THE INHERITANCE OF PRODUCTION CHARACTERS IN MERINO SHEEP

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TABLE OF CONTENTS

PART 1

PART 2

PART 3

SUMMARY

In 1951 a selection experiment was started with Merino sheep by the New South Wales Department of Agriculture at the Agricultural Research Station, Trangie. Flocks of approximately 100 mixed-age ewes and 5 rams were chosen from a large base population; selection being for high (Plus) or low (Minus) expression of one of the following; clean fleece weight, crimp frequency in the wool, body weight at weaning and the degree of skin fold development. In addition to these eight selection flocks, two control flocks of 100 ewes and 10 rams were formed from the same base population: the flocks were then closed and all replacements for the selection flocks were chosen for the character and in the direction appropriate for the particular flock. Selection of replacements in the control flocks was at ~~R~~random.

Over the period of 6 generations examined, 1951 to 1969, realised heritability, estimated from the divergence of Plus and Minus flocks, was in good agreement with heritability estimates obtained in the unselected Trangie population. In three of the four pairs of flocks, realised heritability declined with time (1, 4 or 6 generations of selection), and downward selection was generally more effective than upward selection. Problems introduced into such investigations by overlapping generations were discussed.

Information on the ewes in the selection and control flocks was used to estimate the scope for ewe selection within the Trangie population, as well as the effects of age of ewe and selection on ewe wastage and reproductive performance.

Wastage was lowest among ewes between first and second lambing (4.3 per cent) and increased to 25.5 per cent between sixth and seventh lambing, the last age group considered. Comparing the individual flocks, wastage was highest in the flock selected for high skin fold development, but otherwise wastage was little affected by selection. From least squares analyses it was concluded that ewe survival in the breeding flock was not influenced by her own type of birth, but it was altered by her lambing performance, with ewes having 1 lamb having a higher probability of surviving to the next or subsequent lambings than ewes producing 0 or 2 lambs.

Again from least squares analyses, it was found that age of ewe had a significant effect on reproductive performance, be it the number of ewes lambing, or the numbers of lambs either born or weaned. For all such characters, performance increased up to the fifth lambing when the ewes were six years of age, and then declined. Age of ewe had little effect on lamb survival to weaning, or on ewe lamb survival to 18 months of age.

Age of ewe effects on wastage and reproductive performance were considered together in assessing the consequences of altering the age structure of the flocks for total productivity.

The repeatability of ewe reproductive performance was examined and intra-class correlation estimates for the numbers of lambs born or weaned per ewe joined were similar (.13) when data on either the first five or ten lambings were considered. Higher values were generally obtained when the regression method of estimation was used. When individual pairs of lambings were considered, estimates obtained by either method were found to be significantly heterogeneous, with the repeatability declining as the time between the lambings being correlated increased. The effects of pooling records and of prior selection on repeatability estimates were investigated. Responses in current flock productivity to culling ewes without lambs at individual lambings are likely to be small due to the low repeatability of the character and the generally adverse effects of modifying flock structure.

Twin born ewes were found to give birth to and wean more lambs than single born ewes. Heritability of various measures of ewe reproductive performance was estimated by half-sib analysis of variance separately for each of the first five lambings. The heritability of both lambs born and lambs weaned per ewe joined increased from effectively zero at first lambing to a maximum at third lambing (.26 and .20 respectively), and then showed a variable pattern of decline. When records for a number of lambings were considered concurrently, the heritability at a particular lambing was lower for ewes that survived to a later lambing, than it was when all ewes were included in the analyses. This finding was discussed in relation to the differential probability of ewe survival in relation to their lambing performance. Heritability was estimated for the number of ewes lambing of those joined, and the number of lambing ewes with multiple births using methods appropriate for such Binomially distributed traits.

When the heritability estimates obtained separately for the individual lambings were used, it was found that for a flock of five age groups of ewes, more rapid response would be expected from preferentially selecting twin born ewes to enter the breeding flock, than from culling ewes already in the breeding flock on their own lambing record. The contribution that selecting rams on their dam's performance could make to such programmes was also considered.

Genetic correlations were calculated between the characters under selection at Trangie, fleece weight, crimps, weaning weight and skin fold, and reproductive performance at the first three lambings. These were then compared with the realised genetic correlations, calculated from the correlated responses in reproductive performance in the selection flocks. Possible reasons for the degree of dissimilarity between the two sets of estimates were considered.

INTRODUCTION

This Thesis is primarily a study of factors affecting ewe reproductive performance, and of the determinants of progress in selection programmes which might provide the basis of attempts to improve this trait in Merino sheep. The data utilised in this study have been drawn in the main from animals in selection flocks maintained by the New South Wales Department of Agriculture at their Research Station at Trangie. In view of the selection history of these flocks, the initial Part of the Thesis is concerned with the response which has been obtained to approximately six generations of selection. Apart from providing a description of the populations which are the subject of the subsequent analyses, the major concern here is in the measure of agreement between realised heritability and estimates of genetic variation in the Trangie population before the selection flocks were established. The study of reproductive performance occupies the central Part of the Thesis. Finally to link these two topics, the reproductive performance of the selection flocks will be compared to assess the extent of possible genetic correlations between reproductive performance and the characters subject to selection at Trangie.

Apart from the following section on the history and management of the selection flocks, which is relevant to all of the succeeding Sections, and not withstanding my attempts to integrate the various strands of this study, the topics themselves are somewhat disparate. Consequently the review of literature has been fragmented and presented in conjunction with the corresponding analyses, rather than as a single overall introduction to the Thesis.

PART 1

SECTION 1.1 DESCRIPTION OF THE TRANGIE FLOCKS AND THEIR MANAGEMENT

Since 1951 the New South Wales Department of Agriculture has maintained a selection experiment at the Agricultural Research Station, Trangie. In this experiment, flocks have been selected for either high or low expression of one of a number of characters, and suitable control flocks have also been maintained. The observations to be reported on these flocks were collected over the period 1951 to 1969.

Location and Environment

Trangie Agricultural Research Station is on the central western plains of New South Wales, and consists of approximately 10,000 acres of extremely flat country, lightly timbered with an open savannah type of forest. The soil varies from sandy loam to a heavy black alluvium formed from watercourses spreading out over the flat plain. There is very little natural drainage. In general these soils are extremely fertile and respond very rapidly to rainfall.

Average annual rainfall is approximately 18 inches per year, with a range from 8 to 47 inches. There is no definite seasonal incidence but there is a tendency for the summer rainfall to exceed that in the winter. However, the winter rainfall is the more valuable, partly because of higher evaporation losses in summer, and also because summer rain is often the result of thunderstorms and consequently it can be most variable in incidence.

Summer temperatures are high and recordings of more than

100°F are common from November to February. In winter, temperatures below freezing point and frosts are frequently recorded in June, July and August.

The Trangie flocks are grazed on natural pastures with occasional access to cereal stubble and dry-land lucerne. The natural pasture species have been described in detail by Biddiscombe, Cuthbertson and Hutchings (1954). The dominant species vary considerably according to season. In summer, various Stipa species, annual and perennial Chloris species and various ephemeals provide the bulk of the grazing. In winter, barley, grass (*Hordeum leporinum*), burr clovers (*Medicago* spp.) and some *Stipa* species are dominant. Winter pasture are generally of high quality, make rapid growth in the early spring and are killed off by high temperatures in late spring. The natural hay so produced provides useful feed in the summer. Becuase of extreme temperatures and evaporation, summer rains do not often produce much useful forage.

History of the Trangie Flock

One of the main objectives in establishing the Agricultural Research Station at Trangie was to develop a Merino sheep stud that would help improve the breed and provide sheep of good quality for sale at reasonable prices (Ballard, 1966). The stud, Flock No. 78 in the Australian Merino Flock Register, was founded in 1912 and transferred to Trangie in 1915. In its formation ewes were purchased from the medium-wool Peppin studs, "Cobran", "Bundemar" and "Weemabung", while rams were purchased from these three studs as well as from "Deniliquin Stud". More sheep were obtained from these studs for several years but, from 1920 onwards, no further ewe introductions were made to the flock. Between 1920 and 1943 a total of a further 13 rams were purchased, all from "Bundemar". This is a parent stud of the Peppin Merino strain (Registered Flock No. 11) so that on the classification of Short and Carter (1955), the stud at the Research Station would, by 1951, be termed a daughter stud of "Bundemar".

For many years the flock was managed as a commercial stud. Animals with obvious physical deformities or black wool would have been culled and any selection was for increased fleece weight while maintaining wool quality. Fleece weight in this instance was assessed visually, a procedure of variable but generally low accuracy (Morley, 1955b; Riches and Turner, 1955; Moule and Miller, 1963). For this reason, and also because of the general concern of breeders with characters not directly associated with production, it could reasonably be concluded that the amount of selection applied to production characters was not great (Morley, 1951, p. 38).

In 1943 Morley (1951 _et. seq._) commenced a systematic investigation of the flock at Trangie and especially of the extent to which it might be improved by selection. For this study he collected information on "second stud ewes", those ewes used to breed sale rams. The characters examined included fleece weight, crimp frequency in the wool (a measure of wool quality) and body weight. The information obtained on these characters was used as an aid in selection although the actual intensity of selection was slight (Morley, 1955a). Mating was usually at random although ewes with the best phenotype, based on clean fleece weight with some attention to freedom from skin folds, were mated to a small number of rams whose progeny had been of high performance (Morley, 1955a).

In 1951 pairs of closed single character selection flocks were established and the responses in these flocks between 1951 and 1969 is the subject of the first section of this thesis. Pairs in this context meant that one flock was selected for high expression of the character (Plus) and the other for low expression (Minus). The characters subjected to selection were clean fleece weight, crimp frequency, weaning weight and skin fold and the eight flocks so formed are as follows:

Fleece Plus - selected for high clean fleece weight
Fleece Minus - selected for low clean fleece weight
Crimps Plus - selected for high frequency of crimping in the wool
Crimps Minus - selected for low frequency of crimping in the wool
Weight Plus - selected for high body weight at weaning
Weight Minus - selected for low body weight at weaning
Folds Plus - selected for high degree of skin wrinkling
Folds Minus - selected for low degree of skin wrinkling

A detailed description of how these characters were measured and of the numbers of animals available for selection in 1951 will be given later. Each flock was initially of 80 ewes and in the following year the number was increased to 100, at which level it has remained. The ewes were selected from what will be termed the base population, second stud ewes, born between 1943 and 1950. Each flock of ewes was mated in 1951 to five 1½ year old rams. In the following year ewes born in the base population in 1950 and 1951 were added to some of the flocks and a further selection of rams was made from those born in 1950.

Thereafter, the flocks were closed. Ewe and ram replacements, bred in each flock, were selected only for the appropriate character, and then in the direction indicated by the name of the flock (Plus or Minus). Any animals with black wool or a crippling deformity were rejected.

As already stated, the first mating of these single character selection flocks was in 1951. From 1951 to 1961 the Folds and Weaning Weight groups were mated in the autumn while the Fleece and Crimps flocks were mated in the spring and between 1951 and 1961 these two groups of flocks were known respectively as the Autumn and Spring mated flocks. Corresponding to each group of selection flocks was a control population and these were correspondingly known as the Autumn and Spring mated Random flocks. The Random flocks were formed by choosing 80 ewes and 10 rams, at random, from the base population; in the following year the number of ewes in each was increased to 100. Both flocks were then closed and ewe and ram replacements have since been chosen at random subject to the same restrictions on black wool and physical deformity as applied in the selection flocks. In 1959, 1960 and 1961 five rams were exchanged reciprocally between the Random flocks to minimise inbreeding and random drift between them. From 1962 onwards the number of rams used in each of the Random flocks was increased to 25.

In 1962 the Spring mating was altered to April and the Autumn mating was advanced so that it took place in March. The groups of selection flocks and their appropriate controls have from this time been referred to as March or April mated flocks. For convenience when referring to either group of flocks or just to the Random flocks, the terms March or April mated will be used as a general term for the flocks over the entire period to be considered here, 1951 to 1969 (see Table 1.1.1).

Table 1.1.1

Flocks	Time of Mating		Termed
	1951-1961	1962-1969	1951-1969
Weight Plus	Autumn	March	March-mated flocks
Weight Minus			
Folds Plus			
Folds Minus			
Random			
	1951-1960	1962-1969	1951-1969
Fleece Plus	Spring	April	April-mated flocks
Fleece Minus			
Crimps Plus			
Crimps Minus			
Random			

Policy Regarding Disposal of Ewes and Rams

Between 1951 and 1961, ewes in the selection flocks were not disposed of at a stated age. Each ewe was inspected prior to mating and those considered to be incapable of rearing another lamb were culled. The main reasons for culling were emaciated body condition, faulty udders or teats, and broken mouths. From 1962 onwards a general policy of casting ewes at 6 years of age (after 5 possible lambings) was adopted. Several years elapsed before the policy became fully effective and subsequently it was occasionally relaxed if additional flock matings were required for some special purpose. After it was determined how many ewes were to be culled or cast for age, sufficient maiden (1½ years old) ewes were then selected to maintain flock size.

Rams were used once, at 1½ years of age, in all years other than 1954. In that year the rams used in 1953 were again mated in the March mated flocks as there was no Autumn mating in 1952. Older rams were also used in the Weight Plus and Minus flocks in 1968 and 1969 as these flocks had been mated to Border Leicester rams in 1966 and 1967.

Mating Routine

Two to three weeks prior to the commencement of mating, samples of semen were collected by electro-ejaculation from selected rams in both the single character selection flock and the Random flocks, and from a number of reserves in each. Those failing to produce semen showing rapid wave motion, even after three consecutive daily collections, were rejected in favour of replacement sires.

The following mating procedure was adopted for the selection flock for the years 1951 to 1961. Mating commenced with artificial insemination (A.I.) (Morrant and Dun, 1960). As five rams were mated with 80-100 ewes high sperm dose rates ($100\text{-}300 \times 10^6$) were used. Any collection showing poor motility was rejected. After three weeks of A.I., natural service was allowed for a similar period, joining one ram with 40-50 ewes. The rams chosen for paddock joining had been lightly used during A.I.

From 1962 onwards, the selection flocks were paddock joined for five weeks with one ram to 20 ewes. The rams were fitted with Sire-sine crayons and harness (Radford, Watson and Wood, 1960). Occasionally a ram was replaced if he was not seen to be mounting ewes or if return rates among the ewes appeared unusually high.

Both Random flocks have always been mated by the same method. In the period 1951 to 1961, A.I. was used for three weeks with semen being collected from eight rams. In the following three weeks of paddock joining, two previously unused rams were each joined with 40-50 ewes. From 1962 onwards, 20 out of the 25 rams selected in each flock were used in A.I. which again lasted for three weeks. In the following two weeks of paddock joinings, each flock was joined with five rams, with groups of one ram to 20 ewes in separate paddocks.

There were a number of exceptions to the routines listed above for the March mated flocks. There was no autumn mating in 1952 because of drought. Flooding in 1955 destroyed so much fencing that mating was changed to five weeks of artificial insemination, while in 1956 floods caused the cessation of mating after 17 days.

Lambing Routine

It is again convenient to consider the total period covered in two sections, 1951 to 1961 and 1962 to 1969.

From 1951 to 1961 all ewes in the March or April mated flocks were lambed together, away from all other lambing ewes on the Station. Lambing of each group of 400-500 ewes took place in two 130 acre paddocks. The ewes and their new born lambs were mustered into yards every 2 to 3 days so that lambs could be identified with their dams by observing suckling. This technique is known as 'mothering'. All other ewes were caught and turned up for a detailed inspection of the udder and perinium. On this evidence ewes were classed as having not produced a lamb ('dry'), or having lambed and then lost her lamb(s).

