigation, as has already been pointed out, has been run under good general nutritional and husbandry conditions, this being in contrast to the conditions pertaining to the Merino flocks considered by Young *et al.* (1963) and described by Turner *et al.* (1959). Under these relative severe conditions it might even be expected that the repeatability of barrenness would be low at ages other than the two-tooth.

Recently a large amount of information has accumulated on the relationship between barrenness and liveweight at tupping. Wallace (1961) showed that ewes well fed so as to gain in liveweight from the time they weaned their lambs (mid December) until about three weeks before tupping (mid February) exhibited a smaller incidence of dry ewes than groups less well fed over the same period. Furthermore, examination of the liveweight records of those animals which failed to conceive, demonstrated that these were mainly poorly conditional ewes with tupping bodyweights around the 10[illegible] lb. mark or less. Coop (1962) has obtained similar results from an analysis of the breeding performance of a large number of ewes of a varied history. The data came mainly from Corriedale flocks over a period of 15 years, and showed on average, that 6% of the ewes mated failed to produce lambs.

In relation to liveweight, however, the interesting finding was that the incidence of barrenness in groups of ewes appeared to be relatively independent of the mean liveweight of the ewes at tupping, provided this was above the 90-100 lb. mark. At liveweights below this critical level there existed a rapidly increasing degree of barrenness with decreasing bodyweights. These trends applied to both mature ewes, and to two-tooth ewes mated 2 weeks later than mature ewes.

The significance of these findings is of particular relevence in relation to the two-tooth ewe and points very strongly to the need to rear young ewes well if a high percentage of dry ewes is to be avoided. Similar conclusions have been reached from hogget rearing studies reported by Coop and Clark (1955) Coop (1956a) and Clarke (1958).

Some further Australian work on the Merino is of interest in relation to the relative gains in lifetime performance from selection for twinning and against barrenness.

Barrett and May (1958) reported that in four out of five Merino flocks studied over a number of years the failure of a ewe to lamb was distributed at random. That is, the chance of lambing in any one year was not significantly affected by preceding success or failure to lamb. On the other hand, Turner *et al.* (1958) report that the incidence of twinning in a flock of Merino ewes is not randomly distributed amongst all ewes. Ewes bearing twins on both occasions at 5 and 6 years of age, showed a distribution of multiple births at their subsequent lambings that was significantly different from those bearing singles. The mean number of lambs dropped in each of the two groups during the next 4 years was 5.16 for the twinning ewes and 4.13 for the ewes that bore singles. The intra-ewe correlation coefficient was estimated as 0.30 for the number of lambs per birth. Turner *et al.* (1962) further reported on the subsequent performance of these 2 groups of base ewes. Over the 6 matings when the ewes were 7-12 years old, the twin group produced 31 more lambs per 100 ewes mated than the single group. The difference in the number of ewes failing to bear a lamb was slight, the average over the 6 years being 15% in the twin group and 17% in the single group. This situation is therefore in line with the findings of Barrett and

May (1958), the additional lambs in the present case being due to a higher proportion of multiple births. Over the six years 46% of all parturitions produced multiple births in the twin group compared with only 14% in the single group.

The above work has been considered to demonstrate that an initial difference between zero and one lamb is likely, under certain environmental conditions, to be associated with a smaller difference in subsequent reproductive performance than an initial difference between one lamb and two. Furthermore, environmental conditions, which seem to be related to the nutritional status of the ewe, can apparently also be held responsible for some of the age variations in repeatability.

The within-mob regression studies of Coop and Hayman (1962) provide further evidence for the hypothesis that the repeatability of lamb production may vary with age. These authors demonstrated that ewes producing twins tended, on average, to be lighter in weight at their next tupping than ewes rearing singles. Through the relationship between tupping liveweight and subsequent reproductive performance, those potentially fertile animals may tend to show an inferior reproductive performance at their next lambing (Wallace 1961, Allen and Lamming 1961, Tribe and Seebeck 1962, Coop and Hayman 1962). An effect of this nature acting through liveweight seems likely to be relatively more important between the two-tooth and four-tooth lambings, because of a relatively greater physiological strain of pregnancy and lactation in young ewes. Such an effect may be responsible for the tendency for a lower repeatability of twinning between the two-tooth and four-tooth ages than between the two-tooth and six-tooth ages, demonstrated in the present data.

The effect of nutritional and growth influences associated with an animal's birth rank may also influence the predictive value of the two-tooth lambing record. This aspect will be discussed later.

2. Heritability

It seems once again desirable to consider problems of fertility measurement on an arithmetic scale of visible expression in relation to the heritability estimates obtained. If the inheritance of sterility is of a very different nature from the inheritance of fertility, the use of a linear scale could lead to the wrong relative emphasis being placed on dry, single-bearing and twin-bearing ewes in a selection programme evolved from considerations of heritability estimates calculated on this basis.

Mather (1949), Rae (1946, 1950) Wright (1952), Morley (1953) and Falconer (1960) have discussed problems involved in the choice of an appropriate scale of measurement, in connection with data analysis and interpretation. Although there exist several recognized criteria, at least for the case of characters showing a continuous distribution, Wright (1952) points out that the different criteria are often inconsistent in the scale they indicate, and the same criteria applied to the same character may indicate a different scale in different populations. Mather (1949) proposed that for the purpose of genetic analysis, with particular reference to the estimation of heritability, a scale should be chosen with the object of eliminating all interactions between gene loci. Given sufficiently detailed knowledge of the modes of gene action an appropriate scale could possibly be devised, but since interaction may take different forms, a considerable amount of compromise seems likely to be involved.

Rae's (1950) technique of finding a scale to maximise the regression of offspring on parent is no doubt a useful one in relation to the genetic progress possible from selection. Computational aspects of the method as it applied to data on the number of lambs born to ewes, have been illustrated by Ch'ang (1955). Since heritability estimates determined in this way must include a portion of the epistatic variance in addition to the additive genetic variance, it cannot be inferred that the calculated scales on which an estimate is based are such that the ratio of the additive genetic variance to the total variance is maximised. This would appear to be particularly important in view of the relatively large amounts of epistatic variance that may arise due to the nature of a discrete scale (Dempster and Lerner 1950). Consequently, although the method gave estimates which within any given age group, were higher than those obtained on the basis of a scale of equal intervals (Ch'ang 1955), the significance of these increases in relation to expected genetic advances is in doubt. Furthermore, the heritability estimates obtained can only be applied in relation to the scales accompanying them and, in view of the variable scale estimates found, interpretation is difficult. Nevertheless, the method did appear to indicate that barren ewes were genetically different from other ewes.

A second maximisation procedure tackled by Ch'ang (1955) involved the estimation of the paternal half-sib correlation. It is essentially of the same type as the above, the theory in this case having been dealt with by Fisher (1950). Sampling errors are expected to be large with this method of heritability estimation, and may have been responsible for the negative scale values that were obtained.

Methods of analysis that have been developed for estimating the inheritance of viability in poultry (Lush et al. (1948) and Robertson and Lerner 1949) have also been applied to sheep fertility data by Ch'ang (1955) and Rendel (1956). The latter worker was concerned with estimating the heritability of multiple birth rate, while Ch'ang applied the techniques to estimating the heritability of failure to lamb and twinning. The similarity of the estimates obtained by Ch'ang (they averaged 0.17 and 0.13 respectively on a scale of probits), suggests that a linear scale might satisfactorily represent the situation in this case. The estimates should be considered, however, in relation to the way in which the data was classified. At lambing ewes were divided into those which had produced a lamb and those which were barren. Alternate scores of zero and one were assigned to each of these mutually exclusive classes and the heritability of barrenness estimated. The heritability of twinning was estimated in a similar manner and involved the classification of the ewes which lambed into a further two categories - those producing one and those producing two lambs at birth. Thus the heritability of barrenness represents the genetic portion of the phenotypic difference between ewes producing and ewes not producing at least one lamb at birth, while the heritability of twinning corresponds to the genetic portion of the phenotypic difference between ewes producing one and ewes producing two lambs at birth. For this reason precise interpretation of the estimates is rendered difficult.

(a) Method of Analysis:

In an attempt to investigate scale peculiarities the method adopted has been kept as simple as possible. It is basically similar to the regression approach to repeatability estimation considered in the previous section. Following a given lambing, dams have been classified into those producing zero, one or two lambs at birth. The average lamb production (number of lambs at birth) of those female offspring, which have entered the flock, was then calculated at each lambing for each of these three groups of ewes. The differences between the three groups were studied within year of birth of the offspring ewes. The differences (i.e. between dams producing one lamb and two, and between dams producing zero lambs and one) were then pooled over the different birth years by weighting each inversely in proportion to the sum of the inverses of the number of offspring ewes in each dam category, i.e. in proportion to -

$$1 \Big/ \left(\frac{1}{n_{x_i}} + \frac{1}{n_{y_i}}\right) = \frac{n_{x_i} \cdot n_{y_i}}{n_{x_i} + n_{y_i}}$$

where n_{x_i} equals the number of offspring ewes born in the i-th year and belonging to the first dam category say, and n_{y_i} the number born in the same year but belonging to a second dam category. Dam's records were repeated for the case where more than one of her female offspring entered the flock.

As the analysis proceeded it was discovered that in some years a few sire groups had an abnormally high incidence of barren ewes. Since this effect seemed likely to be due to a low level of fertility on the part of the male, these sire groups were excluded from the main body of the analysis, in those cases where their effect seemed likely to disturb the assumption that the fertility of the male is distributed at random.

The two-tooth lambing records of dams have received the greatest amount of attention, in view of their likely value in selection programmes designed to minimise the generation interval (Dickerson and Hazel 1944).

TABLE 14 Number of Lambs Born per Ewe Mated (LP) Classified According to Age, Year of Birth and Dam's Two-tooth Lambing Status. (Offspring of two-tooth dams excluded).

Year	Lambing Status	2-tooth		4-tooth		6-tooth		8-tooth		Lifetime Lamb Production
		n	L.P.	n	L.P.	n	L.P.	n	L.P.	
1947	0	1	1.00	1	1.00	1	1.00	1	1.00	1.00
	1	21	1.09	15	1.67	15	1.40	13	1.15	1.31
	11	15	1.53	13	1.62	13	1.69	12	1.75	1.64
1948	0	6	0.67	6	1.17	6	1.00	6	2.00	1.21
	1	42	1.09	39	1.26	39	1.28	32	1.56	1.28
	11	21	1.19	20	1.25	20	1.25	19	1.68	1.34
1949	0	10	0.60	10	1.00	9	1.67	9	1.56	1.18
	1	90	1.06	87	1.24	81	1.59	75	1.37	1.31
	11	38	1.16	35	1.26	30	1.63	29	1.52	1.37
1950	0	2	0.00	2	1.00	2	0.50	2	1.50	0.75
	1	5	1.00	4	1.50	4	1.50	4	1.75	1.41
	11	5	1.00	3	1.33	3	1.67	3	1.33	1.29
1951	0	9	1.11	9	1.33	8	1.38	-	-	1.27
	1	24	1.29	25	1.12	24	1.46	-	-	1.29
	11	14	1.14	16	1.38	16	1.44	-	-	1.33
1952	0	8	0.63	8	1.00	6	0.67	6	1.33	0.89
	1	78	0.95	72	1.24	62	1.24	59	1.05	1.11
	11	34	0.76	33	1.15	29	1.34	25	1.44	1.15
1953	0	3	1.33	3	1.33	3	1.33	3	1.33	1.33
	1	38	0.84	36	1.14	34	1.15	32	1.34	1.11
	11	12	0.92	12	1.17	9	1.33	10	1.40	1.19
1954	0	2	1.50	2	1.00	2	1.50	2	1.50	1.38
	1	36	0.94	33	1.15	32	1.19	25	1.20	1.11
	11	12	1.17	13	1.15	12	1.58	10	1.50	1.34

The effect of a ewe's birth rank on her reproductive performance has also been studied. Birth rank refers to whether the individual was born as a member of a twin pair (twin birth rank) or not (single birth rank). It consequently provides information on whether or not the individual's dam produced two lambs or one at that lambing at which the animal under consideration was born. Accordingly the effect of birth rank has been studied in a similar manner to the above method of analysis, ewes in this case being classified into two groups on the basis of their dam's reproductive performance at that lambing at which they were born.

(b) Results:

(i) Lamb production of ewes classified according to the number of lambs born at the two-tooth lambing of their dams.

The number of offspring ewes involved in the analysis together with the mean number of lambs they produced is shown in Table 14, classified according to the year in which they were born. The lifetime lamb production of each of the groups is also given, and represents the total number of lambs produced per ewe per lambing, with no correction for age of ewe at lambing. The three lambing status categories 0, I and II, indicate that the dam of the ewe produced zero, one and two lambs at birth respectively. It is to be noted that ewes born to two-tooth dams have not been included in this analysis, as such animals would contribute to status groups I and II only.

The weighted mean differences between the status categories 0 and I and I and II pooled over birth years, are presented in Table 15.

TABLE 15. Weighted Mean Lamb Production Differences between Lambing Status Categories.
(Barren sire groups excluded)

Status diff.	Age				Pooled over all ages	Lifetime Lamb Prod.	Diff. between Class means
	2-tooth	4-tooth	6-tooth	8-tooth			
I-0	0.26	0.11	0.16	-0.21	0.10	0.10	0.07
II-I	0.05	0.01	0.11	0.23	0.09	0.09	0.10

The pooled weighted mean differences of Table 15 are of the same order as the weighted mean difference in lifetime lamb production, indicating that age effects have not importantly influenced the average differences between the status classifications. The class means refer to the total number of lambs produced per lambing per ewe mated, combined as weighted mean over all ages and birth years.