The major disadvantage of this lambing routine was that it did not enable the identification and recording of lambs that died soon after birth. For this reason, 5.9 per cent of all lambing ewes were recorded as having lost their lambs before mothering. It would also lead to an underestimate of the number of lambs produced by a ewe which still had at least one lamb alive at mothering. Because of the early death of their litter mates, lambs thus recorded as twins could have been born as triplets, while some lambs recorded as singles would certainly have been born as twins.

In 1962 the lambing routine was radically altered although again all of the March and April mated flocks were lambed together. The ewes were lambed in a series of small paddocks. Each day the ewes which had not lambed were separated ('drifted off') from those which had just lambed, and then moved to the next paddock. The ewes with lambs were left behind in small groups and the lambs were then tagged and weighed. Similarly small groups of ewes which had lambed in one of the previous few days were then inspected and all lambs accounted for. All dead lambs were subjected to post-mortem examination (McFarlane, 1961).

This system had a number of advantages over that previously employed. Lambing ewes were inspected during almost all the hours of daylight and assistance could be given more easily to any ewe having difficulty in lambing. In addition, greater confidence could be placed in the numbers of lambs attributed to a ewe, and only 1.2 per cent of lambing ewes were recorded as 'lambed and lost'.

The total number of ewe matings recorded over the period 1951 to 1969 was 17075, and these were obtained from a total of 4248 ewes. All of the ewes involved in these 17075 matings survived the succeeding months to the subsequent lambing. A summary of the outcome of these matings, especially as regards the numbers of ewes not lambing or falling into the 'lambed and lost' category is given in Table 1.1.2. There was a tendency for the proportion 'lambed and lost' ewes to be higher among ewes having a sixth or later lambing (seven years of age and older). However, this was due almost entirely to the small numbers of such ewes lambing between 1962 and 1969, when the level of 'lambed and lost' ewes was low. There was little evidence of any association between age of ewe and the incidence of 'lambed and lost' ewes for ewes lambing between 1951 and 1961.

Lamb Management

All lambs were identified with numbered ear-tags at mothering and from 1962 onwards they were also weighed. In 1951 and 1952, some ram lambs were castrated, but after 1952 all ram lambs were left entire. From 1951 to 1961 lambs were tail-docked at from 1 to 4 weeks of age and 'Mulesed' (to prevent blowfly strike) at weaning. Since 1962, both of these operations were carried out when the lambs were

Table 1.1.2

Summary of the number of lambings where the ewe was recorded as having 'lambed and lost'

Period	Number of mating records	Number 'dry'	Number of 'lambed and lost' records	Lambed and lost		
				as % of all matings	as % of all ewes lambing	as % of all ewes without lambs
All years	17075	4210	716	4.2	5.9	14.5
1951-1961	9347	2261	650	7.0	10.1	22.3
1962-1969	7728	1957	56	0.7	1.2	2.8
All ewes - according to age						
2 year old ewes	3458	1025	124	3.6	5.4	10.8
3 year old ewes	3360	829	116	3.5	4.8	12.3
4 year old ewes	3198	654	124	3.9	5.1	15.9
5 year old ewes	2803	692	122	4.4	6.1	15.0
6 year old ewes	2249	489	96	4.3	5.8	16.4
7 year old ewes	1023	223	76	7.4	10.5	25.4
8 year old ewes	526	168	31	5.9	9.5	15.6
9 year old ewes	304	76	27	8.9	13.4	26.2
10 year old and older ewes	154	54	7	4.5	7.3	11.5

from 4 to 7 days of age, and, within another two days, the lambs and their dams were removed from the drift paddocks.

During the years to be discussed in this Thesis, 1951 to 1969, triplet lambs were only rarely reared as such, usually at least one member of the set was fostered.

The average age of lambs at weaning ranged from 60 to 160 days. In general lambs were weaned later in the early years of the observation. At weaning the lambs were weighed and then shorn. After shearing they were fold scored and then separated according to sex. As the characters selected in the March-mated selection flocks were measured at weaning, all rams not required as prospective sires were disposed of at this time. The remaining rams in the March-mated flocks were thereafter run together and managed as one flock, as were the April-mated rams and both the March and April mated ewe weaners.

Ewes and rams were shorn when they were between 16 and 24 months of age; after shearing they were weighed. Since 1951 shearing has almost invariably been when the sheep were 16 to 17 months of age and carried 12 months' wool. Selection of replacements for the Fleece and Crimps selection flocks was based on performance at this ~~lambing~~ shearing.

General Management

Ewes in the breeding portion of the flocks were shorn each year in May. At all times, all ewes in either the March or April mated flocks were run together and managed identically. The management was such as to keep all sheep in good health. In fact, the only disease problem with a major influence on management is blowfly strike in the spring and summer due to the activity of *Lucilia cuprina*. This is controlled by "Mulesing", (Belschner, 1956; Dun and Donelly, 1965), shearing of weaners, crutching and wigging mature ewes in January and by jetting with insecticide whenever environmental conditions are conducive to strikes.

Internal parasites are rare although *Nematodirus*, the thin-necked intestinal worm, has occasionally led to the death or ill-thrift of weaners. Young sheep are routinely drenched with an anthelmintic as a control measure.

SECTION 1.2 RESPONSE TO SELECTION IN SHEEP POPULATIONS - A REVIEW

Selection experiments have been carried out for a variety of characters in a number of laboratory species, principally Drosophila, Tribolium and mice, and the results reviewed by, for example, Kojima and Kelleher (1963) and Roberts (1965). In addition a small number of studies have been conducted using domestic livestock and those dealing with sheep will be reviewed here.

In the late 1940s and early 1950s a number of workers independently established selection flocks with, it would appear, the following major aims:

(i) Demonstration of quantitative genetic principles

(ii) Testing for possible departures from prediction, and

(iii) Estimation of genetic parameters, especially heritability.

(Morley, 1955; Purser, 1966; Turner, Dolling and Kennedy, 1968). Because of their objectives, the characters chosen for selection were not always directly associated with production or, if they were, selection was usually for one character at a time, and not for the improvement of overall productivity or economic merit. Simultaneous selection for a number of traits (e.g. Turner, Dolling and Kennedy, 1968) or where selection is for various measures of the same character, as in the high fertility flock of Turner <u>et</u>. <u>al</u>. (1962), are rather more suited to evaluating the consequences of commercial selection practices than to the estimation of realized genetic parameters.

Direct response to selection is usually expressed in the form of the realized heritability, calculated as the ratio of accumulated response to total accumulated selection differential. Selection flocks have been of relatively recent origin. Over perhaps a maximum of five or six generations of selection, the agreement between realized heritability and estimates of genetic variation in the base population or a control has generally been quite good (Osman and Bradford, 1965; Pattie, 1965a; Purser, 1966; Robards and Pattie, 1967). Where upward and downward selection lines have been maintained, responses have not always been symmetric (Robards and Pattie, *loc. cit.*). The maintenance of such pairs of lines would appear to be justified on the grounds of an adequate test of genetic prediction theory; usually commercial interest is in the line selected in the direction likely to lead to increased productivity or economic returns.

In view of the scarcity of information on short term responses to selection in sheep, it is perhaps useful to briefly touch on comparable information in laboratory species. In general, for responses over say the first five generations of selection, the agreement between estimated and realized heritability has been quite good (for example, Clayton, Morris and Robertson, 1957; Martin and Bell, 1960) although serious discrepancies have also been observed (Sheldon, 1963; Nordskog, Festing and Verghese, 1967). Sheldon (1963) in fact doubted the value of estimates of heritability to predict changes even in the early generations. In addition, where replicate selection lines have been maintained, considerable variation among them has been reported (see for instance Clayton, Morris and Robertson, 1957).

It is in connection with such between replicate variation that the recent work of Hill (1971a, 1972a,b) on drift variances in selection experiments is of particular interest. He has pointed out that the standard error of the regression of cumulative response on cumulative selection differential, can seriously underestimate the standard error of the realized heritability as the generation means used in such calculations are not independent. The expected variation between replicates is also underestimated if drift resulting from the finite size of the selected populations is ignored. In assessing the measure of agreement between heritability estimates and the realized heritability from a selection experiment, the complication of genetic drift would have to be considered, although its importance would be greater in long term experiments than in the five or six generations of selection applied in the sheep studies mentioned above.

SECTION 1.3 RESPONSE TO SELECTION FOR PRODUCTION CHARACTERS IN THE TRANGIE SELECTION FLOCKS

1. Characters under selection and their measurement

(a) Clean fleece weight

This is the weight of clean scoured wool fibre produced at the hogget shearing, when the rams and ewes were between 16 and 24 months of age and carried 12 months' wool growth. In practice clean fleece weight is estimated as the product of greasy fleece weight, recorded to the nearest tenth of a pound in the shearing shed, and the yield of clean scoured wool as estimated for a mid-side sample of the fleece. Yield was estimated to the nearest per cent after the clean scoured sample had been conditioned at 16 per cent moisture, and clean fleece weight was then calculated to the nearest tenth of a pound.

(b) Crimp frequency

This is the number of crimps per inch in the fleece at the same hogget shearing, and is recorded as the mean of three measurements on staples in the mid-side sample. A flat polygonal disc, with known numbers of serrations per inch on each side, was used to measure staples with crimp frequencies from 5 to 16 per inch. Frequencies outside this range were counted against a ruler.

(c) Weaning weight

This is the weight of the lamb at weaning, measured to the nearest pound, and adjusted for the age of the lamb. Up until

1962, the age adjustment was made by multiplying the ratio of weaning weight to age at weaning by the average age at weaning for all lambs born in that year. From 1962 onwards birth weights were available and the age correction was applied to liveweight gain between birth and weaning.

No corrections were made for type of birth until 1959. Then the difference between single and twin born lambs was calculated separately for each sex among lambs in the March Random flock. This difference, expressed as a percentage of the weight of twin lambs, was then used as a multiplicative correction to twin weights in the Weaning Weight selection flocks. The twin correction varied between 3 to 22 per cent.

(d) Skin fold score

This is the degree of skin wrinkling or body development (Dun, 1964) for which Merino sheep are notable. Scores were allocated using the photographic standards developed by Carter (1943). For animals in the base population, a score ranging from 1 (absence of fold) to 9 was given for fold development in the breech region and selection was based on these scores. From 1951 to 1961 a similar range of scores was used to assess fold development at each of three sites, neck, side and breech, to give a range of possible scores of from 3 to 27. After 1961 lambs were Mulesed before weaning so that only neck and side scores were available, and so the range of possible scores was from 2 to 18. Since 1951, all lambs have been scored at weaning.

Skin fold was scored by the same technician from 1955 to 19~~5~~69; several scorers contributed to the earlier data.

2. Phenotypic and genetic parameters for characters under selection in the Trangie population

Means, variances and coefficients of variation for crimp frequency, fleece weight and breech score in the Trangie base population were presented by Morley (1951), while Pattie (1965a) gave corresponding values for age corrected weaning weights. All four characters showed considerable variation, and average coefficients of variation in these two previous studies were for crimp frequency, 20 per cent, clean fleece weight, 16 per cent, breech fold score, 36 per cent and weaning weight, 12 per cent.

Morley (1951, 1955a) and Pattie (1965a) also estimated the heritability of these four characters. The offspring-parent estimates for clean fleece weight, crimp frequency and breech fold score, obtained by Morley (1955a) were respectively .47, .47 and .50. The heritability of age and type of birth corrected weaning weight was .19 as estimated by half-sib correlation and .30 by offspring-parent regression (Pattie, 1965a). The discrepancy between these estimates was attributed by Pattie to genetically determined maternal effects, a suggestion supported by his studies on milk production of ewes in the Weaning Weight Plus and Minus flocks and on the effects of crossing the two flocks on lamb growth (Pattie and Trimmer, 1964; Pattie, 1965b).

These estimates for the four characters in the Trangie population are similar to those obtained for other Merino flocks (see Brown and Turner, 1968 for review).

Estimates of response to selection and of realised heritability have already been presented for the Trangie Weaning Weight and Crimp frequency selection flocks for respectively the first four and five generations of selection (Pattie, 1965a; Robards and Pattie, 1967). In general the realised heritability estimates (Table 1.3.1) were in quite good agreement with estimates given above, although response in the Crimps Minus flock was not linear.

Table 1.3.1

Realised heritability estimates for age corrected Weaning Weight and Crimp Frequency

	Character under selection	
	Weaning Weight (years 1952 to 1965)	Crimp Frequency (years 1951 to 1961)
Divergence between:		
Plus and Minus flocks		
Rams	0.19	0.29[†]
Ewes	0.31	0.31[†]
Plus flock v. Random		
Rams	0.18	0.38
Ewes	0.33	0.46
Minus flock v. Random		
Rams	0.23	0.13[†]
Ewes	0.22	0.28[†]

[†] These figures were not in fact presented by Robards and Pattie but have been calculated for the same period (1952-1965) using the same method of estimation.

Over the entire period of selection to be considered here, covering both the base population and selection flocks, the measure of fold score and weaning weight, used as the criterion of selection, has varied. As already mentioned, fold score has been successively breech score, a combined score for neck, side and breech, and then a total score for neck and side. Similarly, weaning weights have been adjusted for age by different methods, and type of birth corrections have not always been applied. In this Thesis it will be assumed that in each case, selection has been for different measures of what is genetically the same character. In an attempt to justify this position estimates of the heritability of all of these measurements of both fold score and weaning weight and of the correlations between these measures, have been obtained for data on ewes in the two Random flocks, and in the Fleece and Crimps selection flocks. Data from these latter flocks have been included to increase the amount of information available for analysis, without the danger of producing seriously biased estimates (see Morley, 1951; Pattie, 1965b).

Estimates of the heritability of these three measures of skin fold were similar, and the genetic correlations between them high (see Table 1.3.1). The situation regarding weaning weight is perhaps not so convincing. For those weights in which the age adjustment was applied to weaning weight itself, the heritability of age corrected weaning weight with and without type of birth corrections were respectively .16 (standard error = .040) and .05 (.012) with a genetic correlation between them of 1.096 (.090). When the age adjustment was applied to gain between birth and weaning, the data were necessarily restricted to animals born between 1962 and 1969.

In this analysis estimates of heritability were low and not always positive, so it is not clear to what extent the assumptions stated above hold.

Table 1.3.2

The heritability of and genetic correlation between different measures of skin fold score: Heritability estimates on diagonal, genetic correlations below diagonal with their standard errors

	Fold Score		
	Neck	Neck + Side	Neck + Side + Breech
Neck	.62 (.111)		
Neck + Side	.90 (.047)	.65 (.112)	
Neck + Side + Breech	.96 (.040)	.99 (.031)	.66 (.113)

3. Formation of the Selection Flocks

The two sets of selection flocks, March and April mated, were drawn from the same pool of approximately 1400 ewes, born between 1944 and 1949, although only ewes born in 1947 and later years were included in the April mated groups. In addition, a further 700 ewes born in 1950 and 1951 were available for inclusion in the April-mated flocks at either the first (1951) or second (1952) mating.

For the March-mated flocks, the same age groups were considered as a source of ewes for all flocks, both selection and Random. On the other hand, ewes born prior to 1947 were included in the April Random flock, but not in the April-mated selection flocks, so that the selection flock and the control were not drawn from exactly the same base population. However, as the numerical importance of these ewes born prior to 1947 was small, only 14 of the 80 ewes mated in 1951, and as this was the only year in which they were mated in the Random flock, it will be assumed that within both sets of flocks, both the selection and Random flocks were drawn from the same base population.

Rams for the March mated flock were chosen from 146 born in 1949 (Pattie, 1965a), and were only used once, at the 1951 mating. Rams from the base population were mated twice in the April mated flocks, 1951 and 1952. In 1951, the choice was made from this same group of 146 rams born in 1949. For the 1952 mating, the selection was from a similar number born in 1950 (Robards and Pattie, 1967).

Before any selections were made, the range and distribution was established for each of the four characters, within each drop and sex. For the ewes, the numbers to be included from each drop was determined from the numerical importance of that drop. The flocks were not established in any particular order. If a ewe qualified for inclusion in more than one flock, say the Crimps Plus and Fleece Minus flocks, she was allocated to one or the other alternatively. Rams were used in all flocks for which they qualified.

From the figures presented in Appendix A, Tables A1 to A4, it can be seen that in virtually all age groups, selection was in the direction intended, and that approximately equal numbers of ewes were included in all of either the March or April selection flocks. While a larger number of ewes were available for this initial selection, selection pressure was considerably higher among the rams.

Information was not available on the performance of all ewes, especially those born before 1947. For these animals, a selection differential of zero has been assumed, implying that the allocation to the selection flocks was at random. To the extent that this was not true (see Pattie, 1965a), selection differentials would be underestimated in the March selection flocks. However, because of the small number of such ewes, and the fact that full information was available on all rams used, the effect would be slight.

4. Selection after the formation of the flocks

Numbers of hogget rams and ewes available for selection and of those actually chosen for inclusion in the selection flocks are given in Tables A5 to A12 of Appendix A, along with estimates of selection pressure applied in individual years. In a number of instances, selection was not in the direction indicated by the designation of the flock; this was usually due to the prior selection of ewes for inclusion in nutritional experiments. Selection pressure in the Weaning Weight selection flocks (Tables A9 and A10) has been calculated from age and type of birth corrected weaning weights, even though type of birth corrections were not used until 1959.

The information included in these Tables is summarised in Table 1.3.3, in which it can be seen that lower proportions of males were selected and consequently, that the selection pressure applied was considerably higher among males than among females. The average deviation of the selected males from the flock mean, relative to the corresponding deviation among females, ranged from 1.7 : 1 in the Crimps Minus flock up to 5.3 : 1 in the Weaning Weight Minus flock.

Table 1.3.3

Average proportions of male and female replacements chosen in the selection flocks and corresponding estimates of selection pressure applied

Flock	Proportion selected as replacements (%)		Selection pressure in units of measurement	
	Rams	Ewes	Rams	Ewes
Fleece Plus	18.8	48.2	1.33 lb.	0.42 lb.
Fleece Minus	16.7	46.6	-1.44 lb.	-0.52 lb.
Crimps Plus	17.2	61.5	2.68 cpi	1.01 cpi
Crimps Minus	18.2	56.5	-1.88 cpi	-1.10 cpi
Weaning Wt. Plus	17.8	59.9	9.48 lb.	3.02 lb.
Weaning Wt. Minus	17.9	55.4	-8.62 lb.	-1.62 lb.
Folds Plus	31.4	78.7	4.33 units	0.89 units
Folds Minus	15.7	53.1	-1.91 units	-0.94 units

5. Number of generations of selection

Although rams were generally replaced each year, ewes remained in the flock for a number of years, so that a situation of overlapping generations was produced. In order to estimate the number of generations of selection, a separate score was calculated for each individual. The generation score for all sheep in the base population was taken as zero. Individual generation scores were calculated using the formula:

$$G_I = 1 + \frac{1}{2} (G_S + G_D)$$

where G_I is the generation score of the individual lamb, and $G_S + G_D$ the score of its sire and dam respectively. The average generation score of all lambs born in any year was called the generation score of that drop.

By 1961 a total of approximately 4 generations of selection had been achieved, and by 1969, approximately six generations.

6. Calculation of Selection Differentials

Individual cumulated selection differentials were calculated in much the same way as were the generation scores. This was done in three stages. Firstly, an individual selection differential was calculated as the individual's deviation from the mean for all animals of the same drop and selection flock. For foundation stock, the mean of the appropriate base population drop was used. Secondly, an individual accumulated selection differential was obtained by adding the individual's selection differential to the average of the individual cumulated selection differentials of its parents. This latter was zero for sheep in the base flock. Finally, the flock cumulative selection differential was calculated as the average of the individual accumulated selection differentials of all parents producing offspring in the flock in any particular year.

Pattie (1965a) attempted to scale all deviations so as to allow for the considerable between year variation in performance. To do this, he divided each individual selection differential by the mean for the Random flock in that year. Young (cited by Robards and Pattie, 1967) suggested that the standard deviation was a more generally reliable scaling factor, as the mean was strictly correct only when environmental effects were multiplicative, i.e. when the yearly estimates of the mean and standard deviation in the Random flock had a correlation of +1. Both the mean and the standard deviation have been used to scale individual selection differentials in the subsequent analyses. In addition, selection differentials have also been calculated using the actual individual deviations.

7. Response to Selection and Realised Heritability estimates

In each year cumulated responses to selection were calculated as the difference in performance between the selection flock and the Random flock. As with the selection differentials, response was expressed as the actual deviation from the Random flock, and also as a percentage of both the mean or standard deviation of the Random flock performance in that year.

Realised heritability was calculated as the regression of cumulated response on cumulated selection differential (Falconer, 1960). Separate estimates were obtained for both sexes for the deviation of each selection flock from its corresponding control and for the divergence between each pair of selection flocks. In these latter calculations, cumulative selection differentials and response were obtained by adding the values for each pair of selection flocks.

Realised heritability was calculated after one, four (1961) and six (1969) generations of selection.

8. Drift Variances

The standard errors of the realised heritability estimates have been modified to allow for the contribution of random genetic drift. The appropriate formulae for divergent selection and for unidirectional selection with a control population have been given by Hill (1972a,b). For divergent selection with heritability calculated as the regression of cumulative response on cumulative selection differential, and with the regression passing through the origin, the sampling variance of the realised heritability coefficient (V_b) is given by:

$$V_b = \frac{6}{s^2 t\,(t+1)\,(2t+1)} \left[\frac{2t^2+2t+1}{5}\sigma_d^2 + \sigma_e^2 + \frac{3t\,(t+1)}{2\,(2t+1)} h^2\sigma_e^2 \right]$$

where t = the number of generations of selection

σ_d^2 = the drift variance which accumulates with time

σ_e^2 = the non-cumulative error due to errors in predicting performance with a finite number of individuals, and

s = the selection differential per generation

The drift variance (σ^2_d) has been taken to equal:

$$2\,\sigma^2(h^2\,(1 - h^2)/N_e + h^4/M_e)$$

where h^2 = realised heritability

σ^2 = the phenotypic variance for the character

N_e = the effective population size per generation, and

M_e = the weighted average number of animals measured per generation.

The term $2\,\sigma^2 h^4/M_e$ does not apply where selection is for one generation. The non-cumulative error (σ^2_e) has been taken to equal $2\,\sigma^2(1 - \frac{1}{2}h^4)/M_e$. The terms N_e and M_e refer to the average numbers in the two selection lines.

The formula for the standard error of the realised heritability estimate for unidirectional selection with a control is:

$$V_b = \frac{6}{s^2 t\,(t + 1)\,(2t + 1)} \left(\frac{2t^2 + 2t + 1}{5}\;\sigma^2_d + \sigma^2_e \right)$$

where here $\sigma^2_{\cancel{d}e} = \sigma^2(1 - h^2)/\overset{M_S}{\cancel{M_e}} + \sigma^2/M_C$ and

$$\sigma^2_d = \sigma^2 h^2\,(1 - h^2)/N_S + h^2\,\sigma^2/\cancel{N_S}N_C$$

where N_C and N_S refer to the effective population size per generation, and M_C and M_S to the numbers of animals measured in the control and selected flock. Again, the formula for V_b is for a regression coefficient passing through the origin.

The general assumptions implicit in the use of such formulae have been discussed by Hill (1971a), but a number of additional assumptions are necessary for their application to these sheep flocks. The formulae refer to populations with discrete generations, so the realised heritability estimates refer to sheep flocks with 1, 4 or 6 discrete generations of selection. Effective population size (N_e and N_c) has been calculated from the numbers of animals entering the breeding flock per year, and such figures were then pooled to obtain an average number per generation. The same was done for the numbers of animals measured per generation (M_e and M_c). In calculating the effective size of a population, no account has been taken of the variation in family contributions to the following generation (Latter, 1959). Throughout selection differentials have been assumed to be constant per generation.

Rams from the Random flocks were exchanged in 1959, 1960 and 1961. Effective population size in the Random flocks has been calculated as the inverse of twice the increase in the inbreeding coefficient from the start of the experiment and the completion of 6 generations of selection. The agreement between N_e estimates obtained in this way for the selection flocks and from the numbers of animals entering the breeding flock per generation were felt to be sufficiently good to justify the use of the inbreeding coefficient approach for the Random flocks (see Table 1.3.4).

Table 1.3.4

Effective population size (N_e) and the number of animals measured (M_e) per generation in the Selection and Random flocks

Numbers refer to period of six generations of selection

Flock	N_e Estimated from number of animals mated	N_e Estimated from inbreeding coefficients	M_e
Fleece Plus	44	65	160
Fleece Minus	45	42	182
Crimps Plus	47	50	181
Crimps Minus	47	49	163
April Random	-	132	164
Weaning Weight Plus	36	43	186
Weaning Weight Minus	36	50	189
Folds Plus	38	33	118
Folds Minus	39	42	193
March Random	-	105	211

One final complication encountered was in comparing the standard errors of the regression coefficient and of the realised heritability. The former was calculated for either 10 (4 generations) or 17 or 18 (6 generations) yearly estimates of the cumulative response and selection differential, while the latter was estimated as if for 4 or 6 generation values. A direct estimate of the contribution of drift to standard errors in such experiments has been attempted from the formulae given by Hill (1972a,b) for the expected standard error of a regression coefficient, calculated for 1, 4 or 6 generations of selection.

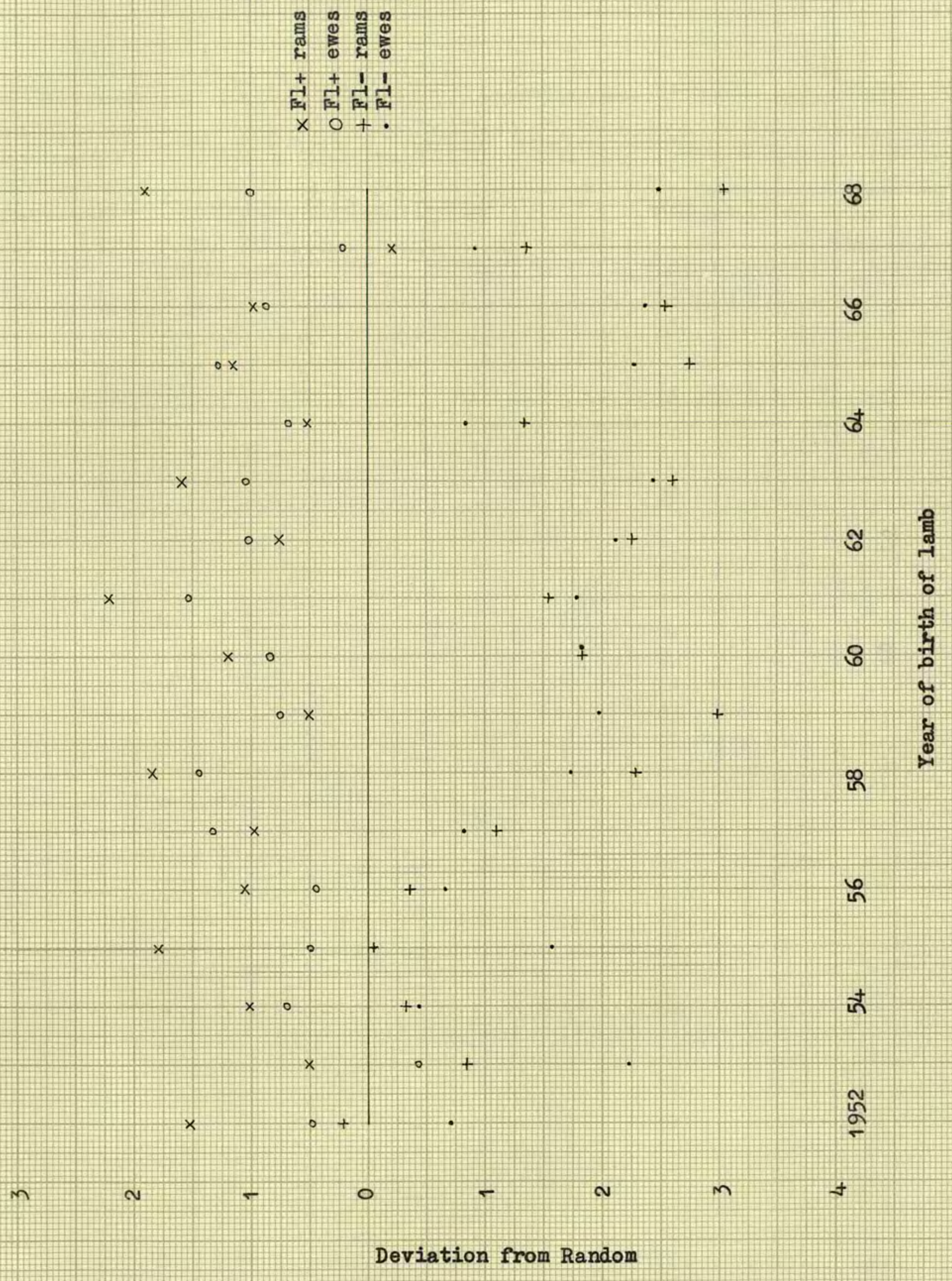
Results

Response to selection for clean fleece weight

A summary of fleece weight information on the Random flock is given in Tables A13 and A14. Over the period 1953 to 1969 (drops 1952 to 1968), average fleece weight declined slightly in both sexes, the pooled estimate of change was -.098 lb. per year. The correlation between yearly means and standard deviations, again pooled over sexes, was .75, indicating that environmental (year) effects were not completely multiplicative in their action (r = 1). When expressed as a coefficient of variation, calculated as the ratio of the standard deviation of year means to the average of the means for all years, between year variation was 31 per cent, considerably greater than the pooled within year estimates.

Fleece weights for the Fleece Plus and Minus flocks are given in Tables A15 to A18, while deviations from the Random flock are

Figure 1.3.1 **Response to selection for clean fleece weight**



presented in Figure 1.3.1. A total of 5.5 lb. of accumulated selection pressure was applied in the Fleece Plus flock, and 6.8 lb. in the Fleece Minus flock. Averaged over the two sexes, the maximum deviation of the Fleece Plus flock from the Random was 2.0 phenotypic standard deviations, or for a heritability of 40 per cent, approximately 5 genetic standard deviations. Corresponding average deviations of the Fleece Minus flock from the Control were 3.0 and 7.5 phenotypic and genetic standard deviations respectively. While the deviation of the Fleece Minus flock was continuous with time, the Fleece Plus flock showed little response from 1958 onwards and the greatest deviation from the Control flock was in 1961.

Selection for fleece weight had only a very slight effect on standard deviation and skewness of the distributions.

Table 1.3.5

Estimates of variation and skewness for fleece weight in the Fleece selection and Random flocks, averaged over the final 10 years of observations

	Random		Fleece Plus		Fleece Minus	
	Rams	Ewes	Rams	Ewes	Rams	Ewes
Standard deviation	1.11	.86	1.25	.93	1.07	.86
Coefficient of variation	16.3	14.4	15.8	13.4	23.2	21.2
Skewness	.08	.10	-.27	.03	.27	.27

Realised heritability estimates, obtained by regressing cumulative response on cumulative selection differential over six generations of selection, are given in Table 1.3.6. There was no consistent pattern in the magnitude of estimates according to the method by which selection differentials and responses were calculated. On average, the standard errors of estimates were higher where all deviations were left in absolute units. Pooled over sexes, the rate of response was higher for the Fleece Minus than for the Fleece Plus flock.