Including ewes born to two-tooth dams in the analysis did not markedly influence the pooled weighted mean differences in lifetime lamb production. Those were 0.09 and 0.07 for the status differences (I-0) and (II-I) respectively, while the difference between class means indicated values of 0.08 and 0.09.

The inclusion of a number of the sire groups which exhibited an abnormally high incidence of barrenness changed the pattern of results obtained, as is shown by the coefficients reported in Table 16.

TABLE 16. Weighted Mean Lamb Production Differences between Lambing Status Classifications.
(Several barren sire groups included)

Status Diff.	Age				Pooled over all ages	Life-time.
	2-tooth	4-tooth	6-tooth	8-tooth		
I-0	0.22	0.06	0.11	-0.25	0.05	0.05
II-I	0.07	0.02	0.14	0.28	0.12	0.12

In this table ewes born to two-tooth dams have once again been excluded. Their inclusion gave lifetime weighted mean differences of 0.05 for (I-0) and 0.09 for (II-I).

(ii) The effect of birth rank on the number of lambs born.

The effect of a ewe's birth rank on her lamb production has been considered separately at each age within different birth years. The same general body of data dealt with above has been included in this analysis, the dam's ages ranging from two-tooths to five year olds.

The number of ewes involved in the analysis, together with their lamb production, classified according to age, birth rank and year of birth, is presented in Table 17. Lamb production has been recorded as the percentage of lambs born per ewe mated, to give results more directly comparable with those of other workers. Single born animals are denoted by S and twins by T.

TABLE 17 Lamb Production of Ewes Classified according to Birth Rank, Age and Year of Birth.

(L.P. = % lamb production)

Age		2-tooth		4-tooth		6-tooth		8-tooth		Lifetime	
Year	Birth Rank	n	LP	n	LP	n	LP	n	LP	Lamb Production	T-S
1947	S	38	121.05	29	155.17	27	125.93	25	120.00	131.93	11.20
	T	46	119.57	38	165.79	37	148.65	35	142.86	142.95	(0.80)
1948	S	62	104.84	59	122.03	59	127.12	49	159.18	126.64	8.78
	T	37	116.22	36	127.78	36	125.00	35	174.29	135.42	(7.05)
1949	S	59	108.48	53	124.53	50	162.00	49	128.57	129.82	-1.37
	T	154	107.14	146	117.81	131	154.96	120	140.00	128.49	(-2.54)
1950	S	11	90.91	7	100.00	7	85.71	7	142.86	105.13	35.33
	T	14	92.86	13	155.85	13	146.15	12	166.67	138.46	(+2.67)
1951	S	50	118.00	52	121.15	50	136.00	-	-	125.00	12.37
	T	32	128.13	34	126.47	33	157.58	-	-	137.37	(13.72)
1952	S	46	95.65	40	125.00	39	130.77	36	122.22	117.39	-11.75
	T	78	80.77	74	114.87	59	116.95	55	116.36	105.64	
1953	S	20	115.00	20	115.00	19	136.84	19	126.32	123.08	-12.55
	T	37	83.78	35	111.43	31	112.90	30	140.00	110.53	
1954	S	38	92.11	36	111.11	36	136.11	27	129.63	116.06	3.94
	T	32	109.38	32	106.25	31	135.48	30	130.00	120.00	

The differences between birth rank classes given in brackets in the final column of Table 17, represent the lambing percentage differences reported in the paper read by Rae and Ch'ang (1955).

The pooled weighted mean differences are presented in Table 18. The separate values within age of dam classes are also given to illustrate the variations found.

TABLE 18. Weighted Mean Differences between the Percentage Lamb Production of Ewes born as Singles and Twins.

Age of Dam	Age of Ewe				Pooled over all ages
	2-tooth	4-tooth	6-tooth	8-tooth	
2-tooth	- 9.99	11.70	23.65	-14.96	3.32
4-tooth	10.14	-11.74	-10.93	35.33	4.02
6-tooth	2.42	10.06	- 3.56	11.37	3.4[illegible]
8-tooth	-10.24	-13.07	- 0.93	1.85	-7.32
Dams of All Ages	- 0.79	0.03	0.93	8.76	1.71

The weighted mean difference in the lifetime lamb production of single- and twin-born ewes averaged 1.75%.

A comparable overall pattern of results emerged when sire groups exhibiting a high proportion of barren ewes were included in the analysis.

(iii) Lamb production of ewes classified on the basis of the twinning records of their dams.

The weighted mean differences between the percentage lamb production of ewes classified into two groups according to whether their dams produced twins (T group), or did not produce twins (N group) at their two-tooth lambing, are presented in Table 19. This data was obtained by combining the appropriate rows of Table 14 with the birth rank data for two-tooth dams, to give the mean percent of lambs produced by the N and T groups of ewes. The differences, (T-N), between the two groups were combined over the birth years represented.

TABLE 19. Weighted Mean Difference in the Percentage Lamb Production of Ewes Classified on the Two-tooth Twinning Performance of their Dams.

Status Diff.	2-tooth	4-tooth	6-tooth	8-tooth	Combined over all Ages	Lifetime
T-N	4.22 (5.20)	4.17 (4.51)	14.00 (16.20)	11.01 (13.48)	7.98 (9.43)	8.08 (9.59)

The range of values obtained was not affected by the inclusion of sire groups exhibiting a high incidence of dry ewes, as is illustrated by the bracketed values presented in Table 19. This was also found to be true when the differences were considered separately for female offspring born to dams at different ages.

When the offspring ewes were classified on the basis of the four-tooth records of their dams the weighted differences presented in Table 20 were found.

TABLE 20. Weighted Mean Difference in the Percentage Lamb Production of Ewes Classified on the Four-tooth Twinning Performance of their Dams.

Status Diff.	2-tooth	4-tooth	6-tooth	8-tooth	Combined over all Ages	Lifetime
T-N	9.50	1.54	-0.29	10.48	5.12	3.79

The number of ewes whose dams produced no lambs at their four-tooth lambing was considered insufficient to justify the presentation of an analysis involving a further subdivision of the N group, whereby those ewes whose dams produce no lambs could be compared with those whose dams produced one lamb at their four-tooth lambing. The difference in lamb production was small and in favour of the former group.

A preliminary attempt has been made to investigate the effect of a dam's twinning sequence at her first two lambings on the lamb production of her female offspring. Ewes were classified into the following four groups:

1. Group NN, whose dams failed to produce twins at both their two- and four-tooth lambings.
2. Group NT, whose dams produced twins at their four-tooth lambing only.
3. Group TN, whose dams produced twins at their two-tooth lambing only.
4. Group TT, whose dams produced twins on both occasions.

The average lamb production for each of these classifications calculated as a weighted mean over the four lambing ages and the eight birth years, is reported in Table 21.

TABLE 21. Mean Lamb Production of Ewes Classified According to the Twinning Sequence of their Dams.

NN		NT		TN		TT	
n.	L.P.	n.	L.P.	n.	L.P.	n.	L.P.
1024	121.88	538	121.93	370	127.84	361	135.18

(c) Discussion:

The estimates reported are consistent with the conclusion that the heritability of the lamb production of ewes is low. They indicate that a difference, between groups of ewes, of one lamb per lambing is on average associated with something less than one tenth of a lamb born per lambing in their offspring. Sampling errors of these estimates have not been reported, but those that were calculated were large in relation to the size of the estimates obtained. This is to be expected on the basis of the variation exhibited in Tables 14, 17 and 18, and the size of the sampling errors reported in the repeatability studies, especially when it is remembered that repeatability studies, in general, gave higher estimates of the effects considered, and were based on a larger volume of data. In this light it becomes obvious that large amounts of data are required to narrow the confidence intervals that can be placed on the estimates of genetic parameters for lamb production.

Assurance can be obtained, however, from the fact that many different statistical procedures have on the whole resulted in similar estimates. This is true for the methods of estimation considered by Ch'ang (1955). Furthermore the present study has had a confirmatory rule, in that the results presented fall within the range of estimates reported by Ch'ang for the same flock of sheep, though they in general tend to congregate at the lower end of this range.

Workers reviewing the literature on the inheritance of fertility in sheep have failed to distinguish between the heritability of number of lambs born and the heritability of multiple births, the reported estimates being low in both cases. The analyses on Swedish breeds conducted by Johansson & Hansson (1943) and Rendel (1956) produced estimates of both these kinds. In general there existed no tendency for the estimates of one kind to be larger than those of the other, on the basis of values applicable to one lambing record. The same is true for the estimates obtained by Ch'ang (1955), and would seem to be confirmed by the present study. Thus, the results reported in Table 15 indicate that a difference of one lamb at a ewe's two-tooth lambing is on average associated with a difference of around one tenth of a lamb at each lambing of her offspring, regardless of whether this initial difference is between zero and one, or between one and two lambs at birth.

The inclusion in the analysis of a small number of sire groups which exhibited a high level of barrenness, has led to a different pattern of results (Table 16). At each age there resulted a slight decrease in the lamb production difference between the status categories 0 and I, and a corresponding increase in the lamb production difference between the status categories I and II. Overall the average effect suggests that in this case, the genetic difference between barren and single-bearing two-tooth ewes is only one half as great as the genetic difference between single- and twin-bearing ewes. While sampling variation might be important in this respect, the consistency of the change in the pattern with age seems to sugge that the male infertility has introduced an element of randomness into genetic assessment of fertility in ewes. While this effect is interesting in that it suggests that some problems may arise under conditions whereby barrenness arises largely as a result of "accidental" influences which have little or no connection with an animals genetic reproductive potential, the existence of this particular possibility has little practical significance. This is because under commercial husbandry conditions, a ewe is given the opportunity of conceiving to any one of several different males during the tupping period.

The indefinite effects reported in the literature for the influence of type of birth on lamb production makes practical recommendations difficult to generalise. The variable influence of this factor is well illustrated by the data presented in Table 17 and 18. The differences in lifetime lamb production presented show close similarity to the values reported in the original paper presented by Rae and Ch'ang (1955) for the same flock of animals. The one exception occurs in the case of the estimate for animals born in 1950 which is, however, based on a relatively small amount of data. The average birth rank effect obtained by Rae and Ch'ang was around the 10% mark, while in the present data the pooled weighted mean differences indicate a much lower average which is of the order of 2-3%. This appears to be mainly due to the extra subsequent years (1952 to 1954) included in the present analysis, and a high value found by the previous workers for animals born in 1946. As is shown in Table 17, the years 1952 and 1953 indicate that twin born animals exhibited an inferior reproductive performance in comparison with their single born contemporaries. Further examination of the data showed that the overall lambing percentage for those animals was below average, especially at their two-tooth lambing.

Evidence exists which suggests that the value of birth rank as a criterion of reproductive potential may depend on environmental conditions, and especially those associated with nutrition. Rae (1963b) has discussed this aspect and suggests that an animal's birth rank not only provides a measure of the dam's fertility for that particular lambing, but also indicates that the animal itself has had a maternally induced environmental handicap imposed on its growth. Many workers have found that effects due to type of birth and rearing are an important source of variation in weaning weight. In the present flock Ch'ang and Rae (1961) have demonstrated that single lambs are approximately 10 lb. heavier at weaning than twin lambs. Under conditions of poor nutrition it is commonly found that at their first tupping twin born two-tooth ewes have a lower average liveweight than single born animals, and this can possibly be attributed to a persistence of the maternally imposed growth handicap. In this way any intrinsic genetic superiority of the twin born ewe may be masked by a positive environmental relationship between tupping liveweight and subsequent reproductive performance. The previously mentioned results of Wallace (1958) are pertinent in this respect. The effect, in turn, may also mean that an animal's two-tooth performance may not necessarily be a good guide to her potential reproductive capacity, whether this be considered in relation to the subsequent performance of the ewe herself or in relation to the performance of her offspring or some other female relative.

In the case of the present flock, however, Ch'ang (pers. comm.) has found that an animal's birth rank is frequently not associated with a liveweight difference prior to the two-tooth mating. Nevertheless the possibility exists that the growth pattern of an animal, as against the cumulative influences measured by bodyweight, may have some bearing on the problem. In this connection the critical hogget rearing period may be important and the fact that this coincides closely with the onset of puberty may have some special significance.

Further evidence demonstrating the possible necessity of assessing a female's birth rank in relation to the environment is provided by Belogradskii's (1940) contention, that the difference between his results and those of Smirnov (1935) was due to poor management under which the genetically higher prolificacy of Smirnov's triplet and quadruplet ewes could not be expressed. This effect can be interpreted as an interaction between heredity and environment, the poor management having a greater depressing effect on the fertility of ewes born in multiple births. Dickerson (1962) has discussed the problems introduced into breeding studies by effects of this nature.

Belogradskii (1940) recommends that ewes should be selected not only because they were born in multiple births, but also on the basis of the fertility levels of the lines or families to which they belong. Sharafeldin (1960) has also suggested that selection on the basis of birth rank information should be applied to the average production of lines, rather than on the records of individuals.

In view of the growth handicap likely to be imposed on twin born ewes it seems that other lambing records of the dams may be of more universal applicability in discriminating between the reproductive potential of young females. The results given in Table 19 do seem to indicate that the twinning performance of the dam at her two-tooth lambing has greater predictive significance, than her twinning performance at that lambing at which the offspring themselves were born. This is suggested on the basis of the generally higher, and less variable, estimates obtained. The average lamb production difference between ewes whose dams produced twins and those whose dams did not, was around the 8-9% mark, and tended to be larger at the six- and eight-tooth lambings of the ewes than at earlier ages.