The estimates of realised heritability following 1, 4 and 6 generations of selection were all in quite good agreement with Morley's estimate of heritability for the Trangie base population (Table 1.3.7). In general, the rate of response declined with time. The standard error of the realised heritability estimate was always higher than the standard error of the regression coefficient, also calculated as if for discrete generations (column 4). The ratio increased from an average of 1.2 for 1 generation to 3.1 for 6 generations of selection.

Table 1.3.6

The realised heritability of clean fleece weight: Estimates of regression coefficients and their standard errors for animals born between 1952 and 1968

Comparison	Method of calculating selection differentials and response: Absolute units	Deviations expressed as percentage of mean in Random flock	Deviations expressed as percentage of standard deviation in Random flock
Fleece Plus v. Fleece Minus			
Rams	.37 (.035)	.37 (.022)	.33 (.021)
Ewes	.30 (.032)	.33 (.027)	.35 (.035)
Pooled	.33 (.035)	.35 (.025)	.34 (.030)
Fleece Plus v. Random			
Rams	.37 (.049)	.41 (.043)	.34 (.039)
Ewes	.24 (.033)	.29 (.037)	.29 (.039)
Pooled	.30 (.045)	.35 (.043)	.31 (.039)
Fleece Minus v. Random			
Rams	.40 (.035)	.40 (.017)	.38 (.020)
Ewes	.37 (.036)	.38 (.026)	.44 (.037)
Pooled	.39 (.036)	.39 (.023)	.41 (.031)
Average of standard errors	(.037)	(.029)	(.032)

Table 1.3.7

Estimates of the realised heritability of clean fleece weight:

Estimates pooled over sexes

	Realised heritability	Standard error of regression[1]	Standard error of regression[2]	Standard error of realised heritability
Divergent selection				
1 generation(s) of selection	.51	-	.057	.074
4 " "	.48	.035	.015	.039
6 " "	.33	.035	.008	.025
Fleece Plus v. Random				
1 generation(s) of selection	.49	-	.177	.194
4 " "	.50	.063	.028	.071
6 " "	.30	.045	.015	.043
Fleece Minus v. Random				
1 generation(s) of selection	.53	-	.168	.184
4 " "	.47	.057	.025	.064
6 " "	.39	.036	.012	.041
Heritability estimate for Trangie population (Morley, 1955)	.47			

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[1] Calculated from yearly estimates of the cumulative response and selection differential

[2] Estimated for 1, 4 or 6 discrete generations of selection.

Response to selection for crimp frequency

Crimp frequency results for the April Random flock are summarised in Tables A19 and A20. Information was not available on individual rams and the information presented in Table A19 has been taken from Robards and Pattie (1967). In both sets of data examined, drops 1952 to 1968 and 1952 to 1965, crimp frequency in the Random flock declined, by an average of .046 crimps per inch per year. The correlation between means and standard deviations was .32 and the between year coefficient of variation 7.3 per cent, considerably less than the pooled within year estimates.

A total cumulative selection differential of 10.8 crimps was applied in the Crimps Plus flock, and 8.9 crimps in the Crimps Minus flock. Averaged over the two sexes, maximum deviations from the Random flock were 2.8 phenotypic standard deviations in the Crimps Plus flock and 2.0 standard deviations in the Crimps Minus flock (see Tables A21 - A24, Figure 1.3.2), and the maximum absolute deviations from the Random flock occurred after 1963.

Selection for increased crimp number increased the standard deviation, while selection for low crimp number reduced the standard deviation (Table 1.3.8). Changes in the coefficient of variation for crimp frequency ~~was~~ were in the opposite direction. In addition to altering measures of variation, the distribution of crimp frequency was skewed to the left (negative values) in the Crimps Plus flock, and to the right in the Crimps Minus flock.

Figure 1.3.2 Response to selection for crimp frequency, expressed as responses to selection, expressed as deviations from the Random flock

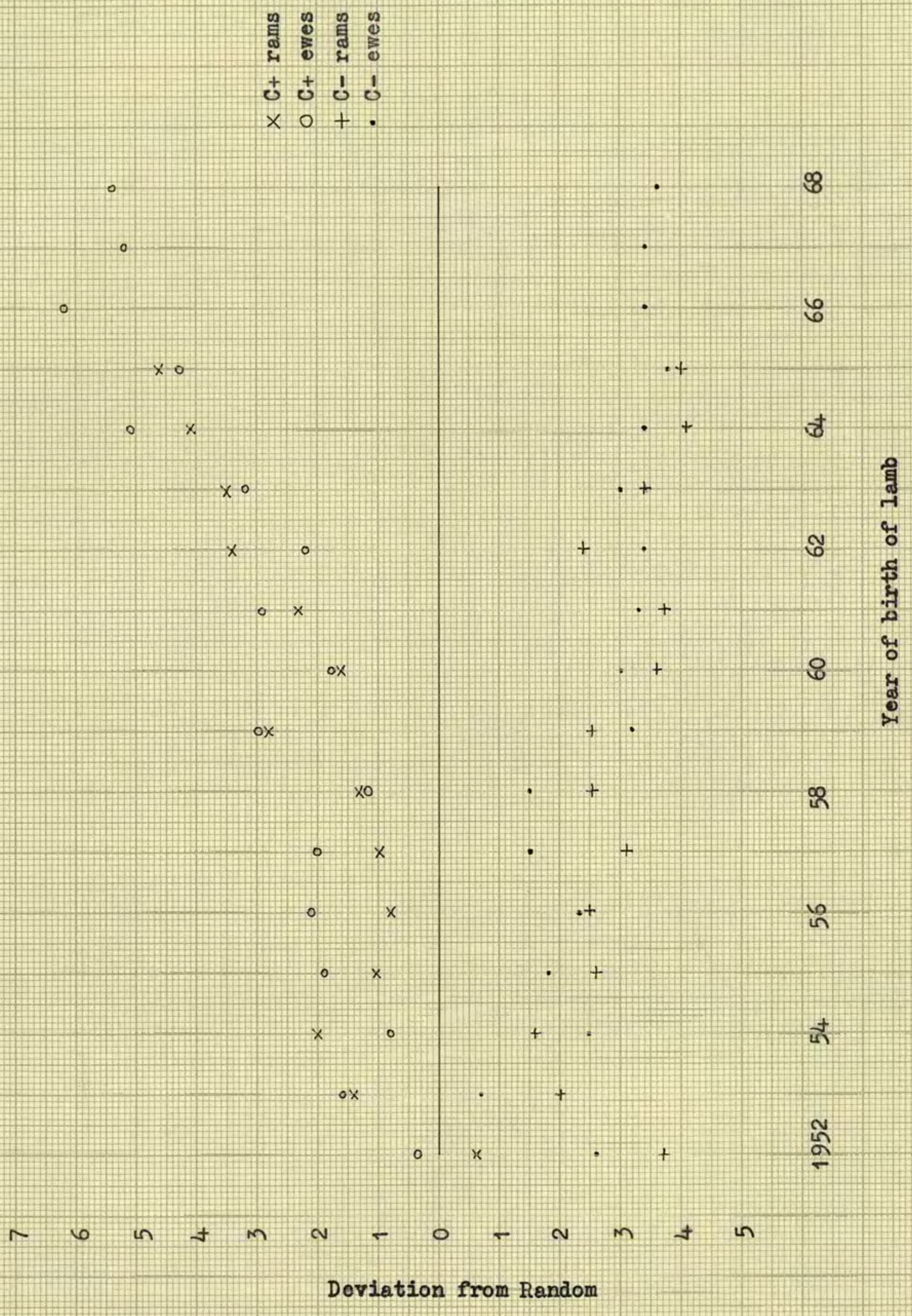


Table 1.3.8

Estimates of variation and skewness for crimp frequency in the Crimps selection and Random flocks, averaged over the final 10 years of observations

	Random		Crimps Plus		Crimps Minus	
	Rams[‡]	Ewes	Rams	Ewes	Rams	Ewes
Standard deviation	2.21	1.76	2.13	2.09	1.67	1.67
Coefficient of variation	20.9	16.9	15.5	14.7	23.2	23.4
Skewness	-	0.31	-.53	-.50	.83	0.80

[‡] Information on variation for final 8 years of observations.

As with the Fleece selection flocks, there was no consistent pattern in the relative magnitude of estimates on the basis of the method used to calculate selection differentials and responses (Table 1.3.9). For the Crimps flocks, the average standard error of the regression coefficients was actually slightly lower when deviations were left in absolute units.

The realised heritability estimates for divergent selection and for the Crimps Minus v. Random comparison declined with time but after 6 generations of selection, the realised heritability estimates for all three comparisons were in good agreement with Morley's estimate for the Trangie population (Table 1.3.10). Response in the Crimps Minus flock were greater than in the Crimps Plus flock, especially after 1 and 4 generations of selection.

As with the Fleece selection flocks, the standard error of the realised heritability estimates were higher than the corresponding error for the regression coefficient; here the ratio ranged from an average of 1.1 after 1 generation of selection to 3.4 after 6 generations.

Table 1.3.9

The realised heritability of crimp frequency: Estimates of regression coefficients and their standard errors for animals born between 1952 and 1968

Comparison	Method of calculating selection differentials and responses		
	Absolute units	Deviations expressed as percentage of mean in Random flock	Deviations expressed as percentage of standard deviation in Random flock
Crimps Plus v. Crimps Minus			
Rams †	.47 (.021)	.47 (.019)	.41 (.021)
Ewes *	.44 (.020)	.45 (.021)	.48 (.026)
Pooled	.45 (.022)	.46 (.022)	.45 (.028)
Crimps Plus v. Random			
Rams †	.39 (.038)	.44 (.043)	.34 (.030)
Ewes *	.45 (.025)	.52 (.031)	.50 (.031)
Pooled	.43 (.029)	.49 (.038)	.44 (.038)
Crimps Minus v. Random			
Rams †	.54 (.048)	.50 (.043)	.48 (.056)
Ewes *	.46 (.028)	.42 (.027)	.51 (.040)
Pooled	.49 (.039)	.45 (.036)	.49 (.050)
Average of standard errors	(.030)	(.031)	(.035)

Table 1.3.10

Estimates of the realised heritability of crimp frequency:

Estimates pooled over sexes

	Realised heritability	Standard error of regression[1]	Standard error of regression[2]	Standard error of realised heritability
Divergent selection				
1 generation(s) of selection	.58	-	.072	.079
4 " "	.48	.032	.020	.051
6 " "	.45	.022	.009	.029
Crimps Plus v. Random				
1 generation(s) of selection	.42	-	.143	.150
4 " "	.30	.089	.034	.075
6 " "	.43	.029	.014	.054
Crimps Minus v. Random				
1 generation(s) of selection	.85	-	.185	.207
4 " "	.65	.065	.029	.071
6 " "	.49	.039	.018	.058
Heritability estimate for Trangie population (Morley, 1955)	.47			

[1] Calculated from yearly estimates of the cumulative response and selection differential

[2] Estimated for 1, 4 or 6 discrete generations of selection.

Response to selection for weaning weight

Information on weaning weights in the March Random flock is given in Tables A25, A26 and A27. Using the results where the age adjustment was applied to weaning weight itself, average weaning weight declined over the period 1951 to 1969 by -0.33 lb. per year. The correlation between yearly means and standard deviations was .54. The between year coefficient of variation of 15 per cent was similar to the pooled within year estimates.

A total of 41.7 lb. of accumulated selection was applied in the Weaning Weight Plus flock, with 38.3 lb. in the Weight Minus flock. Response to selection among rams was greatest in the final year, 1969, when the deviation of both the Weight Plus and Minus flocks from the Random was 1.1 phenotypic standard deviations (Tables A28 and A30; Figure 1.3.3). The largest deviations of the ewe flocks were also equal, at 1.6 phenotypic standard deviations, but this was achieved in the Weight Minus flock in 1956 (Tables A29 and A31).

Selection for weaning weight had only a slight effect on the variation and skewness of weaning weight ~~the fold scores~~, with a slight increase in the standard deviation in the Weight Plus flock and a slight decrease in the Weight Minus flock.

Figure 1.3.3 Response to selection for skin fold score

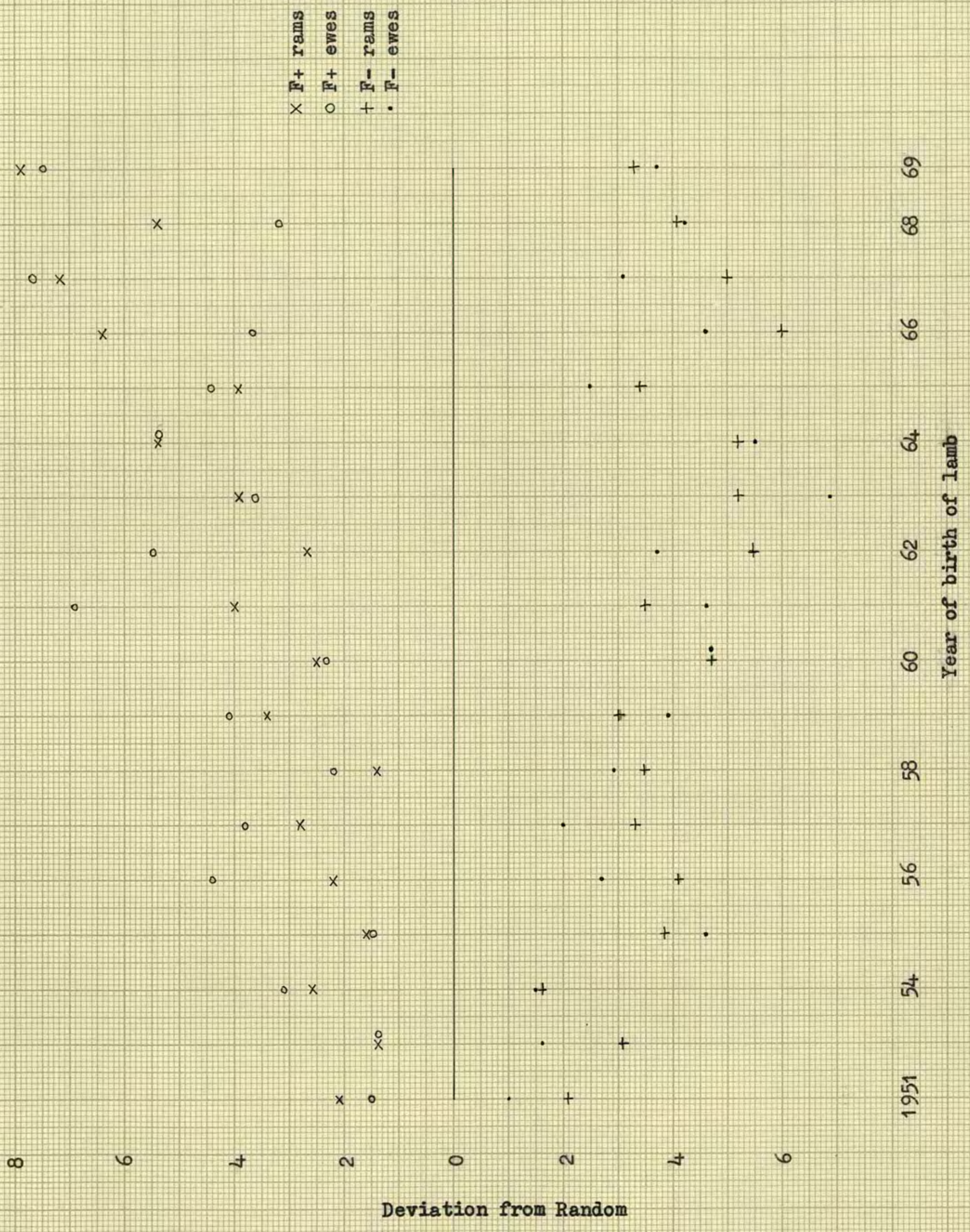


Table 1.3.11

<u>Estimates of variation and skewness for weaning weight (1) in the Weaning Weight selection and Random flocks, averaged over the final 10 years of observations</u>

	Random		Weaning Weight Plus		Weaning Weight Minus	
	Rams	Ewes	Rams	Ewes	Rams	Ewes
Standard deviation	7.40	6.16	8.50	7.53	7.17	6.47
Coefficient of variation	14.2	13.1	14.3	13.9	15.1	15.2
Skewness	0.0	-0.13	-0.46	-0.13	-0.13	0.09

Realised heritability estimates, obtained by regressing cumulative response on cumulative selection differential over six generations of selection, are given in Table 1.3.12. As with the previous sets of selection flocks, the method of estimating selection differentials and response did not systematically affect the relative magnitude of these estimates, nor, in this case, the relative magnitude of the standard errors of these estimates.