Under flock management conditions, whereby animals are mated to lamb for the first time at two years of age, and all female offspring are carried through their first winter, at least two lambing records on the dams will be available on which decisions can be made as to which ewes should be retained for breeding. The results in Table 20 in comparison with those of Table 19, indicate that the four-tooth twinning record of the dam is of slightly smaller predictive value than the two tooth record. The average difference in the lamb production of ewes whose dams produced twins at their four-tooth lambing, and those whose dams did not, was of the order of 4-5%.

This pattern of results would seem to fall in line with Terrill's (1962) suggestion that the changing lambing rate with age provides a clue to selecting for twinning in sheep. Since fewer ewes have twins at their first lambing it is likely that those that do have an average potential for twinning which is higher than those ewes which produce twins at their second or later lambings. Other aspects are pertinent to this problem. The genetic variation of any character may be expected to vary with age if some genes manifest their effects differently according to the age or stage of development of the animal, or if the character is affected by different genes at different ages. Moreover, the modifying influence of environmental factors need not necessarily remain constant with age. For these reasons the heritability ratio may vary with age in either a systematic or completely random manner.

Ch'ang (1955) has reported heritability estimates for number of lambs born, according to the age at which the character was measured. In general, his daughter-dam regression estimates show a decreasing value with increasing age, while those obtained as paternal half-sib correlations show the reverse trend. Since sampling errors are expected to be large the significance of further conjecture on these trends is doubtful.

The heritability estimates of Johansson and Hansson (1943) for the Cheviot breed also provide some indirect evidence on the relative size of heritability in young ewes. They obtained the following estimates based upon within flock, daughter-dam regression:

One lambing at 2 years of age (1324 pairs) = 0.044

Average of three lambings at 2-6 years of age (659 pairs) = 0.178

On the basis of a within flock repeatability estimate of 0.172 the value for the average of three lambings can be reduced to an average estimate of 0.080 for the heritability of one lambing record. Since the number of offspring records averaged, does not influence the size of the regression of offspring on parent, this suggests that the average predictive value for the first three dams' records (0.080) is higher than that for the first lambing record (0.044). On the other hand, peculiarities arising from the small number of categories may have induced a bias into the estimate based on one lambing record, and in addition the authors did not correct for the effect of age on litter size.

Young et al.(1963) presented data which indicates that the heritability of number of lambs born, and number weaned, are higher when measured at three years of age in comparison with two-year old records. They state that the optimal age group from which to select is at present under investigation. Aspects of this problem will be dealt with in the next section.

When selection decisions can be based upon more than one lambing record their accuracy is expected to be greater. This has been shown by Lush (1943), who points out that it is under conditions of low repeatability that performance averages are expected to be of greatest value. This is well illustrated by the higher heritability estimates obtained by Johansson and Hansson (1943) for the average performance at three lambings.

In view of the possible carry-over effects of previous reproductive performance on an animal's current performance, together with the possibility that the inheritance of fertility may vary with age, it seems likely that other methods of combining an animals separate records may be more efficient than a simple average. To this end an attempt has been made to assess the possible predictive value of a ewe's twinning sequence. The means reported in Table 21 do seem to indicate that the genetic difference between twinning and non twinning four-tooth ewes does depend upon their two-tooth twinning performance. It is proposed to investigate, in greater detail, further aspects of this problem in the near future.

C. EXPECTED GAINS FROM SELECTION

In this section it is proposed to consider the way in which the characteristic coarseness of grouping of fertility measurements expressed in terms of numbers of offspring produced, influences the gains to be expected from selection based on this criterion. The use of certain aids to selection for this character will also be discussed.

1. INDIVIDUAL OR MASS SELECTION

(a) Response to Selection:

For discretely distributed characters, the response to selection will depend upon the selection differential as is the case for a continuously varying character. The selection differential, however, will not always depend upon the proportion of animals retained for breeding. This is because the breeder can only discriminate between those individuals that fall into a different phenotypic class; within each phenotypic class he is not able to discriminate between those with high and those with low values (on an underlying scale of potential reproductive capacity). For this reason, unless the proportion of individuals required for breeding is exactly equal to the proportion of animals falling into the desired class (or classes), many (or all) of the selected individuals can only be randomly chosen from the less desired or marginal class. Thus the selection differential is greatest when the number falling into the desired class(es) is exactly equal to the number required for breeding purposes. In this case the ensuring improvement would be expected to be exactly equal to the theoretical situation based on direct selection on the underlying variate. On the other hand, where a larger or smaller number of parents is required, it is expected that the efficiency of mass selection will be lower by an amount depending on the heritability, the intensity of selection and the proportions of individuals in each of the phenotypic classes.

With particular reference to characters classified into two separate classes, Lush et al.(1948), Dempster and Lerner (1950), and Ch'ang (1955) have demonstrated the way in which gains from mass selection depend upon the incidence of the character, in the case where all individuals in the desired class are retained. Those workers postulate a normally distributed underlying scale. Considering, for example, the effect of ewe selection against barrenness, the selection differential on the underlying scale is given by z/p_i, this being the difference between the average of ewes that have lambed and the average of the whole population. Here $(1 - p_i)$ represents the level of barrenness and z the height of the ordinate of a normal curve which truncates p_i of its area. The genetic gain on the underlying scale is given by $\frac{1}{2}(h_x^2 \, z/p_i)$, h_x^2 being the heritability of individual differences in the character on this scale. (Half the heritability is used as ewes only are under selection, and are assumed to be randomly mated to rams of near average genetic merit for fertility). On the assumption that the genetic variance on this scale is the same for both offspring and parents, subtraction of this gain from the distance between the threshold and the mean of the parental generation, gives the incidence of the character in the offspring $(1 - p_o)$. The difference $(1-p_i) - (1-p_o)$ is the genetic gain (reduction in the level of barrenness) on the visible scale, and represents the area of the curve moved across the threshold. Lush (1948) and Lush *et al.* (1948) have given a simpler approximate method of calculating the genetic gain. Letting R represent the value of the normally distributed underlying variate, the regression of p_i on R is given by a sigmoid curve which for small variations in R, ΔR, approximates a straight line of slope z. In the case of the genetic response to selection against barrenness ΔR is given by $\frac{1}{2}h_x^2 \cdot z/p_i$. Consequently the corresponding change in the incidence of barrenness is given by $z\Delta R = \frac{1}{2}h_x^2 \; z^2/p_i$ rather than by $\frac{1}{2}h_x^2 \; z^2/1-p_i$ as given by Ch'ang (1955). Lush (1948) states that the slight bias involved in the approximation results in overestimation of the genetic response for high values of p_i (i.e. for a low initial level of barrenness) and underestimation for low values.

Using a heritability averaging 0.17 on the underlying scale, (1955) calculated the reductions in the percentage incidence of barrenness to be expected per generation when all barren ewes are culled on the basis of one lambing record. These are presented in Table 22 and appear to be correct despite the formula error.

TABLE 22. Expected Reduction in Percentage Barrenness per Generation from Culling those Ewes Failing to Lamb.

Initial level of barrenness (%)	Expected Reduction
50	2.75
40	2.11
30	1.47
20	0.83
10	0.29
5	0.09

These figures demonstrate some of the conclusions reached by Dempster and Lerner (1950) that "Mass selection for a character of high incidence

> (or against one of low incidence) leads to slight gains only. This is due to very low effective heritability, combined with the fact that selection intensity is also perforce low. For intermediate incidence the gains obtained are relatively high, but further shift of incidence does not produce much greater gains, because the decrease in effective heritability offsets and eventually overcomes the increase in selection intensity on this shift."

The above gains have been computed on the assumption that the level of barrenness can be eventually reduced by selection to zero, while in actual fact it is probably more realistic to suppose that there exists an irreducible minimum level of barrenness due to accidents and other factors not associated with an animals inherent fertility potential. This would tend to lower the effectiveness of mass selection even further, particularly when the average incidence is already low (Lush et al. 1948).

On the basis of similar assumptions and reasoning the expect per generation in the level of twinning may be calculated, for the case when only those animals producing twins at a given lambing are retained from amongst those ewes which lambed. These are given in Table 23 and are presented in preference to those of Ch'ang (1955) as the latter appear to be in error.

TABLE 23. Expected Gain in Percentage of Twinning Ewes per Generation from Saving those Ewes Producing Twins.

Incidence of Twinning (%)	Expected Gain.
5	1.38
10	2.00
20	2.55
30	2.62
40	2.43
50	2.07
60	1.62
70	1.12

Due to the way in which the data have been classified and the way the expected gains calculated, the simultaneous consideration of the incidence of twin births and the incidence of barrenness can be used to enhance the overall effectiveness of mass selection for the number of lambs born. The following example has been chosen to illustrate the gain in lambing percentage at birth, through the selection of twin producing ewes from amongst all ewes present at a given lambing.

Suppose the initial position is represented by a 20% level of barren ewes, while of those ewes lambing, 20% produce twins. This corresponds to a lambing percentage at birth of 96%. The expected gains per g given in Tables 22 and 23 indicate that in the offspring generation the incidence of barrenness will be 0.83% less, while at the same time 2.59% more of the ewes lambing will produce twins. This corresponds to a lambing percentage of just under 99% and represents a gain of about 3 lambs born per 100 ewes present at lambing.

It must be emphasised, however, that this example and the figures presented in Tables 22 and 23 are approximations and apply only to the case where all ewes of a given lambing status group are retained for breeding. Furthermore, the method of calculating expected gains requires an estimate of heritability on some hypothetical underlying scale.

Dempster and Lerner (1950) have demonstrated the errors involved in estimating gains on the basis of visible scale heritabilities for the case of characters falling into two mutually exclusive classes. For both the cases when all individuals in the desired class are selected, and when a proportion of individuals in the undesired class must also be retained, they point out that only small discrepancies exist between the actual and the expected gains where the selection intensity is low, and especially where the incidence of the character is near 50% and the additive heritability on the underlying scale is small.

(b) Graphical Representation of Selection Response

The effect of the incidence of barrenness, twinning, selection intensity, and genetic scale peculiarities, on the gains to be expected from selection based on the number of lambs born, will now be illustrated in graphical form.

The graphs given refer specifically to the effect of these factors on subsequent lifetime reproductive performance, through the selection of ewes on the basis of records made at their two-tooth lambing. The same principles apply, however, to the problem of selecting for increased productivity in the offspring generation.

(i) Method of Analysis and Results:

Two initial flock situations have been graphed. These are designated flocks I and II which are assumed to have the following levels of barrenness and twinning, expressed as a percentage of all ewes mated and present at their two-tooth lambing.

	Flock I	Flock II
% Barren Ewes (I_B x 100)	25	10
% Ewes Producing Singles (I_S x 100)	55	40
% Ewes Producing Twins (I_T x 100)	20	50

Expected gains have been calculated as the increase in the number of lambs born per 100 ewes at their next or some other subsequent lambing. The way in which they have been obtained is demonstrated in general terms.

Suppose that barren ewes, single-bearing ewes and twin-bearing ewes exhibit an average of number lambs born per ewe of x, y and z respectively, at some subsequent lambing, and that the flock average in the same year is $\bar{X}$. Then, letting t_b represent the subsequent lamb production difference between single-bearing and barren ewes, and t_t the difference between twin- and single-bearing ewes, the following relationships can be established:

$$(y - x) = t_b \qquad \therefore\ y = (x + t_b)$$

$$(z - y) = t_t$$

$$(z - x) = t_b + t_t \qquad \therefore\ z = (x + t_b + t_t)$$

$$\bar{X} = \frac{(100I_B . x) + (100I_s . y) + (100I_T . z)}{100}$$

$$= I_B . x + I_s . y + I_T . z$$

$$= I_B . x + I_s(x + t_b) + I_T(x + t_b + t_t)$$

$$= x + I_s . tb + I_T(t_b + t_t)$$

$$\therefore (x - \bar{X}) = -I_s t_b - I_T(t_b + t_t) \quad \ldots\ldots\ldots\ldots \quad (1)$$

Similarly

$$(y - \bar{X}) = I_B t_b - I_T t_t \quad \ldots\ldots\ldots\ldots \quad (2)$$

and

$$(z - \bar{X}) = I_B(t_b + t_t) + I_S . t_t \quad \ldots\ldots\ldots\ldots \quad (3)$$

Letting S_B, S_S, and S_T represent the proportion of the barren, single-bearing, and twin-bearing ewes retained for further breeding respectively, and assuming that twin-bearing ewes are retained in preference to single-bearing ewes, which in turn are more desirable than barren ewes, the following formula indicates the gain in lambs born per 100 ewes retained (ΔG):

$$\Delta G = 100S_B(x - \bar{X}) + 100S_S(y - \bar{X}) + 100S_T(z - \bar{X}) \ldots \quad (4)$$

This gain represents the amount by which the average percentage lamb production exceeds the mean lamb production that would result had no culling been practised.

From these four formulae the expected gains for different levels of culling, and for variations in t_b and t_t have been calculated, for flocks I and II. The combinations considered are:

	t_b	t_t
Case a.	0.14	0.14
Case b.	0.08	0.17
Case c.	0.	0.17
Case d.	0.17	0.

and the results have been plotted in Figure 1.