Response in the first generation of selection in the Weight Minus flock was in the opposite direction to the selection pressure applied. For the other two comparisons (4 and 6 generations of selection, response to upwards and downwards selection was similar, and, as with divergent selection, realised heritability was similar to the heritability estimates previously obtained for the Trangie population by Pattie (1965a).

Table 1.3.12

The realised heritability of weaning weight: Estimates of regression coefficients and their standard errors for animals born between 1951 and 1969

Comparison	Method of calculating selection differentials and response		
	Absolute units	Deviations expressed as percentage of mean in Random flock	Deviations expressed as percentage of standard deviation in Random flock
Weaning Weight Plus v. Minus			
Rams	.19 (.010)	.22 (.010)	.20 (.009)
Ewes	.17 (.013)	.22 (.010)	.22 (.012)
Pooled	.18 (.011)	.22 (.010)	.21 (.011)
Weaning Weight Plus v. Random			
Rams	.20 (.017)	.21 (.017)	.21 (.018)
Ewes	.21 (.020)	.25 (.019)	.25 (.018)
Pooled	.21 (.019)	.23 (.018)	.23 (.018)
Weaning Weight Minus v. Random			
Rams	.19 (.021)	.21 (.021)	.21 (.018)
Ewes	.18 (.014)	.22 (.011)	.22 (.013)
Pooled	.19 (.018)	.22 (.015)	.21 (.016)
Average of standard errors	(.016)	(.015)	(.015)

Table 1.3.13

Estimates of the realised heritability of weaning weight:

Estimates pooled over sexes

	Realised heritability	Standard error of regression[1]	Standard error of regression[2]	Standard error of realised heritability
Divergent selection				
1 generation(s) of selection	.11	-	.088	.100
4 " "	.22	.019	.012	.027
6 " "	.18	.011	.007	.023
Weaning Weight Plus v. Random				
1 generation(s) of selection	.32	-	.219	.250
4 " "	.22	.035	.017	.038
6 " "	.21	.019	.013	.037
Weaning Weight Minus v. Random				
1 generation(s) of selection	-.08	-	.192	.192
4 " "	.22	.049	.017	.038
6 " "	.19	.018	.014	.038
Heritability estimates for:				
Trangie population				
half-sib correlation	.19			
Pattie, 1965a)				
offspring-parent regression	.29			

[1] Calculated from yearly estimates of the cumulative response and selection differential

[2] Estimated for 1, 4 or 6 discrete generations of selection

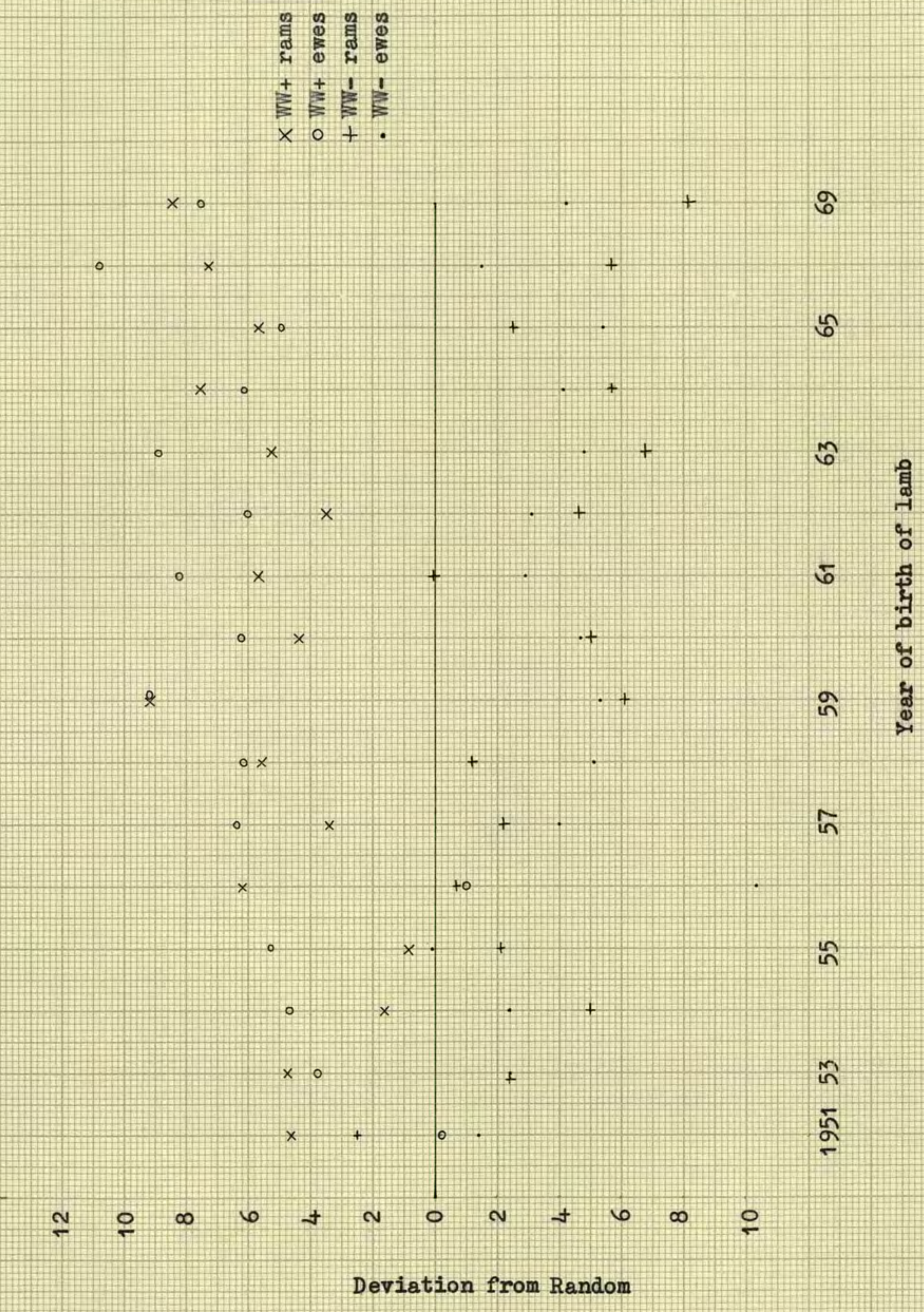
The ratio of the standard error of the realised heritability to the standard error of the regression coefficient ranged from an average of 1.1 for 1 generation of selection to 2.9 for 6 generations of selection.

Response to selection for skin fold score

Fold scores in the March Random flock are summarised in Tables A32 and A33. Over the period 1951 to 1969, average fold score increased slightly in the Random flock, by .07 units per year for the combined score for neck and side. The correlation between means and standard deviations was 0.73. The between year coefficient of variation for neck plus side scores was 22.8 per cent, considerably less than the pooled within year estimates.

The total accumulated selection pressure applied to skin fold score was 19.1 units in the Folds Plus flock and 9.4 units in the Folds Minus flock. These figures are the sum over three periods of selection, when the criterion of selection was in sequence breech score (base population), combined score for neck, side and breech (1951 to 1961) and then the combined score for neck plus side. Averaged over the two sexes, a maximum response of 2.2 phenotypic standard deviations was achieved in the Folds Plus flock, and 2.5 standard deviations in the Folds Minus flock (Tables A34 to A37; Figure 1.3.4). The total range of possible scores for neck and side is 17 units (2 to 18). By 1960 the divergence between the selection flocks was 7.6 units, averaged over the sexes, by 1969 this had increased to 11.2 units.

Figure 1.3.4 **Response to selection for Weaning Weight**



Perhaps the most noticeable aspects of the performance of these selection flocks are the low average scores of the Folds Minus flock and skewness of the distribution of individual scores, even in the early years of the experiment (Table 1.3.14). Again the degree of skewness of scores in the Folds Plus and Random flocks was similar in the first eight years of observation, but after this time scores in the Folds Plus flock were markedly skewed to the left.

Table 1.3.14

Variation and skewness of skin fold scores in the March Random and Folds selection flocks: Combined score for neck + side

	March Random		Folds Plus		Folds Minus	
	Rams	Ewes	Rams	Ewes	Rams	Ewes
1. First eight years of observation (1951 to 1969)						
Standard deviation	2.86	2.69	3.71	3.32	1.51	1.41
Coefficient of variation	42.1	43.3	40.1	36.4	38.3	37.6
Skewness	0.52	0.70	0.27	0.33	1.11	1.20
2. Last 10 years of observation (1960 to 1969)						
Standard deviation	3.59	3.10	3.31	3.77	1.65	1.32
Coefficient of variation	45.2	42.6	25.9	32.5	47.6	44.1
Skewness	0.54	0.77	-0.45	-0.51	1.60	1.78

Because the criterion of selection varied in these selection flocks with time, responses to selection can strictly speaking, only be regarded as correlated responses to selection, even though the heritability of all three measures of fold score used is similar, and the genetic correlation between the scores high. For this reason, the heritability of the combined score for neck and side has been estimated but only where selection differentials and response have been expressed as a percentage of the standard deviation of performance in the Random flock (Table 1.3.15). Unfortunately only 12 rams were scored in the Random flock in 1951, so little confidence could be placed in the estimate they provided of the standard deviation for fold score. Consequently the pooled within-year estimate of the standard deviation has been used in estimating response to 1 generation of selection. The rate of response to selection in both directions declined with time. The ratio of the standard error of the realised heritability to the standard error of the regression coefficient increased with selection, from an average of 1.3 for 1 generation to 3.1 for 6 generations of selection.

The realised heritability of breech fold following one generation of selection was .62 for upward selection with a control (standard error of the realised heritability, .164), 1.03 (.313) for downward selection, and .77 (.203) for the divergence between the Folds Plus and Minus flocks.

Table 1.3.15

Estimates of the realised heritability of fold score: Combined score for neck plus side. Estimates pooled over sexes

	Realised heritability	Standard error of regression^1	Standard error of regression^2	Standard error of realised heritability
Divergent selection				
1 generation(s) of selection	.60	-	.104	.131
4 " "	.42	.080	.021	.054
6 " "	.36	.038	.011	.035
Folds Plus v. Random				
1 generation(s) of selection	.50	-	.132	.172
4 " "	.33	.064	.047	.109
6 " "	.33	.033	.015	.044
Folds Minus v. Random				
1 generation(s) of selection	.69	-	.235	.311
4 " "	.66	.072	.050	.140
6 " "	.53	.042	.034	.113
Heritability estimate for Trangie population - breech fold score Morley (1955)	.50			

[1] Calculated from yearly estimates of the cumulative response and selection differential

[2] Estimated for 1, 4 or 6 discrete generations of selection

Discussion

Before considering the results it is perhaps necessary to establish that the methods of predicting response to selection are, in fact, appropriate for these particular flocks. In outlining their formation, it was pointed out that the flocks were established at the same time from essentially the same base population. If this was the case, then the prediction equations would hold. If on the other hand the flocks were formed sequentially, the validity of response predictions depends on the equality of genetic and phenotypic regressions of the character subsequently selected on the character initially subject to selection (Robertson, 1966). Even with sequential selection, a strong argument could still be made for the validity and accuracy of response predictions for the characters under selection at Trangie. Firstly, the sequential selection would have applied only to the base ewe population and the selection pressure applied came mainly from between ram selection. Secondly, from the phenotypic and genetic correlations estimated for pairs of these characters in the Trangie population (Morley, 19~~54~~55a; Pattie, 1951b), the genetic and phenotypic regressions are similar in magnitude as well as in sign, with the possible exception of the relationship between folds and weaning weight. Splitting the base ewe population into four and establishing Plus and Minus flocks for one character from one such sub-flock, would have been a preferable method of establishing the selection flocks.

Over the six generations of selection, realised heritability estimates, calculated from the divergence of the selection lines, were in quite good agreement with heritability estimated on the Trangie base population. For the Fleece weight, Crimps and Folds selection lines, the rate of response declined with time. Scaling the responses and selection differentials, by the mean or standard deviation of the Random flock, did not improve the precision of the realised heritability estimates other than for the fleece weight selection lines. It is worth pointing out that the between year variation in the Random flock was also greatest for fleece weight.

Comparing the symmetry of response to upward and downward selection, realised heritability was greater for downward selection in Fleece, Crimps and Folds lines. This is not likely to be due to directional selection in the April Random flock for fleece weight (Pattie and Barlow, personal communication) or crimps (Robards and Pattie, 1967), nor, from the cumulative selection differentials presented in Table 1.3.16, for folds in the March Random flock. Inbreeding could lead to the greater response to downward selection.

Table 1.3.16

<u>Cumulative selection differentials for skin fold score in the March Random flock</u>
<u>Calculations have been made using yearly unscaled deviations for the flock mean</u>

			Year		
	1951	1956	1961	1965	1969
Cumulative selection differential	-0.03	-1.07	0.36	0.72	-0.29

Morley (1954) examined data on the Trangie population and showed the expression of all three characters to be somewhat reduced by inbreeding;

by 1969 the level of inbreeding in the selection flocks ranged from 6.0 to 9.2 per cent.

In the Fleece, Crimps and Weaning Weight selected lines, upward selection increased the phenotypic variance while downward selection reduced it. The changes produced in the variance were not felt to be sufficient to consider transforming the scale of the observations, such as Falconer (1954) did for body weight in mice. In any case, the effect on the realised heritability estimates are likely to be small. A better case exists for transforming skin fold scores, or at least devising a more satisfactory measure of response to selection. With only a limited number of scores, it is only to be expected that the distribution in the selected lines will become skewed as the limits are approached. Under such conditions, response to upward and downward selection is largely determined by the response of the control line to environmental conditions, rather than to a change in average performance of the selected lines.

Some attempt has been made to account for the contribution of genetic drift to the reliability with which realised heritability was estimated. With overlapping generations, the major difficulty in comparing the relative magnitude of standard errors of the regression coefficient and of the realised heritability is that the two are not estimated from the same information. Where the latter standard error was compared with the expected standard error of the regression, the contribution of drift could readily be appreciated. In both of these calculations, as in the actual calculation of the standard error of the regression of cumulative response on selection differential, the standard errors of the estimates declined as the selection experiment was continued. However, because of the contribution of drift, the increased precision with which realised heritability was estimated, as a result of keeping lines for additional generations is not as great as indicated by the decline in the standard error of the regression coefficient.

PART 2

SECTION 2.1 SELECTION FOR IMPROVED EWE REPRODUCTIVE PERFORMANCE

In this part of the Thesis, it is intended to examine ways of improving ewe reproductive performance and to consider the effectiveness of the various forms of selection which can be applied. These related topics have received considerable attention in recent years (see, for instance, Turner, 1969a, b) and the major stimulus for such investigations is the poor reproductive performance of most sheep breeds. Increasing the average number of lambs annually produced by each ewe is likely to increase the profitability of sheep relative to alternative enterprises as the proportion of the ewe maintenance costs borne by each lamb would be reduced. In addition, by increasing the number of replacements available for selection, there would be greater scope for improving other production characters.

Ewe reproductive performance differs from the characters previously subject to selection at Trangie in that it is sex-limited. Selection can be practised among rams but it would usually be based on their dam's performance, or more generally, on that of their female relatives. In its simplest form, and one which is often recommended (for example, see Young and Turner, 1965), rams are selected from the largest litters. Progeny testing of rams is generally not considered to be practicable, which is apart from the undesirable effects progeny testing would have on inbreeding and the generation length. In future, it may be possible to select for some character which is highly correlated genetically with ewe reproductive performance, but which can be measured directly on the rams (Ch'ang and Rae, 1972; Land, 1973). For the time being this possibility will not be considered.

Two forms of ewe selection can be envisaged. The first is analagous to the ram selection mentioned above, in which the selection criterion is the performance of the ewe's dam or other female relatives, and this would normally be applied in choosing replacements for the breeding flock. However, selection could also be practised on ewes already in the breeding flock, on the basis of their own lambing performance. The optimum policy would probably be one which incorporated both these forms of selection.

The factors determining the response to selection for ewe reproductive performance are the same as those previously mentioned in connection with the selection flocks; the intensity of selection, the heritability of the character and the generation length. While the factors determining genetic progress may be the same, their relative importance is altered because we are dealing with a sex-limited trait. The most obvious change is the greater importance of between ewe selection relative to between ram selection. There are two reasons for this. Firstly, ewe selection can take place both before and after entering the breeding flock, and secondly, there is the difficulty in assessing the ram's breeding value.

Because of the enhanced contribution that ewe selection can make to the success of such programmes, a considerable amount of attention will be devoted to estimating the scope for ewe culling in the Trangie flock. In all such considerations, and in estimating response to selection, it will be assumed that the flock under investigation is self-contained; that is that no replacement ewes are brought in. The repeatability and heritability of ewe reproductive performance will be considered after the scope for selection has been established.

SECTION 2.2 THE SCOPE FOR SELECTION IN SHEEP POPULATIONS - A REVIEW

Perhaps the most useful measure of the scope for between ewe selection is the net reproduction rate (N.R.R.) of the population. This is defined on the average number of female replacements that each female produces in her lifetime. If the N.R.R. of a population is 2, each ewe entering the breeding flock at say 1½ years of age would in her lifetime produce on average 2 female offspring to the same age. Given that only one replacement is required to maintain numbers, the population will either increase in size or half the possible replacements could be culled. The rate at which the population would grow is described by the innate capacity for increase (r_m) (Andrewartha and Birch, 1954). This statistic is a summary of a number of physiological functions of the ewes in a population; the frequency with which they breed, their fecundity (the average number of young produced each time they breed) and their longevity.

The calculation of N.R.R. and r_m in sheep population has been described by Moule (1971). Age specific schedules of births and deaths are drawn up in which the numbers of ewes dying within specified age intervals are calculated, as are the numbers of ewe lambs which survive to the age of first mating produced by ewes in the same age intervals. With sheep the most convenient age intervals to work with are between successive matings.

Comparatively few estimates of net reproduction rate or of the innate capacity for increase are available for sheep populations (Dun, 1964; Turner and Young, 1969; Moule, 1971) or can be calculated from information provided on age specific reproductive performance and wastage rates from the breeding flock (Purser and Roberts, 1959) (see Table 2.2.1). These figures are for breeds of allegedly poor reproductive performance and/or are for flocks run under comparatively adverse environmental conditions, so that they should not necessarily be taken as representative of the species as a whole. While the populations described by Moule (1971) and Purser and Roberts (1959) did little more than maintain numbers, in the Cunnamulla flock it was possible to cull 66 per cent of hogget ewes. Taking the Folds Minus flock as the more representative of the Trangie population, the comparable figure obtained by Dun (1964) was 56 per cent. A modified version of N.R.R. has also to estimate the effect of early nutrition on lifetime productivity at Trangie (Giles, 1968).

Both N.R.R. and r_m provide an overall assessment of a population's ability to survive under a given set of conditions. Apart from giving an appreciation of the numbers of replacements required and available for selection, which is important when considering selection programmes, the same information is necessary when deciding on an optimal flock structure for current productivity. For instance, only four age groups of ewes (2 to 5 years of age) were necessary to maintain the Cunnamulla flock at constant size. Increasing the numbers of age groups not only increased the net reproduction rate, but also the numbers of young rams and hogget ewes available for disposal. On the other hand, fewer ewes were cast for age and they were older when cast. When information such as this is considered along with age of ewe effects on both wool quality and quantity, and also on the growth (Bichard and Cooper, 1966) and hence perhaps value of an individual lamb, then some decision on optimal flock structure could

Table 2.2.1

Estimates of net reproduction rate and the innate capacity for increase in sheep populations

Author	Breed of Sheep	Number of age groups of ewes*	Net reproduction rate	Innate capacity for increase
Dun (1964)	Australian Merino (Trangie), Folds Plus Folds Minus selection flocks	not stated; till ewes were dead or cast for age	Folds Plus, 1.238 Folds Minus, 2.270	- -
Turner and Young (1969) ‡	Australian Merino (Cunnamulla flocks)	9	2.920	0.183
Moule (1971)	Australian Merino	7	1.128	0.026
Purser and Roberts (1959)	Scottish Blackface	5	1.222	0.043

* These were the maximum number of age groups considered by the different authors

‡ Figures for this flock have been slightly modified from those given by Turner and Young, to accord with the method of calculation set out by Andrewartha and Birch (1954).

be arrived at.

As far as selection is concerned, increasing the number of age groups to give the greatest scope for selection may not enable the most rapid genetic progress to be made, as the generation length would also be increased.

Having discussed the calculation of N.R.R. estimates, its two components will now be considered, age specific rates of ewe wastage and of ewe reproductive performance. There are two main reasons for this. Firstly, there is considerably more information available on the components, and especially on ewe reproductive performance, than there is on N.R.R. itself. Secondly, selection is to be practised for ewe reproductive performance and if environmental factors which influence performance can be identified, then the accuracy with which breeding value can be predicted is increased. This discussion will not be restricted entirely to the estimation of age of ewe effects on wastage and reproductive performance.

Ewe Wastage

Comparatively little information is available on ewe wastage and the figures which have been presented refer to only a few types of populations, mainly hill breeds in Britain and the Australian Merino. For the British breeds, annual death rates of from 3 to 5 per cent have been reported (Gunn, 1967; Purser and Roberts, 1959), with little evidence that death rates varied with the age of the ewe (Purser and Roberts, loc. cit.), at least up to 6 years of age. Higher estimates of overall flock losses were reported by Bichard and Cooper (1966) for a crossbred lowland flock. Estimates of annual death rates in Merino flocks show rather more variation. Turner (1951) summarised losses in a number of commercial flocks and found that the average rate for all age groups was never less than eight per cent, a figure which can be compared with the five per cent reported for the experimental flocks at Cunnamulla (Turner, Dolling and Sheaffe, 1959). The incidence of ewe mortality increased as the ewes became older in the flocks investigated by both Turner, Dolling and Sheaffe (loc. cit.) and Granger (1944) although, in the former study, this trend was most marked in a drought year (1957-58) when losses were high.

In most commercial flocks some form of ewe culling is practised and this constitutes an additional source of wastage from the breeding flock. Generally, ewes are culled for such reasons as damaged udders or teats, broken mouths or generally poor body condition. In each case, culling implies that the expected productivity or probability of survival of the ewe is below average for her age group. Purser and Roberts (1959) reported that the average culling rate for all age groups of a Scottish Blackface flock was 11 per cent and that it increased from 3.4 per cent for ewes between first and second mating to 25.6 per cent between fifth and sixth mating.

Ewe Reproductive Performance

The measure of ewe reproductive performance which enters directly into the calculation of N.R.R. is the number of hogget ewes produced by each ewe joined. While there is a dearth of such estimates, considerable information is available on the number of lambs produced to various earlier ages, in particular birth, tail-docking and weaning. In addition to treating such traits as characteristics of the ewe, lamb survival will also be considered separately.

It is both customary and valuable to consider ewe reproductive performance both in some overall measure, such as the number of lambs weaned per ewe joined, and to also examine the components of such characters. Turner (1958, 1969a, b) has given considerable attention to the orderly presentation of such information and also to the nomenclature and abbreviations which can gainfully be applied in such investigations. The same nomenclature will be employed here, although the slight modifications to her suggested abbreviations have been considered desirable for ease of understanding.

Before reviewing the literature on ewe reproductive performance, the terminology and abbreviations will be summarised. Taking the number of lambs weaned per ewe joined as the overall measure of performance, this is equal to the following product; the probability of a ewe lambing of those joined, the number of lambs born per lambing ewe, and the number of lambs that survive from birth to weaning. In the notation to be employed in this thesis:

$$L_{WJ} = E_{LJ} \times L_{BL} \times L_{WB}$$

Other measures of performance to be used are:

L_{BJ} = number of lambs born per ewe joined (= $E_{LJ} \times L_{BL}$), and

E_{ML} = number of lambing ewes with multiple births.

In discussing lamb survival, it is customary to consider lambs from different litter sizes separately as the probability of survival is usually influenced by type of birth. Hence:

S_{WB} = number of single lambs weaned per single lamb born, and

T_{WB} = number of twin lambs weaned per ~~single~~ twin lamb born.

A further subdivision is possible so that sexes are treated separately within each type of birth. In this situation we have:

$S_{WB.R}$ = number of single ram lambs weaned per single ram lamb born,

and so on for $T_{WB.R}$, $S_{WB.E}$ and $T_{WB.E}$.

Published information on the association between age of ewe and reproductive performance now covers a wide range of breeds in a large number of countries and has been reviewed by Reeve and Robertson (1953) and Turner (1969a, b). Whichever measure of performance has been used, be it lambs born or weaned, and expressed relative to ewes joined or ewes lambing, a similar pattern has emerged with an increase in performance with age to a peak, followed by a decline. This pattern of association is also true for the Australian Merino, where both commercial and experimental flocks have been examined (Table 2.2.2). However, from the results presented in Table 2.2.2, it can be seen that the age of peak performance shows considerable variation.

Where information on the components of either L_{WJ} or L_{BJ} was available (Turner and Dolling, 1965; Lax and Brown, 1968; De Haas and Dunlop, 1969; Mullaney and Brown, 1970), the pattern of their association with age was generally the same as for the overall measure of performance. One notable exception was the finding by De Haas and Dunlop (loc. cit.) that while the normal pattern of association with age was shown for the number of lambs born per ewe joined, no

Table 2.2.2

Summary of the available data on the relationship between age of ewe and ewe reproductive performance in the Australian Merino

Author	Characteristic recorded	Oldest age group	No. of flocks	No. of flocks in which peak occurred at:				
				4 Years	5 Years	6 Years	7 Years	8 Years
Riches, 1958	Lambs marked per ewe mustered at marking	5	5	3	2	-	-	-
		6	10	-	6	4	-	-
		7	5	-	2	2	1	-
		8	2	-	-	1½	-	½
Kelley, 1939	Lambs born	11	1	-	-	-	-	1
Turner (1962) and unpublished data. (cited by Turner & Dolling)	Lambs born per ewe joined	8	2	-	½	1½	-	-
	Lambs weaned per ewe joined	8	2	-	-	2	-	-
Turner & Dolling, 1965	Lambs born per ewe joined	10	1	-	-	-	1	-
	Lambs weaned per ewe joined	10	1	-	-	1	-	-
Mullaney and Brown, 1970	Lambs born per ewe joined	8*	4	-	-	4‡	-	-
	Lambs weaned per ewe joined	8*	4	-	-	4‡	-	-

* Ewes first mated when 2½ years of age

‡ Results for the four flocks were not treated separately.

association was observed for the percentage of ewes conceiving to first service.

It should be pointed out that the information presented in many of these studies was obtained over a small number of years so that only a few cohorts were studied and then for only a portion of their life. The danger in employing this method is that information from one cohort, exposed perhaps to abnormal management or environmental conditions, can bias the age group comparisons and sampling problems of this sort probably account for the conflicting results obtained by Mullaney and Brown (1969, 1970). The greater the between year variation in fertility, the more important such sampling considerations are likely to be.

Turner (1969b) concluded that in flocks or breeds with a high average level of performance, ewes may reach their peak performance at an earlier age. However, because of the dearth of reliable comparative data available, it is not really clear to what extent the variation which has been observed in this relationship is genetic in origin, although Dunlop (1963) observed differences among Merino strains which were born and reared together. Within breeds there is again little information on the genetic correlation between lambing performance at different ages which would indicate the extent to which the pattern of association could be changed. It is not known whether selection for L_{BJ} has produced any changes in the association (Wallace, 1964; Turner, 1966).

So far in this discussion, no distinction has been made between age of ewe effects and what might, in fact, be a parity effect.

Where age of ewe effects have been reported, ewes have always been mated as a flock at regular yearly intervals so that any individual effects that age of ewe or parity might have could not be isolated. One way of making this distinction would be to delay or enhance the age of first mating of one half of the flock, but, where such a design has been used, the numbers of animals involved have been too limited for such a question to be answered (Spencer, et. al., 1942; Cannon and Bath, 1969).

Coop has suggested that the association between reproductive performance and age of ewe is largely a reflection of the association between body weight of the ewe at mating and (Coop & Hayman, 1962). such measures of performance as L_{BJ}, L_{BL}, and to a lesser extent E_{LJ}. Certainly, for ewes of the same age, body weight has been shown to be associated with these characters even when body weight changes immediately prior to mating (flushing) have been removed (see for instance, Killeen, 1967). Nevertheless, in the majority of studies, age of ewe effects have persisted when body weight differences have been removed (De Haas and Dunlop, 1969; McLaughlin, 1970).

Attempts to distinguish age of ewe from parity effects and to assess the importance of ewe body weight at mating are simply two approaches to the question of the physiological basis for the association between age of ewe and reproductive performance. There appears to be no published estimates of ovulation rates and either embryo or foetal mortality for ewes of different ages or more fundamentally of circulating hormone levels. However, the analyses conducted by De Haas and Dunlop (1969) suggests that the difference in reproductive performance between ewes of different ages may be, at least, partially behavioural in origin as no age effects were observed for the percentage of ewes conceiving to first service. The more extended period of oestrus in older ewes has also been suggested as the reason for the higher proportion of them which lamb (Lambourne, 1956; Connors and Giles, 1970).

Finally, the association between birth type of a ewe, whether single, twin etc., and her own reproductive performance will now be discussed. This topic more properly belongs in the Section on genetic influences on performance, but is presented here as in the analysis of data on the Trangie population, type of birth effects were considered along with age of ewe effects.

Differences have been reported in the lambing performance of ewes born in litters of different sizes and a summary of these differences between single and twin born ewes is given in Table 2.2.3. In the majority of these, reproductive performance was positively correlated with birth type, and where the birth type classification has been extended to cover ewes born as triplets or quadruplets (see Turner, 1969b for review), this positive correlation has still been evident. The genetic interpretation of such differences will be discussed later when considering the heritability of reproductive performance. However, from a practical point of view, the results presented in Table 2.1.3 indicate that by selecting twin born ewes in preference to singles, the lambing performance of the flock would, in general, be increased.

Table 2.2.3

Difference in lambing performance (L_{BJ}) of ewes born as singles or twins

Author	Breed	Age at which performance compared	Twins - Singles
Kennedy (1959)	Australian Merino (Trangie)	2-7	0.09
Turner et. al. (1962)	Australian Merino	2-7	0.06
Dun and Grewal (1963)	Australian Merino (Trangie)	Sum of performance at 2 and 3 years	0.18
Wallace (1964)	New Zealand Romney	2-4	-0.06 to -0.10
Hallgrimsson (1966)	Icelandic	2-6	0.09
Vakil et. al. (1968)	American Rambouillet and Crosses	Mixed	0.14
Lax and Brown (1968)	Australian Merino	2-10	0.02

Lamb Losses

Information on lamb loss to weaning has been obtained from many of the studies used to estimate the importance of various factors on ewe reproductive performance, especially age of ewe effects. Where such comparisons have not been confounded with differences in the average litter sizes of the groups being compared, then ewes of intermediate age (3 to 7 years) have generally weaned the highest proportion of lambs (Goot, 1951; Sidwell, Everson and Terrill, 1962). Information on age of ewe effects on lamb survival in the Australian Merino is summarised in Table 2.2.4, where again survival is highest from ewes of intermediate age. Turner and Dolling (1965) concluded that, in their study, age of ewe effects on lamb survival were not as marked as age of ewe effects on ewe reproductive performance. However, the results obtained by Lax and Turner (1965) indicated that the importance of age of ewe effects on survival may vary in relation to the absolute level of lamb survival in the flock.