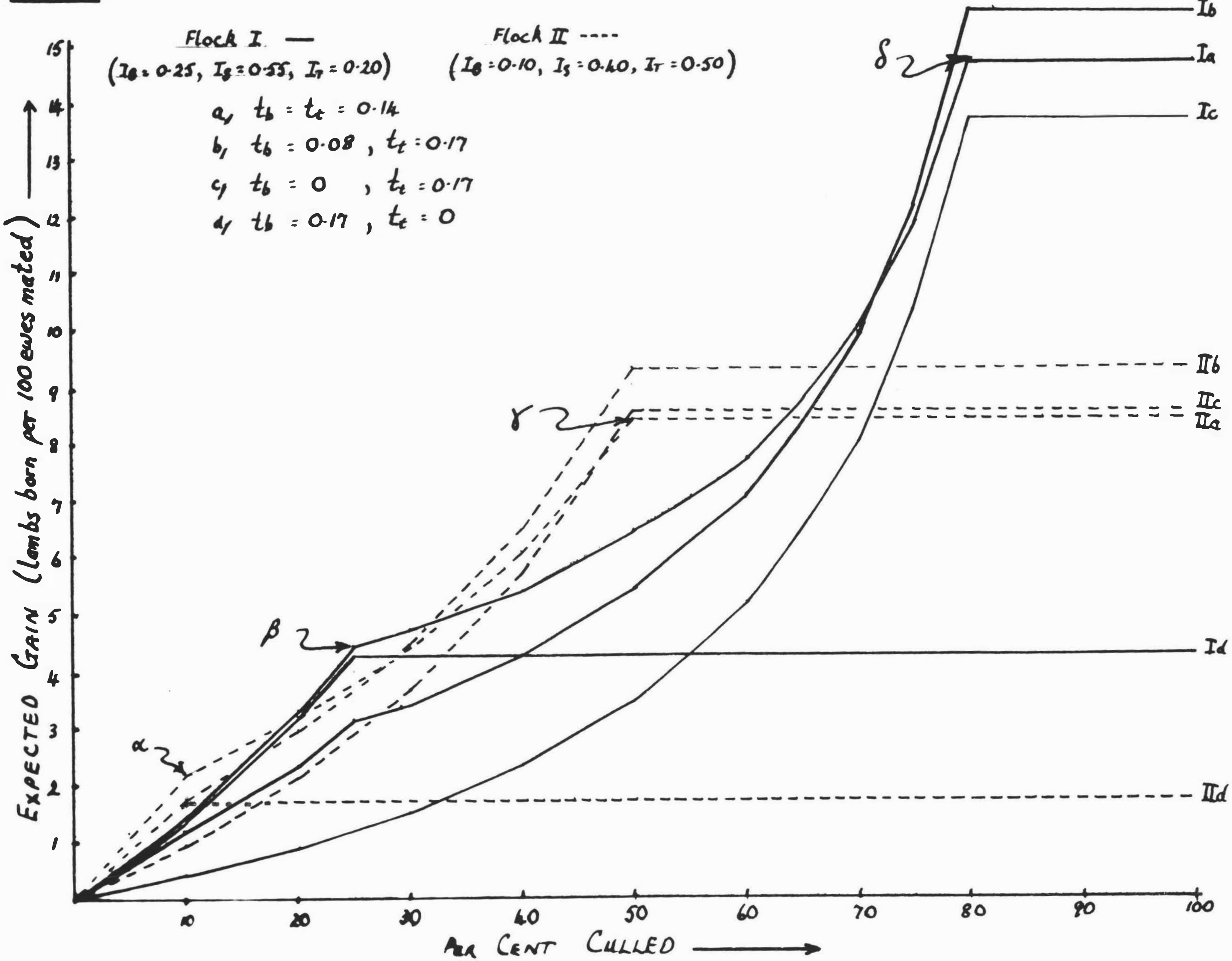
(ii) Discussion:

The graphs will be discussed separately for each of the situations studied.

Case a. (Graphs Ia and IIa):

In both flocks the gains rise to a plateau with increasing culling, demonstrating the principle that for threshold characters the amount of gain is a maximum when the incidence of the desired class (I_T) equals the proportion of the population saved for further production. For less intense levels of selection the expected gains fall off due to the less desirable animals diluting the effect of retaining the superior class. This fall off is rapid at first, especially in flock I which exhibits a low level of twinning, due to the dilution effect of including animals at random from the larger group of singles. The rate of decline in expected gains decreases with further

FIGURE 1. EXPECTED GAIN IN LAMB PRODUCTION FROM SELECTION OF EWES ON ONE LAMBING RECORD



drop in selection intensity, until when the proportion culled equals the level of barrenness, the gains are once again equivalent to those obtainable could the selection be based upon a continuously graduated phenotypic scale, showing the same coefficient of repeatability. With a further drop in the intensity of selection, the gains fall off at greater rate which gradually diminishes with decreasing intensity of selection.

Four critical points (labelled α, β, γ and δ) are shown in Figure 1. These represent the points through which the plot of expected gains against selection intensity would pass, could selection be based on a continuous scale of phenotypic values, providing the repeatability on this scale is also 0.14. The discrepancies between this hypothetical line and the graphs given for flocks I and II thus give an idea of the reduced selection efficiency that results from the coarse classification of fertility data measured on a scale of lambs born. These discrepancies are seen to be greatest whenever the percentage of animals to be saved for breeding falls within one of the broad phenotypic classes and especially if this class is a large one.

With respect to the selection of replacements to enter the breeding flock as two-tooths, a culling rate of around 40-50% seems applicable for quite a wide range of variations in lambing percentage, and the mortality rate of ewes and lambs (Goot 1947, Hickey 1960). It is interesting to note that for this level of selection intensity, the expected gains from selection based on one lambing record of the dams, are never far below this hypothetical maximum in flock II, although in flock I they may differ by 2-3% lambs born per 100 ewes. Hickey (1960) has demonstrated the way in which the culling rate amongst young replacements is influenced by the level of flock fertility. Thus in flock II, a culling rate of the order of

50-60% might be more applicable, this being the area of the graph where the largest discrepancies occur for this flock, at least with respect to the efficacy of ewe selection.

It is to be noted that with respect to ram selection on dam's information, where a selection intensity of the order of 1-2% is more likely (Goot 1947), the differences in the expected gains are quite marked.

Comparisons of flocks I and II demonstrates Terrill's (196) suggestion that age group variations could profitably be made use of in selective breeding for increased lamb production. These graphs, however, demonstrate that the optimum age group from which to select, depends on the proportion of replacements required, as well as the number of individuals in each category. It also depends on the relative selective advantage of the animals in each of the groups, this influence being demonstrated in the remaining graphs of Figure 1.

Case b. (Graphs Ib and IIb):

This situation has been studied in view of the possibility that the predictive value of the difference between one lamb and zero lambs, is lower than the predictive value of the difference between two lambs and one. The genetic parameters chosen are those suggested by the average predictive values for the two-tooth record presented in Table 11.

The differences between the expected gains for this situation and those of case (a) above, are in general, small throughout in both flocks. For flock I, which has the higher level of barrenness, the difference is greatest when the level of culling corresponds to the incidence of barrenness. At this level of culling the gains represented by Graph Ib are lower, and it is not until a level of culling of 70-75% is reached that the advantage of the slightly higher predictive value for twinning overcomes the lower predictive value of barrenness, both twinning and barrenness being considered relative to the subsequent performance of single-bearing ewes. In flock II, however, the greatest difference occurs at selection intensities corresponding to the level of twinning or higher. The difference in this case corresponds to the difference between the t_t values of 0.17 and 0.14 and is the same as that occurring in flock I at selection intensities greater than 0.20.

Cases c and d. (Graphs Ic, IIc, Id and IId):

For comparison of the relative gains arising from the selection against barrenness and the selection for twinning, two further series of graphs have been presented. Graphs Ic and IIc correspond to a zero predictive value for barrenness and Graphs Id and IId to a zero predictive value for twinning, in relation to single-bearing ewes.

Comparison of Graphs b and c within flocks I and II illustrates the effect of a zero value for t_b. This is seen to be greatest in flock I which has a higher incidence of barren ewes and a lower level of twinning than flock II.

Comparison of Graphs c and d indicate that at low levels of culling a positive t_b value is more important than a positive t_t value of the same size. In flock II this is true for culling levels up to about 16-17%, but in flock I this position holds for rates as high as 55%.

In all the Graphs presented gains rise with increased culling rate until a plateau level is reached, which is dependent upon the relative selective advantages of the three classes of animals and the proportions of animals in each. Where the twin class has no predictive advantage over the single-bearing ewes, this plateau is reached when the level of culling is equal to the incidence of barrenness.

In some cases a fourth phenotypic fertility class may be available on which to base culling decisions - namely a class involving triplet-bearing ewes. The effect of this extra class is expected to be of relatively greater advantage when high intensities of selection are possible, due to the small number of triplet-bearing ewes in most breeds of sheep. For example consider a flock with the following proportions of animals in the four categories:

Barren ewes	10%
Single-bearing ewes	40%
Twin-bearing ewes	45%
Triplet-bearing ewes	5%

The selection differential corresponding to a 95% culling rate is 1.55, and with a repeatability of 0.14, the gain expected from retaining all the triplet bearing ewes is 21.6 lambs per 100 ewes. The expected gain for a 40% culling rate is 6.6. lambs per 100 ewes and this is only 0.6 of a lamb higher than the corresponding figure given by Graph IIa.

(c) Subdividing the Phenotypic Classes:

The proceeding discussions have demonstrated that special difficulties in breeding for threshold characters arise from the coarseness of the phenotypic distribution. No new principles are involved, but merely a difficulty of recognising underlying variations in potential reproductive capacity.

Terrill (1962) has presented data which suggests that this problem of broad categories may be overcome to some extent. On the basis of their two year old reproductive performance, he classified Rambouillet ewes into the following six phenotypic classes:

1. Infertile
2. One still-born lamb
3. One live lamb born but not weaned
4. One live lamb weaned
5. One still-born lamb but foster lamb weaned
6. Twin lambs born

With respect to their subsequent lamb production from three to six years of age, these classifications represented a gradually increasing scale of fertility.

Unfortunately, however, such classifications do not consistently exhibit regularity of potential performance for different groups of sheep, and as a consequence the breeder is faced with the problem of how best to weight each of the classifications for any given situation. Taylor (1961) is faced with similar problems in his attempt to find a scale of reproductive capacity which will facilitate comparisons between different flocks. The scale of measurement chosen in a particular case would seem to depend upon the definition of fertility being considered, and this must necessarily be related to the purpose for which fertility is being recorded.

2. THE USE OF AIDS TO MASS SELECTION:

Breeders have long been acquainted with methods of evaluating breeding value in ways other than the individuals own phenotype. Lush (1943) quotes examples of early attempts, although it was not until the theory of population genetics was developed that a rationale became available for comparing different methods.

When selection is ostensibly directed to the improvement of a single trait, information about the breeding worth of an individual may be sought from its own phenotype and from the phenotypes of its relatives. Broadly speaking, these are the only two bases for direct selection procedures, direct selection implying that the selection criterion is based on values of the character in which improvement is desired. The basis for the use of these additional items of information is the genetic similarity which exists between relatives, the degree of which is measured by the coefficient of relationship.

Many workers have shown that the accuracy of estimating an animal's breeding value can be increased by the use of records on relatives.
Lush (1943, 1947) first considered selection based on individual merit and family average and derived optimal weighting coefficients enabling these two methods to be combined. His formulae marked out the general domains in which these methods are expected to be most useful and showed that optimally combined selection was never less efficient than selection on the individuals record alone. He also demonstrated that when the heritability is low family selection could be more effective than mass selection, especially when the family size is large.

Various systems of selection combining information on the individual and its relatives, have since been investigated by Lerner (1950), Legates and Lush (1954), Osborne (1957a, 1957b), Jardine (1958), Skjervold and Odegard (1959) and Young (1961). These studies have shown that the proper amount of attention to be paid to different relatives in a selection programme depends upon their closeness of relationship to the individual in question, the number of relatives included and how completely the merit of each relative is known. In particular, this work has demonstrated that the use of these additional items of information is expected to be of greatest value for characters exhibiting low heritability estimates.

In the case of many economically important characters in farm animals, information on the performance of relatives is all that is available to guide the breeder in his selection decisions. This is true for characters which are sex-limited and for characters which cannot be measured on the live animal. In addition, records on the ancestors of an animal, are often useful when it is desirable to select animals early in their life and this aspect becomes particularly significant for characters which are capable of direct expression only in the mature animal.

Therefore, since lamb production is sex-limited, has a low heritability and is capable of direct expression only in the sexually mature ewe, selection procedures utilising information on relatives are expected to be of considerable value. In breeding flocks where an adequate identification of an individual's pedigree is possible, the following items of information could be made available:

1. The lambing performance of an animal's female offspring.
2. The lambing performance of an animal's dam.
3. The lambing performance of the maternal grandam and possibly the paternal grandam as well.
4. The lambing performance of the paternal half-sisters of an animal in those cases where the sire is mated to more than one ewe.

The use of these items of information will now be considered.

(a) Progeny Testing:

The variation between sires in the fertility of their female offspring demonstrated by several workers is encouraging with respect to the progeny testing of rams. There is no doubt that this is the most accurate way of determining the breeding value of a ram, due largely to the fact that a ram can have many offspring. In the average of these offspring many of the errors of estimating additive genetic merit (for exampl, those due to environmental, dominance and epistatic variance) have the opportunity to cancel each other. For the same reasons, however, the progeny testing of ewes is expected to be of relatively little value due to the small number of offspring produced per ewe each year.

Selection on the basis of progeny test information cannot be carried out until the individual has progeny mature enough for their phenotypes to be observed. In the case of the character lamb production,this involves a delay which is serious enough to impair the efficiency of ram progeny testing in terms of the expected annual genetic response (Dickerson and Hazel 1944). This has been illustrated with reference to New Zealand conditions by Rae (1956b), who points out that the disadvantage would tend to varnish if ewes and rams were mated to lamb for the first time as yearlings or if artificial insemination were to become a useful technique in sheep breeding.

(b) Family Selection:

In the case of discretely distributed characters it seems that family averages are likely to be particularly helpful whenever a choice must be made between individuals falling into the same phenotypic class. In the absence of family information, this choice must necessarily be random with respect to the discrete character, but if information on collateral relatives is also available, the selection of individuals from the highest producing families can be practised.

Lush *et al.*(1948) suggested that the same weighting factor developed for continuously distributed characters, be used to weigh each family deviation for variation in family size. However, breeding problems for the threshold character disease resistance, which was being considered by those workers, are not exactly the same as those arising for the number of lambs at birth. Apart from the difference between two and three phenotypic classes, mortality occurring before the age of puberty effectively prevents further reproduction. In their case then, mass selection can do no more than discard all defective individuals or a random sample of them and the sib test allows the breeder to go further, only if there is freedom for further culling. It is particularly useful when the incidence of defective types becomes less and less. In the case where the threshold effect does not prevent the possibility of further reproduction, however, defective individuals from extremely good families may be kept for breeding. This leads to the problem of combining more than one source of information.

(c) Information on Ancestors:

Information on ancestors is of no use where defective individuals are prevented from becoming ancestors this being the case of breeding for resistance to early mortality. In the case of lamb production, however, information on ancestors, if available, is likely to be of some value.

Lush (1943) has shown that the proper amount of attention to be paid to each ancestor depends on the correlation of that ancestor's phenotype with the breeding value of the individual concerned, and also on the correlation of that ancestor's phenotype with the phenotypes of other ancestors. In the case of information on just one ancestor this correlation will depend on the genetic relationship of the ancestor with the individual, and the number of records available on that ancestor. Of all ancestors the parents will be most closely related to the individual. Repeated items of parental information are likely to be most valuable in selecting for the sex-limited character lamb production.

(d) Combined Selection Schemes:

Whenever there is the opportunity of employing more than one criterion of selection, two questions must be resolved by the breeder. Firstly, are the selection gains expected under the more complex selection schemes sufficiently greater than those obtainable from the simpler ones, to justify the cost involved in their application? Secondly, if the more elaborate schemes are more efficient, what are the respective weights to be given to each item of information so that selection response is maximised? These are problems which can be answered on theoretical grounds, being most easily handled as aspects of selection index theory. This has been demonstrated by Hazel in his original selection index study, and by Henderson (1952, 1961), Legates and Lush (1954) and Dickerson (1950). In this case the procedure is to consider the particular items of information as separate, but correlated variables.

VI THE SELECTION INDEX APPROACH

A. INTRODUCTION

Although the idea of a yardstick or selection index for measuring the net merit of breeding individuals is almost as old as animal breeding itself, (Hazel 1943), many of the early attempts involved the mere assignment of purely arbitrary scores to the series of factors believed to contribute to productive worth. Beginning with Pearson's multiple regression methods and Fisher's concept of discriminant functions, the principles of index construction were first developed by Smith (1936) and Hazel (1943).

The various sire indices that have been proposed and are widely used for selecting bulls for butterfat and milk production are examples of indices designed for the improvement of one trait, but using information based on several related individuals.

Henderson (1952) gave the first detailed application of the principles of the selection index approach to this type of problem. He showed that the approach was capable of making use of all information and that the effects of inbreeding on additive genetic variances and covariances could be allowed for. He also suggested that environmental trends and age effects could be eliminated. Cochran (1951) has discussed many of the mathematical and statistical problems encountered in index construction. Henderson (1961), has further extended these theoretical considerations, and has discussed in detail several important properties of the selection criterion. The same worker has also been involved in empirical sampling investigations of selection index problems (Heidhues and Henderson 1961, 1962).

B. SELECTION INDEX THEORY

1. DERIVATION OF INDEX EQUATIONS:

Letting $y_1, y_2, \ldots\ldots, y_N$ represent the items of information available, an index of the form -

$$I = b_1 (y_1 - \mu_1) + b_2 (y_2 - \mu_2) + \ldots\ldots + b_N (y_N - \mu_N)$$

is required to discriminate between the additive genetic values of the individuals available for selection. In this formula the μ's represent the mean values of the corresponding y's, while the b's denote the optimum weighting factors requiring estimation.

The principle of index construction rests upon the fact that improvement in the additive genetic merit of a population (ΔH) through truncation selection on the index estimates of breeding value, is maximised by choosing that index which has a maximum correlation (r_{IH}) with additive genetic merit (H) (Hazel 1943, Lush 1948). This is true provided that H and I can be assumed to follow a joint bivariate normal distribution. The regression of H on I is then given by,

$$E (H - \mu_H) = B_{HI} (I - \mu_I)$$

where μ_H and μ_I are the mean values of H and I respectively, over all individuals in the population. Letting the corresponding standard deviations be σ_H and σ_I, this may be formulated as,

$$\Delta H = r_{IH} \, \sigma_H \, \frac{(\mu_I' - \mu_I)}{\sigma_I}$$

μ_I' being the mean index value of those individuals retained for breeding. This formulation is merely an extension of the simple linear prediction equation (Lush 1961).

The final term of the above relationship represents the standardised selection differential or the intensity of selection (i). Provided the breeder uses the same diligence in selecting by truncation on I, regardless of what I is, this term will be constant for a given population. Since the additive genetic variance (σ^2_H) will also be constant, the accuracy of a given index is directly proportional to r_{HI}.

Differentiating log r_{HI} with respect to $b_1, \ldots\ldots, b_N$, and equating the derivatives to zero, gives the index equations whose solution produces the optimum weighting coefficients. These are:

$$\begin{aligned}
b_1\sigma^2_{y_1} + b_2\sigma_{y_1y_2} + \ldots\ldots\ldots + b_N\sigma_{y_1y_N} &= \sigma_{y_1H} \\
b_1\sigma_{y_2y_1} + b_2\sigma^2_{y_2} + \ldots\ldots\ldots + b_N\sigma_{y_2y_N} &= \sigma_{y_2H} \\
\ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots & \\
b_1\sigma_{y_Ny_1} + b_2\sigma_{y_Ny_2} + \ldots\ldots\ldots + b_N\sigma^2_{y_N} &= \sigma_{y_NH}
\end{aligned} \qquad \ldots\ldots (5)$$

where σ^2_{yi} is the variance of y_i; $\sigma_{y_iy_j}$ is the covariance between y_i and y_j; and σ_{y_iH} is the covariance between y_i and H.

These equations are seen to be the same as the normal regression equations of $y_1, \ldots\ldots y_N$, on H, with population variances and covariances in place of sample sums of squares and products.

The same general equations are applicable to an index designed for the simultaneous selection of several characters. The only difference involves the definition of breeding value (H) and the fact that the present application requires that only the additive genetic variance need be estimated. Population genetics theory can then be invoked to infer the appropriate variances and covariances. Henderson (1961) has shown that the right hand members of the equations are given by the relation,

$$\sigma_{y_i H} = a_{i\alpha}\sigma_H^2 ,$$

where $a_{i\alpha}$ is the relationship of the animal with the i-th item of information, to α, the animal being evaluated. This allows simplification to the following system:

$$\begin{pmatrix} 1 + F_1 h^2 & a_{12}h^2 & \cdots\cdots & a_{1N}h^2 \\ a_{21}h^2 & 1+F_2 h^2 & & a_{2N}h^2 \\ \cdots & \cdots & \cdots & \cdots \\ a_{N1}h^2 & a_{N2}h^2 & & 1+F_N h^2 \end{pmatrix} \begin{pmatrix} b_1 \\ b_2 \\ \cdot \\ b_N \end{pmatrix} = \begin{pmatrix} a_{1\alpha}h^2 \\ a_{2\alpha}h^2 \\ \cdot \\ a_{N\alpha}h^2 \end{pmatrix}$$

where F_i is the inbreeding coefficient of the i-th individual and a_{ij} is the relationship between animals with the i-th and j-th items of information. On this basis r_{IH} is equal to $\sqrt{b_1 a_{i\alpha} + \dots + b_N a_{N\alpha}}$

This formulation implies the assumptions that no selection has occurred since the period of defining the initial population; that all genetic variance is additive; that there is no correlation between the additively genetic and environmental values of the same individuals; and that the environmental values of related individuals are also uncorrelated (Henderson 1961).

Henderson has also indicated ways in which the equations must be modified when more than one record is available per animal, and when group means are used for estimating breeding value. In the first case the i-th diagonal element of the matrix becomes $\dfrac{1 + (n_i - 1)T}{n_i} + F_i h^2$, where n_i is the number of records averaged and used in the index equation, and T is the coefficient of repeatability. In the second case, which is appropriate to the problem of family selection, the i-th diagonal element becomes $\frac{1+(n_i-1)T}{n_i} \Big/ p_i$

$$+ \left(F_i h^2 + (p_i-1)\, a_{ii} h^2\right) \Big/ p_i$$

where, n_i in this case represents the number of records on each member of the group; p_i is the number of individuals in the group; F_i is the inbreeding coefficient of each member of the group; and a_{ii} is the intra-group relationship. This implies that every member of the group has the same relationship with any other individual whose record is used in the selection index. When $n_i = 1$ the expression becomes $\left(1 + F_i h^2 + (p_i-1)\, a_{ii} h^2\right) \Big/ p_i$

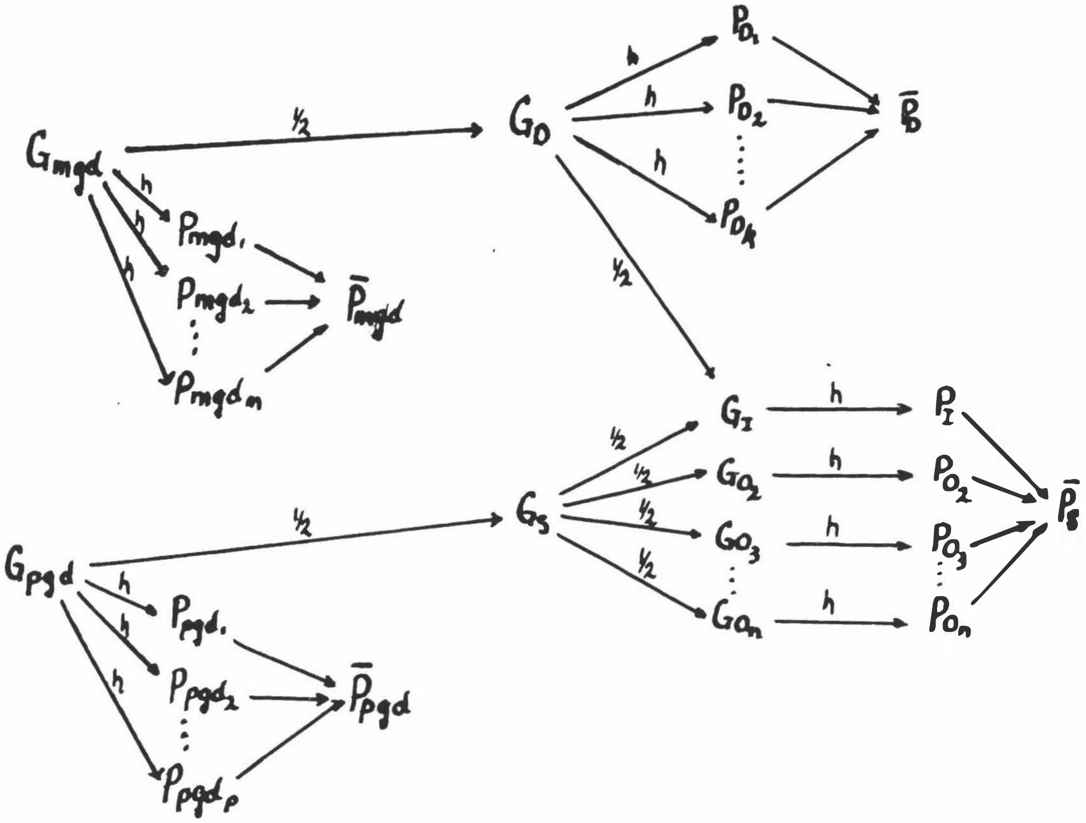
2. SELECTION INDICES FOR LAMB PRODUCTION:

Several selection indices, based on information pertaining to the number of offspring produced, will now be considered for the purpose of selecting young ewe and ram replacements to enter a breeding flock. In particular indices utilising the following information have been derived:

1. The number of lambs born per lambing of the animal's dam.
2. The number of lambs born per lambing of the half-sisters of the animal.
3. The number of lambs born per lambing of the animal's grandams.

The biometrical relationships concerned are presented in terms of the path coefficient diagram of Figure 2, for the case of a large random mating population with no environmental correlation between generations. The correlation coefficients applicable to these items of information are presented in the following matrix:

FIGURE 2. BIOMETRICAL RELATIONSHIPS BETWEEN AN INDIVIDUAL ITS ANCESTORS AND ITS COLLATERAL RELATIVES, IN A RANDOM MATING POPULATION.



P = phenotypic value and G = additive genetic value of the animal indicated by the subscript:

I = the individual being evaluated
O = offspring of the individual's sire
D = dam of the individual
S = sire " " "
mgd = maternal grandam
pgd = paternal grandam

$\bar{P}_D$ = mean of the k records of the dam
$\bar{P}_S$ = mean performance of n paternal half-sibs
$\bar{P}_{mgd}$ = mean of the m records on the maternal grandam
$\bar{P}_{pgd}$ = mean of the p records on the paternal grandam
h : $\sqrt{\text{heritability}}$

$$
\begin{array}{cccccc}
 & G_I & \bar{P}_D & \bar{P}_s & \bar{P}_{mgd} & \bar{P}_{pgd} \\
G_I & 1 & \frac{1}{2}h\sqrt{K} & \frac{1}{4}h\sqrt{N} & \frac{1}{4}h\sqrt{M} & \frac{1}{4}h\sqrt{P} \\
\bar{P}_D & & 1 & 0 & 0 & 0 \\
\bar{P}_s & & & 1 & 0 & \frac{1}{4}h^2\sqrt{NP} \\
\bar{P}_{mgd} & & & & 1 & 0 \\
\bar{P}_{pgd} & & & & & 1
\end{array}
$$

where $K = \frac{k}{1 + (k-1)T}$, (T being the repeatability coefficient;

$N = \frac{n}{1 + (n-1)t}$, (t being the intra-class correlation between haf-sibs);

$M = \frac{m}{1 + (m-1)T}$; and $P = \frac{p}{1 + (p-1)T}$.