There appears to be general agreement on the effect of sex and type of birth on survival, with females superior to males and singles superior to twins (Table 2.2.5). No information on the survival of triplets or higher order lambs appears to be available for the Australian Merino where, of course, such occurrences are comparatively rare. Lamb survival would have to be considered in assessing the desirability of attempts to increase ewe reproduction. For instance, if the survival of twins was only half that of singles, then increasing the proportion of ewes producing twins might not increase the number of lambs alive at weaning, unless some appropriate

Table 2.2.4

Influence of age of ewe on lamb survival in the Australian Merino breed

Source	Age of dam (years)	Survival to	Differences of survival rate of lambs: From ewes of various ages	Differences of survival rate of lambs: From youngest to peak age group of ewes	Comments
Kennedy and Bettenay (1950)	3ƒ to 5	4-5 days	3 year old ewes below others	0.05	Sexes pooled
		5 days to marking	No differences.	Nil	Sexes pooled
Turner and Dolling (1965)	2 to 10	Weaning	Rise and decline: Single males and females, peak at 5-6	0.12	Sexes and type of birth kept separate
			Twin males and females, peak at 6-7	0.12	
Lax and Brown* (1965) (1)	2 to 7	Weaning	Rise and decline: Peak at from 4-6	0.14	Single lambs only
(2)	2 to 7	Weaning	Rise and decline: Peak at 5	0.11	Single lambs only
(3)	2 to 7	Weaning	Little trend with age, maximum at 7	0.04	Single lambs only
(4)	2 to 8	Weaning	Rise and decline: Peak at 5	0.08	Single lambs only
Mullaney and Brown (1969)ø	3ƒ to 9	Weaning	Rise and decline: Single lambs, peak at 5 Twin lambs, peak at 4	0.10 0.13	Sexes pooled

ƒ Ewes first mated at 2½ yrs. of age.

ø Information included from 4 flocks.

* The flocks and locations included from this study are as follows:

(1) Five strains at Cunnamulla

(2) Five strains at Armadale

(3) Five strains at Deniliguin

(4) Selection flock at Armadale

change was also made in lamb management. However, Turner (1969a) has pointed out that there are no reports in which the differential between single and twin mortality is as great as this, although Mullaney and Brown (1969) did find twin survival to be only 59 per cent that of singles. In Britain, Bichard and Cooper (1966) reported that in the Clun Forest breed increasing the proportion of triplets in the flock would also increase the numbers of lambs alive at weaning.

Table 2.2.5

The influence of sex and type of birth on lamb survival in the Australian Merino

Source	Survival to	Difference in survival rate	
		Female-Male	Single-Twin
Moule (1954)	3-4 days	0.03	0.18
Turner and Dolling (1965)	Weaning	0.02	0.18
Lax and Turner (1965)	Weaning	0.04	-
Mullaney and Brown (1969)	Weaning	-	0.34

Little information is available on survival between weaning and age at first mating. Purser and Roberts (1959) estimated wastage at 6.8 per cent in a Scottish Blackface flock, while Turner and Young (1969) used a figure of 6 per cent for the Australian Merino. Granger (1944) calculated that 10 per cent of ewes died between weaning and first lambing in the commercial Merino stud flock that he studied.

SECTION 2.3 THE EFFECTS OF AGE OF EWE AND SELECTION ON EWE WASTAGE RATES IN THE TRANGIE FLOCK

In estimating wastage rates for ewes of different ages, data were obtained on ewes born between the years 1951-1966 in the single character selection flocks and in the two Random flocks. Wastage was estimated between lambings so that by 1969, all ewes considered had the opportunity of at least two lambings.

As already mentioned the policy of ewe disposal on the Research Station has varied over the years. From 1951-1961 ewes left the flock through death or were culled if, at a routine inspection prior to mating, they were considered incapable of rearing another lamb. Culling was used to give flexibility to flock management. For instance, culling rates were increased in 1954 as part of a general preparation for drought (Dun, 1964). In his comparison of the Folds selection flocks over the period 1951-1961 Dun (loc. cit.) found death to be twice as important as a cause of loss than was culling, with wastage rates of 9 and 5 per cent respectively for these two sources of loss in the Folds Plus flock and 5 and 2 per cent respectively in the Folds Minus flock.

From 1962 onwards the policy was to dispose of ewes after they had been in the flock for five years. This policy took several years to become generally effective and has occasionally been waived when additional matings have been required for some special purpose.

The data available simply indicated the presence or absence of a ewe at lambing. If absent, no information was available of the time or cause of disappearance from the flock. The possibility of bias in the data due to ewes eluding matings, and so being recorded as 'dead', is slight because of the frequency with which ewes were inspected and the comparatively small size of the paddocks. In addition, the numbers of ewes losing both ear tags and having to be culled due to loss of identity are negligbly small.

The numbers of ewes included in the analysis of survival between successive pairs of lambings and the number of cohorts in which the animals were born, are given in Table 2.3.1. It is clear that after the fifth lambing the amount of information was considerably reduced and for this reason the effects of selection have only been considered from the first to the fifth lambing. It is also obvious that analysis of these data will not give a complete description of wastage in the breeding flock of this population as no account has been taken of wastage from the time of selection, at perhaps 18 months of age, to the age at which ewes first lamb, at two years of age.

Age of ewe effects on the data pooled over flocks have been extended to cover wastage to the seventh lambing. However, much of the data on survival from the fifth to the seventh lambing came from the period when the policy of ewe disposal was in the process of changing to one of culling all ewes after five years. The decision to consider a ewe for inclusion in these analyses was made on the basis of whether other ewes of that age group and flock were mated for a sixth or seventh time.

Table 2.3.1

Numbers of ewes included in the ewe survival study, survived over drops

Measure of Survival	March Mated flocks		April Mated flocks		Total
	No. of Ewes	No. of Drops Included	No. of Ewes	No. of Drops Included	No. of Ewes
Survival from lambings 1-2	1535	15	1360	15	2895
Survival from lambings 2-3	1412	14	1205	14	2617
Survival from lambings 3-4	1254	13	1024	13	2278
Survival from lambings 4-5	1027	12	874	12	1901
Survival from lambings 5-6	415	7	331	5	746
Survival from lambings 6-7	140	2	174	3	314

Statistical Analysis

Chi-square tests have been used to assess the significance of age of ewe effects on the data pooled over flocks. This procedure was considered adequate for the purpose as the number of contributing cohorts and the number of 1½ year old ewes included were virtually the same for all flocks (see Table 2.3.3, page 79).

Variation among both the March and April mated flocks was also assessed by Chi-square heterogeneity tests. However, as the flocks were the result of a consistent, continuing and directional regime of selection, it was felt that comparisons of appropriate pairs of flocks (Plus v. Minus, Plus v. Random, Minus v. Random) were also justified. At the same time, no attempt has been made to relate any differences observed to the amount of selection practised, as any effect of selection on ewe wastage would be counteracted by the change in the policy of ewe survival and, probably to a lesser extent, by the closer supervision of ewes at lambing from 1962 onwards.

In examining the effect of selection, survival has been estimated from first lambing to some later lambing, and not between consecutive pairs of lambings, so that the comparisons involving any one pair of flocks are not independent. Nevertheless, when applying such a large number of tests, there are still difficulties in adjudging as statistically significant a difference observed in any individual comparison.

Least squares analyses were used to investigate the effects of a ewe's type of birth (single or twin) and of her own lambing performance, on the probability of her surviving to various ages up to and including the fifth lambing. The stimulus to investigate a possible relationship between lambing performance and subsequent survival came originally from estimates of the heritability of lambing performance which will be presented later in this thesis. As the number of lambs a ewe had at mothering was the character generally considered in these heritability analyses, it has also been used as the measure of lambing performance here. Ewes that 'lambed and lost' before mothering would thus be classed as having failed to produce a lamb. However, a number of additional analyses have also been conducted in which ewes which lambed and lost before mothering have been excluded and in these all ewes classed as having no ewes would, in fact, have failed to lamb.

The model used in these analyses was:

$$X_{ijklm} = u + f_i + y_j + t_K + p_l + tp_{Kl} + e_{ijklm}$$

where X_{ijklm} = an individual observation

u = overall mean

f_i = the effect of the i^{th} flock

y_j = the effect of the j^{th} year of birth of the ewe

t_K = the effect of the K^{th} type of birth of the ewe

p_l = the effect of the l^{th} lambing performance of the ewe

tp_{Kl} = the interaction between type of birth and lambing performance, and

e_{ijklm} = random error of observations

Again, no attempt has been made to identify any time trend in selection effects, for the reasons set out above.

Since these data are Binomially distributed, the calculation of standard errors in a manner appropriate for normally distributed characters is open to criticism, as are significance tests based on these standard errors. Nevertheless, some idea of the sampling variation can be obtained from the standard errors and they have generally been included.

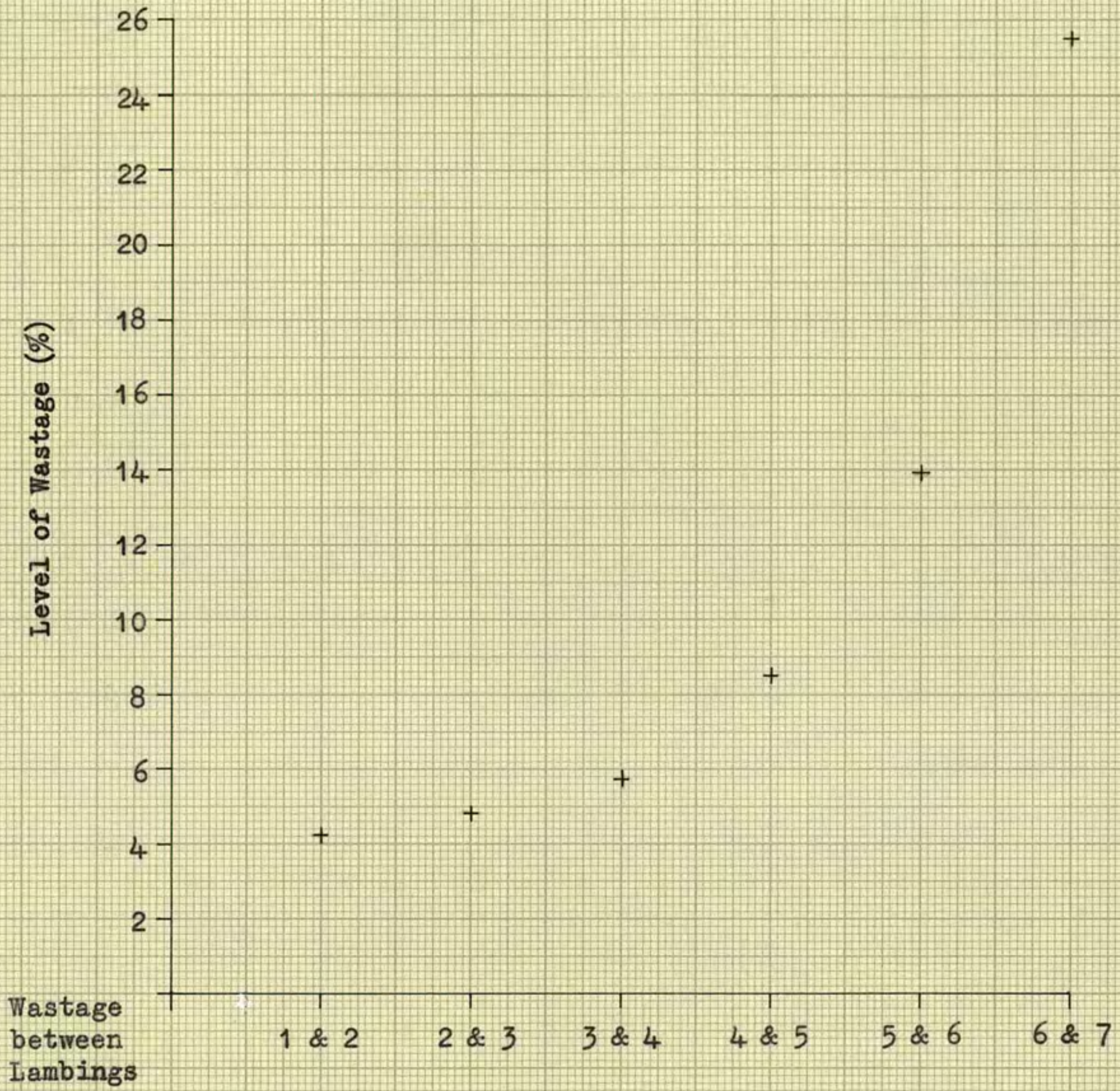
Results

Ewe wastage between successive pairs of lambings between the first and fifth lambs were 4.2 per cent between the first and second lambing, 4.8 between the second and third, 5.7 between the third and fourth and 8.5 per cent between the fourth and fifth (Chi-square, 3 d.f. = 8.17, $P < .05$). Corresponding losses between the fifth and sixth and seventh lambings were respectively 13.9 and 25.5 per cent and the variation among the six estimates was statistically significant. This pattern of a rise in wastage with age of ewe is illustrated in Figure 2.3.1.

From these results estimates can be obtained of the probability of survival to some specified later lambing by multiplying the probabilities of survival between successive pairs of lambs up to and including the desired later lambing. Alternatively, corresponding estimates can be obtained for ewes born sufficiently early in the experiment to have had the chance of surviving to the nominated later lambing during the period under investigation. The two sets of estimates are in quite good agreement (Table 2.3.2) and indicate that by the fifth lambing, between 20 and 25 per cent of ewes alive at the first lambing have been lost. Using the first of these methods, the estimated percentages of ewes surviving to have a sixth and a seventh lambing were respectively 67.8 and 50.5.

Estimates of ewe wastage in the individual flocks are given in Table 2.3.3. Losses in the March and April flocks were similar and there were no significant differences between the March and April Random flocks in percentage survival up to the fifth lambing. The March mated flocks were found to be significantly heterogeneous for percentage survival to the third lambing ($X^2 = 9.72$, 4 d.f., $P < .05$). When the pairwise contrasts between the selection flocks were made, the only significant differences involved the Folds selection groups. Survival to both the third and the fourth lambing was significantly

Figure 2.3.1 **Wastage rates among ewes in the breeding flock, with regard to age**



lower in the Folds Plus flock than in either the Folds Minus or March Random flock and the Folds Plus and Minus flocks also differed significantly in percentage survival to the fifth lambing ($P < .05$). Some of the contrasts between the Crimps Plus and April Random flocks approached this level of significance.

Table 2.3.2

<u>Estimates of ewe survival to various ages</u>

Measures of survival	Probability[1] of survival	Estimate of[2] survival
Survival to second lambing	95.8	95.8
Survival to third lambing	91.2	90.5
Survival to fourth lambing	86.0	84.8
Survival to fifth lambing	78.7	75.8

[1] Estimated on the product of the probability of surviving between successive pairs of lambings.

[2] Calculated for those ewes which had the opportunity to survive to that particular lambing.