Substitution of these correlations in the formulae presented in relation (5) above, gives the appropriate weighting factors. The multiple correlation coefficients may then be calculated. It is immaterial whether these equations are considered as a matrix system involving variances and covariances, or as one involving correlations. Skjervold and Odegard (1959) and Young (1961) have approached the problem in correlation terms, calculating the weighting and multiple correlation coefficients appropriate for different combinations of records.

To illustrate the method of computation and the equivalence of the correlation approach and the modified formulae of Henderson, the derivation of an index combining dam and half-sister information is presented, for the case where each half-sister has but one record.

Correlation method - ($\bar{P}_D = y_1$; $\bar{P}_s = y_2$)

The two simultaneous equations are:

$$b_1\sigma^2_{\bar{\bar{P}}_D} + b_2\sigma_{\bar{\bar{P}}_D\bar{\bar{P}}_S} = r_{\bar{\bar{P}}_D G_I}\,\sigma_{\bar{\bar{P}}_D}\,\sigma_{G_I}$$

$$b_2\sigma_{\bar{\bar{P}}_S\bar{\bar{P}}_D} + b_2\sigma^2_{\bar{\bar{P}}_S} = r_{\bar{\bar{P}}_S G_I}\,\sigma_{\bar{\bar{P}}_S}\,\sigma_{G_I}$$

Since in a random mating population $\bar{\bar{P}}_D$ and $\bar{\bar{P}}_S$ will not be correlated as a result of genetic causes, and since environmental correlation is assumed zero, $\sigma_{\bar{\bar{P}}_S\bar{\bar{P}}_D} = \sigma_{\bar{\bar{P}}_D\bar{\bar{P}}_S} = 0.$

$$\text{i.e. } b_1\sigma^2_{\bar{\bar{P}}_D} = \tfrac{1}{2}h\sqrt{K}\,\sigma_{\bar{\bar{P}}_D}\,\sigma_{G_I} \quad \therefore\ b_1 = \frac{\frac{1}{2}h\sqrt{K}\,\sigma_{GI}}{\sigma_P\sqrt{1/K}} = \tfrac{1}{2}h^2K$$

$$\text{and } b_2\sigma^2_{\bar{\bar{P}}_S} = \tfrac{1}{4}h\sqrt{N}\,\sigma_{\bar{\bar{P}}_S}\,\sigma_{GI} \quad \therefore\ b_2 = \frac{\frac{1}{4}h\sqrt{N}\,\sigma_{GI}}{\sigma_P\sqrt{1/N}} = \tfrac{1}{4}h^2N$$

where σ^2_P is the phenotypic variance of one lambing record.

<u>Hendersons formulation</u> $(\bar{\bar{P}}_D = y_1;\ \bar{\bar{P}}_S = y_2)$

$$\begin{pmatrix} \frac{1+(k-1)T}{k} + F.h^2 & a_{12}h^2 \\ a_{21}h^2 & \frac{1+F_2h^2(n-1)a_{22}h^2}{n} \end{pmatrix}\begin{pmatrix} b_1 \\ b_2 \end{pmatrix} = \begin{pmatrix} a_{1\alpha}h^2 \\ a_{2\alpha}h^2 \end{pmatrix}$$

Since, $a_{12} = a_{21} = 0$, $F_1 = F_2 = 0$, $a_{1\alpha} = \frac{1}{2}$, $a_{2\alpha} = \frac{1}{4}$, $a_{22} = \frac{1}{4}$, and $a_{22}h^2 = t$, this reduces to -

$$\begin{pmatrix} \frac{1+(k-1)T}{k} & 0 \\ 0 & \frac{1+(n-1)t}{n} \end{pmatrix}\begin{pmatrix} b_1 \\ b_2 \end{pmatrix} = \begin{pmatrix} \frac{1}{2}h^2 \\ \frac{1}{4}h^2 \end{pmatrix}$$

$$\therefore\ b_1 = \tfrac{1}{2}h^2K \qquad b_2 = \tfrac{1}{4}h^2N,$$

and $r_{III} = \sqrt{b_1 a_{1\alpha} + b_2 a_{2\alpha}} = \sqrt{\frac{1}{4}h^2K + 1/16h^2N}$

$= \frac{1}{4}h\sqrt{4K + N}$, as given by Young (1961).

Following the same basic principles the indices given below have been calculated:

1. Index utilising dams' information alone:

$$I_1 = b\,(\bar{P}_D - \bar{\bar{P}})$$

$$b = \tfrac{1}{2}h^2K \qquad r = \tfrac{1}{2}h\sqrt{K}$$

2. Index combining the performance of the dam and the maternal grandam:

$$I_2 = b\,(\bar{P}_D - \bar{\bar{P}}) + b_2\,(\bar{P}_{mgd} - \bar{\bar{P}})$$

$$b_1 = \tfrac{1}{2}h^2K \qquad r = \tfrac{1}{4}h\sqrt{4K + M}$$

$$b_2 = \tfrac{1}{4}h^2M$$

3. Index combining the performance of the dam and the paternal half-sibs:

$$I_3 = b_1\,(\bar{P}_D - \bar{\bar{P}}) + b_2\,(\bar{P}_S - \bar{\bar{P}})$$

$$b_1 = \tfrac{1}{2}h^2K \qquad r = \tfrac{1}{4}h\sqrt{4K + N}$$

$$b_2 = \tfrac{1}{4}h^2N$$

4. Index combining the performance of the dam, paternal half-sibs and the maternal grandam:

$$I_4 = b_1\,(\bar{P}_d - \bar{\bar{P}}) + b_2\,(\bar{P}_s - \bar{\bar{P}}) + b_3\,(\bar{P}_{mgd} - \bar{\bar{P}})$$

$$b_1 = \tfrac{1}{2}h^2K$$

$$b_2 = \tfrac{1}{4}h^2N \qquad r = \tfrac{1}{4}h\sqrt{4K + N + M}$$

$$b_3 = \tfrac{1}{4}h^2M$$

5. An index combining information on the dam, the paternal half-sibs and both grandams is considerably more complex due to a genetic relationship

between the paternal grandam and the paternal half-sibs. Thus, the weighting factors for half-sisters (b_2) and for paternal grandams (b_4) become,

$$b_2 = \frac{h^2N\,(4-h^2P)}{16 - h^4\,NP} \qquad b_4 = \frac{h^2P\,(4-h^2N)}{16 - h^4\,NP}$$

In these indices $\bar{\bar{P}}$ represents the population average lamb production.

3. RELATIVE EFFICIENCY OF LAMB PRODUCTION INDICES:

The expected values of the multiple correlation coefficient ($r_{II'}$) provide a basis for choosing an index which is of an accuracy which is consistent with its practical utility in terms of the cost and labour involved in its construction and application.

The theoretical values of the multiple correlation coefficients for the first four indices given above are presented in Table 24. They have been calculated on the assumption that each individual has 10 half-sisters (i.e. n = 10) with one lambing record, and that four records are available on the maternal grandam. Heritability and repeatability have been taken as 0.125 and 0.25 respectively.

TABLE 24. Multiple Correlation Coefficients for Four Lamb Production Indices.

No.of Dams Records	I_1	I_2	$\frac{100I_2}{I_1}$	I_3	$\frac{100I_3}{I_1}$	I_4	$\frac{100I_4}{I_1}$
k = 1	0.177	0.222	125	0.304	172	0.332	188
k = 2	0.224	0.261	117	0.333	149	0.359	160
k = 3	0.250	0.283	113	0.353	141	0.376	150
k = 4	0.267	0.299	112	0.364	136	0.388	145

This table demonstrates the relatively small gain in accuracy which is expected from the inclusion of grandam's information in comparison with the advantage to be had from 10 half-sister records. This, together with the fact that the records on an animal's grandam are less likely to be readily available and complete, suggests that contemporary half-sister records will be a more useful adjunct to information on the dam. The above table also indicates that information on 10 paternal half-sisters might be particularly useful when only a small amount of dams information is available, (i.e. when k is small).

In an attempt to further assess the value of including half-sister information in a lamb production index based on the performance of the dam, the relative efficiencies of I_3 and I_1 have been studied in greater detail. This relative efficiency is given by:

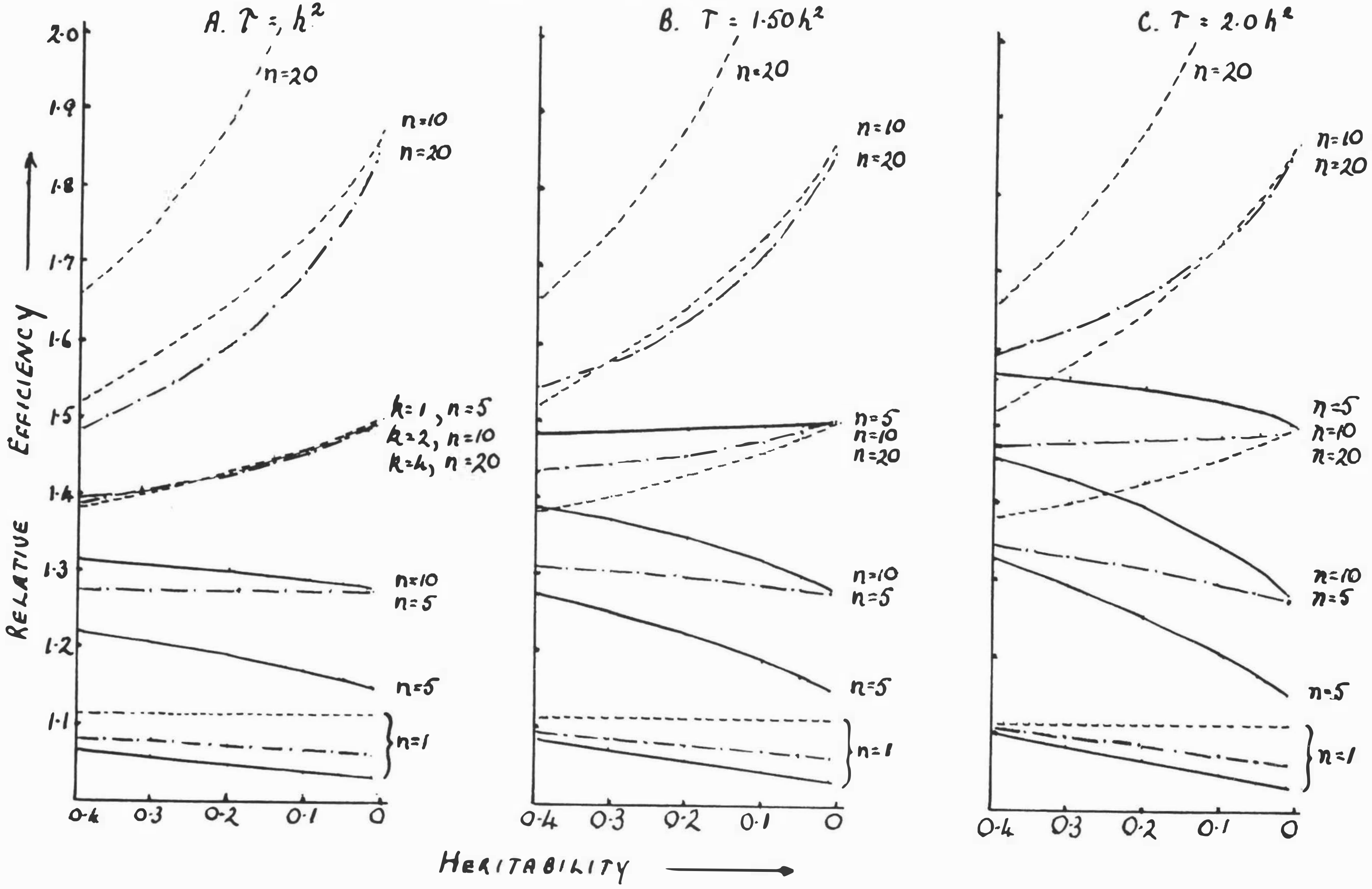
$$E = {}^{r_{G_I I_3}}\!\Big/\!{}_{r_{G_I I_1}} = \frac{\frac{1}{2}h\sqrt{4K + H}}{\frac{1}{2}h\sqrt{K}} = \frac{1}{2}\sqrt{4 + {}^{H}\!/\!{}_{K}}$$

$$= \sqrt{1 + \left(\frac{n\left(1 + (k-1)T\right)}{k\left(4 + (n-1)h^2\right)}\right)}$$

As is implicit in the theory of index construction, values of K and H are never less than unity and, as Young (1961) has shown, their values increase with increasing k and n. The exact rate of increase depends upon the ratio $\frac{n\left(1 + (k-1)T\right)}{4k\left(1 + (n-1)t\right)}$. This is not independent of the heritability because the intra-group correlation (t) is given by the relation $t = rh^2 + c^2$. In this formula r represents the genetic relationship, and c^2 an environmental component of the correlation which has been assumed absent in the present study due to the nature of the experimental design. This assumption is also likely to hold under the husbandry conditions operating on commercial sheep farms where sire groups seldom receive differential treatment.

FIGURE 3. RELATIVE EFFICIENCY OF COMBINING HALF-SIB INFORMATION WITH RECORDS OF THE DAM

(- - - - - indicates one record of the dam, —·—·—· indicates two, and ——— indicates four)
n = number of half sisters



The exact relationships between T, h^2, n and k have been considered over the following range of values:

h^2 varying from 0.01 to 0.4

T equal to h^2, $1.50h^2$ and $2.0h^2$

n equal to 1, 5, 10 and 20.

k equal to 1, 2 and 4.

The results are presented in graphical form in Figure 3.

For the case when k = 1, E is given by

$$E = \sqrt{1 + \frac{n}{4 + (n-1)h^2}} \, .$$

The relative efficiency is therefore, expected to be large when n is large. This is indicated by the dotted lines of graphs A, B and C. These graphs also indicate that a considerable gain is expected from the inclusion of information on 10 or more half-sisters, especially when the heritability is low.

When $k > 1$, the size of the repeatability exerts an effect upon the relative efficiency. For the case when $T = h^2$ (graph A) approximately the same relative gain is obtained from the inclusion of half-sister records for each of the following combinations of n and k:

$k = 1$; $n = 5$; $k = 2$; $n = 10$; $k = 4$; $n = 20$; i.e. when $^{n}/_{k} = 5$. That is, the inclusion of five times as many half-sisters as the number of dam's records available, is expected to give a 40-50% increase in the relative efficiency of the index. Furthermore, the size of this increase would seem to be relatively independent of heritability over the range chosen. Similarly, the graphs indicate that inclusion of 10 times as many half-sisters is expected to give a 50-80% increase in the relative efficiency of estimating breeding value, although in this case the increase is especially evident at low values of the heritability.

These same general relationships are also approximately true for the case where $T = 1.5h^2$ (graph B) and where $T = 2.0h^2$ (graph C), especially at the lower end of the heritability range.

4. RELATIVE WEIGHTING FACTORS FOR AN INDEX BASED ON DAM'S AND HALF-SIBS' PERFORMANCE:

The emphasis to be placed on half-sister information relative to the performance of the dam is given by the ratio -

$$b_2/b_1 = \tfrac{1}{4}h^2N/\tfrac{1}{2}h^2K = N/2K.$$

Some characteristics of this ratio for variations in n, k, h^2 and T are also indicated by the graphs of Figure 2. This is true because -

$$E = r_{G_I I_3} \Big/ r_{G_I I_2} = \frac{\sqrt{\tfrac{1}{2}b_1 + \tfrac{1}{4}b_2}}{\sqrt{\tfrac{1}{2}b_1}} = \sqrt{1 + \frac{b_2}{2b_1}}$$

i.e. E is a function of b_2/b_1

Graph A indicates that approximately the same relative emphasis should be given to half-sister records when n = 5 and k = 1, when n = 10 and k = 2, and when n = 20 and k = 4. This relative emphasis has been calculated to be approximately 2.3. The same approximate relationship holds true when the repeatability is of the order of $1.50h^2$ (graph B).

It is also to be noted that the lines of graphs A and B are relatively flat until the ratio of n/k reaches a value of 5. This indicates that until this ratio is reached there is little change in the relative emphasis to be placed on half-sister records with changes in the heritability over the range 0.01 to 0.40. On this basis the approximate relative emphasis values shown in Table 25 have been calculated.

TABLE 25. Approximate Emphasis to be placed on Half-sisters' Performance Relative to Dam's Average Production

Value of n/k	Approximate Relative Emphasis b_2/b_1
5	2.3
3	1.6
2.5	1.4
2	1.0
1	0.5

These approximations hold most closely when heritability is of the order of 0.10 and repeatability is not much higher.

5. DISCUSSION:

The investigations of Henderson and Heidhues (1951) have been concerned with the problem of the amount of information which can usefully be included in a selection index. Although it might be expected from theoretical considerations that the inclusion of additional items of information on the animal's relatives will not decrease the accuracy of estimation, Cochran (1951) has pointed out that the sampling errors involved in the determination of the weighting factors might cancel much of the extra accuracy expected. Heidhues and Henderson found that it was in fact, advantageous to neglect those relatives which were known to have small partial correlations with the true breeding value of the individual being evaluated, when the sample size was small.

This suggests that empiracal investigations are necessary to critically examine the efficiency of any given index.

C. APPLICATION OF TWO LAMB PRODUCTION INDICES

1. INDEXING PROCEDURE:

(a) Information on the Dam:

Rae (1958b) has presented in tabular form a lamb production index utilising information on the dam. His table is based on the index formulation previously derived, which for heritability and repeatability coefficients of 0.125 and 0.25 respectively, reduces to -

$$I = \frac{k}{4(k+3)} \left(\bar{P}_D - \bar{\bar{P}}\right)$$

$$= \frac{K}{4(k+3)} - \frac{k\bar{\bar{P}}}{4(k+3)} \quad \ldots\ldots\ldots \quad (6)$$

In this formula K is the total number of lambs produced by the dam in k lambings. The second term of this relationship is constant for all animals whose dams have the same number of records and in an attempt to correct for age variations in fertility, Rae has chosen different values of $\bar{\bar{P}}$ for each of these cases.

The logic behind the application of additive age correction factors and their incorporation into a table of index values is illustrated in the following relationships.

Suppose that there exists in a population the following lamb production values:

Age	Number of Ewes	Total Lambs Produced	Mean Lamb Production
Two-tooth	n_1	P_1	x_1
Four-tooth	n_2	P_2	x_2
Six-tooth	n_3	P_3	x_3
Mature Ewes	n_4	P_4	x_4
Total	$M = (n_1+n_2+n_3+n_4)$	$M\bar{\bar{P}}$	$\bar{\bar{P}}$

Correcting individual lamb production records to their mature equivalent, requires the additive correction factors shown below:

Two-tooths : $x_4 - x_1 = a_1$
Four-tooths : $x_4 - x_2 = a_2$
Six-tooths : $x_4 - x_3 = a_3$

Since the total age corrected lamb production of the population ($M\bar{\bar{P}}_c$) equals the total uncorrected lamb production ($M\bar{\bar{P}}$) plus the corrections for age, the following relationship may be written:

$$M\bar{\bar{P}}_c = M\bar{\bar{P}} + n_1a_1 + n_2a_2 + n_3a_3$$

where $\bar{\bar{P}}_c$ = the average age corrected lamb production. Similarly the age corrected lamb production ($\bar{P}_{ic}$) for the k_i lambings of the i-th ewe may be written as:

$$\bar{P}_{ic} = \bar{P}_i + \frac{a_1 + \dots + a_{ki}}{ki}$$

TABLE 26. Lamb Production of Ewes Classified According to Age and Year. (L.P. = total lambs born per 100 ewes mated and present at lambing).

Age Year	Two-tooth		Four-tooth		Six-tooth		Eight-tooth	
	n	L.P.	n	L.P.	n	L.P.	n	L.P.
1946	132	127						
1947	186	115	136	131				
1948	24	100	197	110	124	123		
1949	87	123	18	150	167	149	111	168
1950	104	109	82	150	2	150	26	142
1951	214	107	100	124	79	142	-	-
1952	25	92	200	120	100	125	72	142
1953	83	122	20	135	182	157	88	161
1954	128	86	87	124	20	125	172	136
1955	192	104	118	121	84	146	19	158
1956	71	100	59	115	57	121	45	151
1957			69	109	53	123	52	138
1958					68	135	53	134
1959							58	129
Age Group Means	1246 (1267)	109 (108)	1086 (1137)	122 (122)	936 (985)	140 (138)	696 (733)	146 (147)

The problem is one of finding a value (X) with which a ewe's uncorrected lamb production ($\bar{P}_i$) is to be compared such that $(\bar{P}_{ic} - \bar{\bar{P}}_c) = (\bar{P}_i - X)$.

i.e. such that $X = \bar{P}_i + \bar{\bar{P}}_c - \bar{P}_{ic}$ which on substitution becomes -

$$= \bar{\bar{P}} + \frac{n_1a_1 + n_2a_2 + n_3a_3}{N} - \frac{a_1 + \dots + a_{ki}}{ki}$$

Algebraic simplification of this relationship gives the appropriated values of X for ewes with different numbers of lambings on the assumption that all ewes lamb for their first time as two-tooths and once annually thereafter until they are mature.

Number of Records On the Dam	Value for X
1	x_1
2	$\frac{1}{2}(x_1+x_2)$
3	$\frac{1}{3}(x_1+x_2+x_3)$
4	$\frac{1}{4}(x_1+x_2+x_3+x_4)$

Table 26 reports the mean lamb production of ewes classified according to the age and year in which their records were made. The age group averages given in the final row of this table, represent the weighted means over the years shown. The inclusion in this analysis of ewes which lambed to sires exhibiting a high level of barrenness, and of ewes which lambed for their first time as four-tooths, made little difference to these overall means, as is demonstrated by the bracketed figures given in the final row of Table 26.

From these age group means the appropriate age-adjusted population means have been calculated and incorporated in the index values presented in Table 27.

This table has been calculated from formula (6), each value being coded by multiplying by 1000 and adding 100 units. This has been done to avoid small and an excessive number of negative values respectively.

TABLE 27. Lamb Production Index Based on the Dam's Records.

Number of Lambs (K)	Number of Lambings			
	1	2	3	4
1	94	34	- 13	- 49
2	157	84	29	- 13
3	219	134	70	23
4		184	111	59
5		234	154	94
6		284	195	130
7			236	166
8			279	201
9			320	237
10				273

(b) Information on Dams and Half-sisters:

Due to the independence of these two sources of information, the latter can be used to supplement the above index values in a simple additive manner. This is true provided the half-sister factor is also coded by multiplying by 1000, the combined index then being given by -

$$I = 1000 \frac{k}{4(k+3)} (\bar{P}_D - \bar{P}) + 1000 \frac{n}{n+31} (\bar{P}_s - \bar{P}) + 100.$$

In table 28 factors for adjusting for differing numbers of half-sisters (n) are given for use when their two-tooth lamb production is expressed as the percentage of lambs born per ewe.

TABLE 28. Factors for Adjusting for Differing Numbers of Half-Sisters.

Number	Factor	Number	Factor	Number	Factor	Number	Factor
1	0.31	9	2.25	17	3.54	25	4.46
2	0.61	10	2.44	18	3.67	26	4.56
3	0.88	11	2.62	19	3.80	27	4.66
4	1.14	12	2.79	20	3.92	28	4.75
5	1.39	13	2.95	21	4.04	29	4.83
6	1.62	14	3.11	22	4.15	30	4.92
7	1.84	15	3.26	23	4.26	31	5.00
8	2.05	16	3.40	24	4.36	32	5.08

Since in this case only the two-tooth records of the half-sisters are being used, there is no need to consider the problem of age corrections.

2. ESTIMATES OF INDEX EFFICIENCY:

(a) Method of Analysis:

The efficiency of the above two lamb production indices in ranking individuals according to their breeding values has been considered in terms of a simple linear prediction equation. Thus, if $\bar{I}$ is the average index value of all individuals available for selection and I' is the average value of those individuals retained for breeding, the expected gain in lamb production per generation (ΔP) is given by $\Delta P = b_{PI} (I'-\bar{I})$, b_{PI} being the regression of the lamb production of the animals (P) on their index value (I). In this formula ΔP represents the amount by which the lamb production of those individuals retained for breeding (P') exceeds the lamb production that would have resulted had no selection taken place ($\bar{P}$).

$$\text{i.e. } \Delta P = (P'-\bar{P}) = b_{PI} (I'-\bar{I}) = r_{PI}(i)\,\sigma_p$$

where σ_p = the standard deviation of lamb production
σ_I = the standard deviation of the index
(i) = the intensity of selection

Accordingly the efficiency of the two lamb production indices has been studied in terms of the least squares linear regression and correlation coefficients, b_{PI} and r_{PI}. That is, the linear association between the index values of individuals and their actual average annual lamb production ($\bar{P}$) has been calculated. This has been done in an attempt to simulate the practical problem of selecting young female flock replacements prior to their first mating as two-tooths. Under this system of flock management at least two lambing records of their dam will be available on which to construct an index of their breeding value. The maximum number of records on the dam will be four, since the ewes of this flock have been cast for age following their fourth lambing.

Since the lamb production of the animals has been assessed as an average based on different numbers of lambings, the correlation coefficients will not form an appropriate basis for comparing the efficiency of two indexes unless they are calculated on the same sample of animals. In this case the regression coefficients are the appropriate basis for comparison, provided that both indices have the same or similar standard deviations. This is because the averaging of lamb production records affects the correlation in such a way as to cancel exactly its effect on the standard deviation of lamb production, with the result that the regression coefficient is independent of the number of records averaged.

Both correlation and regression coefficients have been calculated separately for groups of animals born in the same year. Pooling has been accomplished by combining the intra-year sums of squares, sums of products and degrees of freedom.

(b) Results:

(i) Index based on records of the dam:

The within year of birth correlations utilising all available information are reported in Table 29 to illustrate the variation found. Those based on less than five pairs have been excluded.

TABLE 29. Correlations between Index Values and Mean Lamb Production (Index based on dam's records alone; all available daughter-dam pairs utilised).

Year of Birth	Number of Dam's Records Entering the Index							
	2		3		4		2 to 4 Combined	
	n-1	r	n-1	r	n-1	r	n-1	r
1946	-	-	-	-	5	.328	6	.430
1947	48	-.072	34	.335	-	-	85	.183
1948	13	.597	76	-.023	30	.031	121	.046
1949	48	.101	96	.003	66	.161	212	.062
1950	12	.478	8	-.173	-	-	24	.299
1951	34	.403	28	.198	21	.095	86	.245
1952	-	-	64	.007	55	.130	125	.069
1953	6	.149	7	.158	45	-.154	60	-.089
1954	20	.020	14	.295	36	.099	72	.111

TABLE 30. Pooled Correlations Between Index Values and Mean Lamb Production

(Index based on dams records alone)

	A Number of Dams Records Entering Index				B Number of Dams Records Entering Index				C Number of Dams Records Entering Index			
	2	3	4	2-4 Combined	2	3	4	2-4 Combined	2	3	4	2-4 Combined
d.f.	181	327	258	791	154	250	236	661	117	237	175	546
σ_I	38.14	47.01	44.75	45.04	38.61	46.32	44.41	44.56	37.35	45.61	44.29	44.23
σ_P	0.377	0.410	0.417	0.403	0.388	0.408	0.403	0.398	0.336	0.388	0.360	0.367
r	0.188	0.062	0.082	0.099	0.204	0.069	0.060	0.102	0.165	0.060	0.072	0.080
100xb	0.186	0.054	0.076	0.088	0.205	0.061	0.055	0.091	0.148	0.052	0.058	0.066

The pooled values of the correlation and regression coefficients are presented in Table 30 together with the corresponding standard deviations and degrees of freedom. Section A of this table represents the values obtained when all available daughter dam pairs were included in the analysis. Section C shows the corresponding values when pairs exhibiting non-consecutive annual lambing records, and pairs in which either member was mated to an apparently infertile sire, were excluded. Section C includes only those pairs in which the average lamb production assessment was based on four consecutive annual lambing records of the daughter ewes.

(ii) Index based on records of the dam and the half-sisters:

The pooled values of the correlation and regression coefficients over the different birth years are recorded in Table 31.

TABLE 31. Pooled Correlations Between Index Values and Mean Lamb Production (Index based on combined dam and half-sister performance)

Basis of Analysis	d.f.	I	$\bar{Y}$	r	100 x b
Including all available daugter dam pairs	605	65.41 (45.32)	0.410	0.088 (0.098)	0.055 (0.088)
Excluding ewes mated to infertile rams and ewes with non-consecutive records	499	66.22 (45.20)	0.401	0.087 (0.090)	0.053 (0.080)
Including only those daughter ewes with four consecutive records	408	66.42 (44.24)	0.378	0.057 (0.076)	0.033 (0.065)

The figures reported in brackets refer to the corresponding statistics when the same sample of animals was indexed on the basis of their dam's performan alone.

(c) Discussion:

The low values for the estimates reported show that their exists little linear association between an animal's predicted breeding value and its subsequent reproductive performance. This is to be expected in view of the low heritability of lamb production.

Due to the possibility that male infertility may have introduced an element of randomness into the assessment of an animal's breeding value, the initial analysis was repeated excluding females mated to sires associated with a high incidence of barrenness. Ewes which did not show consecutive annual lambing records were also excluded in view of the assumption made in the calculation of the age correction factors. These effects, however, made little difference to the pattern of results, as is indicated by the regression coefficients of Tables 30 and 31. A similar pattern was also obtained when only those animals with four consecutive lambing records were studied. (Tables 30 C and 31).

The regression coefficients reported in Table 30 suggest that an index based on two lambing records of the dam, exhibits a closer relationship with the animal's ability to produce lambs, than one based on three or four records. This is contrary to theoretical expectation, sampling variation being the only possibility the writer can suggest as an explanation. This suggestion is based upon the variation shown by the within-year correlations of Table 27.

This same variation also suggests that the response to selection for lamb production on the basis of an index of parental performance is likely to be quite erratic. Nevertheless, the small but consistently positive pooled values do indicate that, on average over a number of years, some progress can be expected. The magnitude of this response has been calculated for the two lamb production indices, using the values of the pooled statistics obtained from the analysis of all available daughter-dam pairs. The method of calculation involves the assumption that the index is normally distributed and that selection is entirely on the basis of the index ranking of the animals. It is based on the standardised selection differentials reported by Lush (1943). The expected progress per generation is presented in Table 32, for different intensities of selection.

TABLE 32. Expected Gain per Generation in the Number of Lambs Born per 100 Ewes Mated.

% of Population Saved	Index	
	Dam's Information Alone	Combined Dam and Half-sister Performance
70	1.98	1.79
60	2.54	2.30
50	3.17	2.88
40	3.81	3.45
30	4.60	4.17
20	5.55	5.04
10	6.98	6.33
5	8.16	7.41
2	9.67	8.78

These figures demonstrate that the use of either index for the selection of female flock replacements is expected on average to produce, per generation of selection, a gain of approximately 2½ lambs per 100 ewes mated when the culling rate is of the order of 40%. Assuring that the intensity of selection of the sires is around the 5% mark, the total gain per generation will be of the order of 10-11 lambs per 100 ewes mated.

It is disappointing from the point of view of *maximising* selection response to find that the inclusion of half-sister records in a combined lamb production index has apparently not produced the expected increase in efficiency. The correlations reported in Table 31, and the expected gains of Table 32 indicate that no advantage has accrued from their use. This is unlikely to be due to a lack of half-sister information, each individual averaging between 10 and 30 half-sisters in all but one of the five years on which half-sister information was available. Apart from the possibility of sampling variation, no adequate explanation of this situation appears to be available.

An important question which arises in the use of the index method of selecting for lamb production, is whether the tables of index values presented can be satisfactorily applied over a wide range of flocks which are likely to differ in their basic genetic parameters and in the adjustments required for age effects.

In this connection the consistency found for the value of the relative weighting to be given to dam and half-sister information for variations in heritability and repeatability, suggests that some degree of generality might be valid. The simulation studies of Heidhues and Henderson (1961) provide further pertinent information. These workers found that the single trait selection index method was relatively insensitive to errors of estimation of the true population heritability. This lends support to the conclusion that any reasonable heritability estimate may be used in setting up selection programmes of this nature.

An attempt has been made in this study to assess the adaptability of the table of index values based on dam's information, to flocks which differ in their lamb production pattern. To this end, index tables were constructed separately for each of the years in which the dams of the animals being evaluated were born. For example dams born in 1945 made their lambing records in the years 1947 to 1950 inclusive. Accordingly, the average lamb production figures of all animals with this pattern of performance formed the basis of the averages incorporated in the index tables.

Correlation and regression analysis demonstrated that this modification produced little change in the genetic ranking of the animals. This is illustrated by the correlation coefficient of 0.077 which was obtained when only those animals with four consecutive lambing records were included in the analysis, the comparable coefficient for the index of Table 27 being 0.080. Further evidence of the equivalence of the index rankings was afforded by the correlations between the index values of the various tables derived. These were of the order of 0.97 - 0.99, even for the case of the two tables based on the most extreme lamb production averages.

These considerations suggest that the index values presented in Table 27 have sufficient adaptability, to allow their general use over quite a wide variety of flock conditions.

VII. DISCUSSION

The objectives and methods of sheep breeding must take account of the kind of husbandry that is possible, the environments in which the animals are required to live and the purposes for which they are kept. Despite the variation that exists in these characteristics, the prolificacy of ewes is an important factor controlling the level of financial returns in virtually all Romney flocks of this country. The importance of prolificacy over a wide range of husbandry conditions operating in the sheep industry of Great Britain, has recently been stressed by the Committee on Sheep Recording and Progeny Testing (Harris 1961), and by the Livestock Breeding Conference (1962) organised by the National Agricultural Advisory Service. It is interesting to note from these reports that many British farmers are far from satisfied with levels of lamb production which are far in excess of those obtained by Romney flocks in this country.

How then, may a breeder of New Zealand Romney sheep effect an improvement in the reproductive efficiency of his flock? Firstly, it is well established that much can be gained from the application of proven husbandry methods. Secondly, since the individual flock owner has to practise selection and culling if he has stock surplus to his requirements, this potential can also be directed to achieving an increase in the lambing abilities of his animals.

In order to avoid any sub-optimum productivity, it is logical to expect that the ideal method of selection should allow breeders to identify those animals to be retained prior to them being first mated, and that the most efficient method will be that which strikes a balance between the early recognition and the accurate assessment of desirable breeding values.

Aspects of the efficiency of various methods of within-flock selective breeding have been discussed in previous sections. From this work it may be concluded that direct selection procedures are capable of producing a response in the population, at least with respect to the improvement of lamb production in the short-term of a few generations. At the same time, however, it is evident that, the rate of genetic change on an annual basis will be very small, quite erratic, and that it will require the application of the breeder's entire selection potential. To pay much attention to other aspects of productivity is tantamount to abandoning the task of improving fertility by direct methods of selection. For this same reason, individual breeders must be quite convinced that this singularity of purpose will be rewarding in financial terms. They should also ensure that their level of husbandry is high enough to exploit the inherent fertility of their stock to the full.

The problem of which of the several procedures available will be embarked upon, in effect, largely reduces to deciding upon the amount of effort the breeder can afford to apply to the collection, interpretation and application of the necessary records upon which they are based. It is obvious that all of the methods discussed require that certain records be available, traditional methods of visual appraisal being entirely unsatisfactory.

As far as pedigree sheep breeders are concerned, the identification of animals allows the pertinent information to be relatively easily collected, and involves comparatively little in the way of additional work. In commercial flocks, however, the extent to which the various methods can be practised depends upon whether or not a practical method of identifying animals can be undertaken. Fortunately, the majority of methods considered do not require the permanent identification of individuals, but merely of classes of sheep which differ in their lamb production potential. As Rao (1963b) has pointed out, dry ewes may be relatively easily identified and allocated to separate mobs following lambing. The identification of birth rank classes is less easily undertaken, although under intensive shepherding conditions twin-born animals could be marked with coloured tags immediately following birth. Another possibility which exists under these conditions involves the "shedding" of ewes and their lambs shortly after lambing into comparable fertility groups, followed by the ear-marking and tagging of lambs according to their birth rank and the concurrent tagging of dams according to their lamb production. This method is at present being used by at least one Romney ram breeder in this country, who believes that the "shedding" is best undertaken when the lambs are 10-14 days old. His technique involves the gathering together of about six sets of twins and their dams, and quietly working them towards the gate and thence into the appropriate mob. He states that one man is capable of grouping from 200-300 ewes per day by this method (Parker pers. comm.). The method also allows preferential treatment to be given to the different fertility groups, and should therefore, be a useful aid to flock management.

In view of the slow response obtainable from direct selection procedures, together with the delay involved in obtaining information on the animals themselves and the work involved in obtaining information on their relatives, recent research has been concerned with the possibility that some indirect measures may be more profitably applied to breeding for lamb production. In particular, indirect criteria which allow an early assessment of animals are expected to be of considerable value. At present face-cover, body weight and the occurrence and number of oestrus cycles in ewe lambs are under investigation. In order to determine the usefulness of these techniques, information is required on the phenotypic and genetic relationships between each of the characters and lamb production, and also on their heritabilities. This allows the determination of the value of each item as an independent source of information, and whether their combined use is likely to be profitable. The available information on the phenotypic association between face-cover and lamb production is promising (Barton 1954, Coop 1956b, Inkster 1956, Cockrem et al. 1956, Cockrem 1958), although further research on its inheritance and its genetic association with lamb production seems desirable before accurate selection procedures can be specified with assurance. The outcome of further work on the inter-relationships of body weight and lamb oestrus with lamb production is awaited with interest, preliminary investigations appearing most encouraging (Ch'ang pers. comm.).

Crossbreeding is a further tool that has been used in livestock breeding for many years, and recent research on crossbreeding has done much to demonstrate the economic importance of lamb production even under the relatively more severe environments of this country. Although the advantages of a first cross ewe with respect to lamb production would seem to be of fairly widespread occurrence (Peren et al. 1951, Coop 1958, Clarke 1962), further information is needed to establish the role of selection in maintaining this level in subsequent generations. The vital question on the application of crossbreeding revolves around the ways in which it can be integrated into the breeding structure of the sheep industry. To this end detailed specification of purebred and crossbred performance under various environmental conditions is needed. The possible value of ~~three-breed~~ crosses also merits investigation.

It is important to emphasise that the fertility measure employed in this study is far from being a complete description of the ability of individuals, or of groups of individuals, to produce lambs. Rather it is a compound aspect of a complex series of events which was chosen for its ease of measurement and for the fact it is largely under the control of the female parent. Other aspects of the complete chain of events must also be considered before a complete understanding of the genetics of lamb production can even be attempted. The complexities involved in work of this nature are extremely well illustrated by the recent work that has been reported on the genetics of litter size in mice (Falconer 1960, Roberts 1960 and 1961, Bowman and Falconer 1960, Falconer and Roberts 1960).

Lamb production in turn, is only one aspect of overall productivity in New Zealand Romney sheep, net financial return being also influenced by the level and quality of wool production. Furthermore, it has been demonstrated that fleece weight shows a negative genetic relationship with lamb production in this breed (Ch'ang 1955). Thus if the breeder confines his attention to lamb production, he runs the risk of a probable deterioration in wool production, the maximisation of financial returns requiring that a balance be struck between the two characters. This further complicates the formulation of selection plans for sheep breeding and reduces the amount of progress that can be made in any one character (Hazel and Lush 1942).

Further complications to selective breeding arise with respect to the efficiency of animal production. Present day selection methods are all based on ranking the highest producing animals as the most desirable types, no account being taken of the possibility that the highest producers may not in fact be the most efficient. The concept of animal efficiency, which is no doubt, a useful one in determining the costs involved in producing a given increment of production, is by no means easy to define and is even more difficult to measure.

These complications to the genetic improvement of livestock in general, and to the improvement of lamb production in particular, indicate that a complete understanding of the factors involved is necessarily a goal for the future. Their solution is dependent upon basic research, intensive in application, but broad in conception, and embracing an active exchange of ideas and information between pure and applied scientists and practical husbandrymen. In the meantime, it is necessary for the practical breeder to rely upon methods of breed improvement which are now at his disposal.

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