Table 2.3.3

Wastage rates for ewes in the Individual Flocks, 1951 to 1969

Population examined	Lambing Interval							
	1-2		2-3		3-4		4-5	
	No. of Ewes	Death rate%	No. of Ewes	Death rate%	No. of Ewes	Death rate%	No. of Ewes	Death rate%
March mated flocks								
Random	360	4.0	288	3.5	259	5.4	235	11.1
Weaning Wt. Plus	306	6.2	287	3.5	260	6.9	196	10.2
Weaning Wt. Minus	293	6.5	274	2.9	250	5.2	196	5.1
Folds Plus	315	4.1	275	9.4	232	7.8	187	9.6
Folds Minus	328	1.9	288	6.2	253	5.9	213	8.0
TOTAL	1535	4.6	1412	5.1	1254	6.2	1027	8.9
April mated flocks								
Random	286	2.4	267	3.7	228	3.5	188	8.5
Fleece Plus	274	3.7	230	5.2	193	7.2	165	6.1
Fleece Minus	254	4.7	224	3.6	190	3.2	171	7.6
Crimps Plus	282	4.6	249	6.0	210	6.7	171	9.4
Crimps Minus	264	3.8	235	3.8	203	2.5	179	8.9
TOTAL	1360	3.8	1205	4.5	1024	5.0	874	8.1

The effects of both the birth type of a ewe and her lambing performance on the probability of survival between successive lambings are summarised in Table 2.3.4. Differences in survival between single and twin born ewes were small, not statistically significant and not consistent in direction (Table 2.3.5). Using the estimates of survival between consecutive pairs of lambings, the probability of ewes which entered the breeding flock surviving to have a fifth lambing was 73.2 per cent for single born ewes and 73.8 per cent for twins.

There was significant variation in the probability of ewes with different lambing performance surviving to the next lambing for all except that relating to performance at the fourth lambing and survival to the fifth (Table 2.3.5). This association was found regardless of whether ewes which 'lambed and lost' before mothering were included in or excluded from the analyses (Table 2.3.4). Ewes having twins at their first lambing had the greatest chance of surviving to have a second lambing, but in all other analyses, ewes producing single lambs had the highest probability of surviving to the next lambing. When performance at each of the first three lambings ~~were~~ was examined separately, in each instance ewes with 0 lambs had the lowest probability of surviving to have a fifth lambing (Table 2.3.5) while ewes with 1 lamb generally had the highest chance of survival.

Discussion

The major aim of the analyses reported here was to characterise this Merino population as regards wastage in the ewe

Table 2.3.4

Summary of the least squares analyses of lambing performance and type of birth effects on ewe survival.
Estimates of overall mean (u) plus least squares deviation (lsd), and standard errors of the least squares deviations (s.e.)

Main effects	Probability of survival from first to second lambing		Probability of survival from second to third lambing		Probability of survival from third to fourth lambing		Probability of survival from fourth to fifth lambing	
	u+lsd	s.e.	u+lsd	s.e.	u+lsd	s.e.	u+lsd	s.e.
Analysis 1 - lambing performance taken as number of lambs with ewe at mothering								
Lambing performance*								
No.lambs	.928	.007	.922	.007	.885	.009	.870	.011
One lamb	.961	.006	.960	.006	.947	.008	.911	.010
Twins	.980	.010	.940	.008	.920	.009	.889	.011
Type of birth								
Single	.956	.006	.943	.005	.910	.006	.892	.008
Twin	.957	.006	.938	.005	.925	.006	.889	.008
Overall Mean	.951		.945		.924		.892	
Analysis 2 - lambing performance taken as number of lambs with ewe at mothering all ewes 'lambed and lost' excluded								
Lambing performance*								
Ewe did not lamb	.937	.007	.928	.007	.891	.009	.851	.011
Ewe with one lamb	.958	.006	.959	.006	.943	.007	.905	.010
Ewe with twins	.981	.009	.941	.007	.922	.008	.868	.011
Overall Mean	.955		.949		.931		.874	

* Lambing performance recorded at the first mentioned lambing; e.g. for survival from second to third lambing, lambing performance recorded at the second lambing.

Table 2.3.5

Summary of the analysis of variance examining the effect of lambing performance and type of birth and ewe survival

Lambing performance taken as number of lambs with ewe at mothering

Source of Variation	Performance at first lambing survival to second lambing		Performance at second lambing survival to third lambing		Performance at third lambing survival to fourth lambing		Performance at fourth lambing survival to fifth lambing	
	d.f.	Mean Square x 10^2	d.f.	Mean Square x 10^2	d.f.	Mean Square x 10^2	d.f.	Mean Square x 10^2
Flock	9	5.88	9	15.61	9	2.82	9	7.45
Year	15	18.54*	14	18.30*	13	23.70*	12	37.56*
Lambing Performance (LP)	2	36.75*	2	32.84*	2	64.28*	2	24.39
Type of Birth (TB)	1	0.07	1	1.02	1	9.16	1	0.28
Interaction (LP x TB)	2	0.26	2	9.61	2	2.46	2	5.14
Residual	2804	4.52	2620	5.05	2299	6.83	1914	9.41

Table 2.3.6

Summary of the least squares analysis of lambing performance effects on subsequent ewe survival.

Estimate of overall mean and least square deviation plus the standard error of the least squares deviation

		Probability of survival to second lambing		Probability of survival to third lambing		Probability of survival to fifth lambing	
		u+lsd	s.e.	u+lsd	s.e.	u+lsd	s.e.
Lambing performance at first lambing	0	.928	.007	.878	.010	.699	.016
	1	.961	.006	.919	.009	.772	.014
	2	.980	.010	.907	.014	.755	.021
Lambing performance at second lambing	0			.922	.007	.714	.014
	1			.960	.006	.830	.012
	2			.940	.008	.781	.015
Lambing performance at third lambing	0					.759	.013
	1					.853	.012
	2					.851	.013

Table 2.3.7

Effect of differential ewe survival on retrospective ewe reproductive performance (L_{BJ})

1. Adjacent pairs of lambings

	Lambing			
	1	2	3	4
Average performance for age group (all ewes)	.743	.903	1.011	.960
Performance given that ewe survived to the following lambing	.754	.907	1.021	.967

2. For ewes surviving to have a fifth lambing

	Lambing			
	1	2	3	4
Average performance for age group (all ewes)	.746	.921	.996	.960
Performance given that ewe survived to have a fifth lambing	.770	.946	1.025	.967

breeding flock. The data available to estimate survival to the fifth lambing were extensive and the pattern observed was one of increasing wastage as the ewes became older (Figure 2.3.1). Using the information on survival between successive pairs of lambings, an estimated 78.7 per cent of ewes alive at first lambing were still alive at fifth lambing. Although there is some evidence of statistical heterogeneity among the flocks in survival to various ages, the differences between flocks had little effect on this figure. For instance, the probability of ewes in the Random flocks surviving to have a fifth lambing was 79.5 per cent, while excluding Folds Plus ewes from the data on all ten flocks only increased the probability of survival to fifth lambing to 79.9 per cent. In other words, losses of from 20 to 22 per cent from first to fifth lambing would seem to be quite an accurate characterisation of ewe wastage in this population.

This pattern, of an increase in ewe wastage with age, was maintained when losses between the fifth and seventh lambings were examined. An estimated 50 per cent of ewes alive at first lambing in this population have died or been culled before the seventh lambing. While deaths were approximately twice as important as a source of wastage in the overall figures presented by Dun (1964) for the Folds selection flocks, it seems likely that the probability of a ewe being culled increases with age. This has been reported by Purser and Roberts (1959) whose criteria for culling were essentially the same as those used in the present investigation. If this suggestion is correct, then the pattern of ewe wastage presented in Figure 2.3.1 would overestimate the relationship between age of the ewe and the probability of dying before the next lambing.

The losses recorded here are considerably higher than those reported by Turner, Dolling and Sheaffe (1959) for similar experimental flocks of Merinos and also higher than in the commercial stud flock examined by Granger (1944). The culling of ewes from the Trangie flock would be implicated in the differences in wastage rates between it and the Cunnamulla flocks but, from Dun's (1964) figures on the relative wastage from culling and death, it is unlikely to explain all of it. In addition, Turner, Dolling and Sheaffe (loc. cit.) excluded from their major analyses losses in a drought year. In the present analyses no such exceptions have been made as the aim has been to estimate losses in a representative sample of years encountered by the breeding flock. Finally, while the conditions of supervision and management are generally more intensive at Trangie, at Cunnamulla the ewes were lambed in pens. As ewe deaths around lambing probably represented a considerable proportion of all losses in a year (Gunn, 1967) this may also help to explain the apparently lower losses at Cunnamulla.

The manner in which the selection flocks were compared provided a relatively insensitive test of the effects of selection, as no attempt was made to relate any differences observed to the amount of selection practised. The major reasons for not employing a more sophisticated form of analysis were the changes in culling policy, time of lambing and general degree of supervision at lambing, which occurred in 1962. In this context, it was noticed that in the least squares analyses, ewe wastage over all flocks was consistently lower after 1962 than in the period 1951 to 1961.

The poorer viability of Folds Plus ewes relative to those in the Folds Minus flock, reported by Dun (1964) for the period 1951-1961, was again noted and the Folds Plus flock was also shown to differ significantly from the unselected March Random flock. In comparing the Folds selection flocks, Dun (loc. cit.) suggested that the increased wastage among Folds Plus ewes could be due to the higher birth weight of their lambs (Dun and Wall, 1962) which was often associated with dystocia. He suggested that this not only led directly to the death of lambing ewes but also predisposed them to infections of the uterus and mammary glands and generally led to chronic loss of body condition.

In comparing the subsequent survival of ewes of differing lambing performance, the general pattern could be described as one of stabilising selection, with ewes producing an intermediate number of lambs, one, being most likely to survive birth to the next lambing and also to the fifth lambing. From the numbers of ewes producing 0, 1 or 2 lambs, it can be shown that the average performance of ewes which survive, either to the next lambing, or to the fifth lambing, is higher than the average performance for all ewes present at any lambing between the first and the fourth (Table 2.3.7). A more rigorous examination of the possible effect that this differential ewe mortality could have on associations between age of ewe and reproductive performance will be presented in the next Section.

In these comparisons, the most consistent and clear cut distinction is between ewes which did not lamb and those which did.

This suggests that the reasons leading to a ewe not lambing may be associated with or the same as those predisposing her to be lost from the flock. In this context it must again be stressed that any culling in this population was not on the basis of a ewe's lambing performance per se but only on body condition. For a more complete understanding of the reasons for these differences in the probability of subsequent survival for ewes of different lambing performance, it is obviously important to establish the reason for a ewe's non-appearance at the next lambing and also to classify individual deaths according to the time of the year at which they occur.

Finally there is the need to consider the likely consequences that a selection programme for increased reproductive performance would have for ewe wastage rates. The relationships obtained could not be used to predict wastage in future generations since they are phenotypic and not genetic. However, they could be used to estimate the effects of selection for lambing performance within a cohort of ewes on the probability of ewes within that cohort surviving to a given age. For instance, using the information included in Table 2.3.4, culling all ewes without a lamb at their first lambing (33 per cent of ewes) would increase the probability of the remaining ewes in that cohort surviving to have a fifth lambing from 74.6 to 77.0 per cent, provided, of course, that there were no alterations in the criteria normally adopted for culling in the flock. If it can be assumed that the phenotypic and genetic relationships between lambing performance and the probability of ewe survival are of the same order of magnitude, then the results presented in Tables 2.3.4 and 2.3.6 suggest that selection for increased reproductive performance is not likely to influence ewe mortality to any marked extent.

SECTION 2.4 THE EFFECTS OF AGE OF EWE AND TYPE OF BIRTH ON EWE REPRODUCTIVE PERFORMANCE AND ON LAMB SURVIVAL IN THE TRANGIE FLOCK

In examining age of ewe effects on reproductive performance, data have been drawn from all matings of both the selection and control flocks over the period 1951 to 1969. All ewes from the base population mated in these years were also included. In all, information was available on a total of 17075 matings on 4242 ewes, an average of 4.0 matings per ewe. The distribution of these matings according to age of ewe is given in Table 2.4.1, together with the number of cohorts sampled.

Information was available on the survival to weaning of all lambs born as a result of these matings. Records were not available on the fate, after weaning, of ewes born in 1969 and so information on these ewes could not be included in the analysis of factors affecting survival to hogget shearing.

Methods of Analysis

From the information obtained on the numbers of lambs born and lambs weaned from ewes joined and alive at lambing, the following measures of ewe reproductive performance were recorded:

Numbers of ewes lambing of those joined (E_{LJ})
Number of lambs born per ewe joined (L_{BJ})
Number of lambs born per lambing ewe (L_{BL})
Number of lambing ewes with multiple births (E_{ML})
Number of lambs weaned per ewe joined (L_{WJ})
Number of lambs weaned per ewe lambing (L_{WL})

Table 2.4.1

Number of ewes joined in each age group, summed over all flocks and years

Age of ewe at lambing (years)	Number of ewes joined	Number of cohorts* from which data were obtained
2	3,458	36
3	3,360	36
4	3,198	36
5	2,803	36
6	2,249	36
7	1,023	16
8	526	10
9	304	7
10 and over	154	6

* In these calculations, March and April mated flocks have been taken as making separate contributions.

In these analyses, triplet lamb survival has been treated as a characteristic of the dam, even if the lamb was fostered. For both L_{BL} and E_{ML}, ewes which 'lambed and lost' their lambs before mothering were discarded from the analysis as far as that mating was concerned.

Least squares analysis were used to estimate the relative importance of various factors affecting these measures of ewe reproductive performance. In addition to analyses utilising all available information, a separate set of analyses was conducted on data obtained from the matings between 1962 to 1969, because of the greater confidence which could be attached to records obtained in that period.

The following model was used in these analyses:

$$X_{ijkl} = u + f_i + a_j + y_k + e_{ijkl} \qquad (1)$$

where X_{ijkl} = an individual observation

f_i = the effect of the i^{th} flock

a_j = the effect of the j^{th} age group of ewes

y_k = the effect of the k^{th} year of lambing, and

e_{ijkl} = a random error

Least squares analyses were also used to compare the reproductive performance of ewes born as singles or as twins. All lambings from 1953 to 1969 were included in this comparison, ewes born before 1951 being excluded as no information was available on their type of birth. The model employed was the same as Model 1. with additional terms for type of birth of the ewe and the first order interaction between type of birth and the age of the ewe at lambing.

From the numbers of lambs weaned, estimates were obtained of the number of lambs weaned per lamb born (L_{WB}). As for all measures of lamb survival, two analyses were conducted, one covering the period 1951 to 1969, and the other the years 1962 to 1969. The following model was used to examine L_{WB}:

$$X_{ijklmn} = u + f_i + a_j + y_k + t_l + s_m + ts_{lm} + e_{ijklmn} \qquad (2)$$

where the terms X_{ijklmn}, u, f_i, a_j and e_{ijklmn} have the same meaning as in Model 1. and where:

y_k = the effect of the k^{th} year of birth of the lamb

t_l = the effect of the l^{th} type of birth

s_m = effect of the m^{th} sex, and

ts_{lm} = the first order interaction between sex and type of birth.

Lambs dying before mothering were not included in these analyses. In addition, triplet lambs were not considered, as usually at least one member of the set was fostered, while the small number of ram lambs which were castrated were also excluded.

The lambs were then sorted according to sex and type of birth and survival was estimated separately for singles and twins (S_{WB} and T_{WB}) and then for male and female lambs within each of these type of birth categories; single born rams ($S_{WB.R}$), single born ewes ($S_{WB.E}$), twin born rams ($T_{WB.R}$) and twin born ewes ($T_{WB.E}$). Model 1 was used to examine these characters with 'years' in this case referring to year of birth of the lamb.

The same form of analysis and statistical model (1) were employed in examining ewe survival to hogget shearing. Survival to this age was assessed indirectly, from the presence of a fleece or body weight record. As shearing and weighing occurred on separate days, there was little chance that a ewe alive at that age would elude mustering and recording on both days.

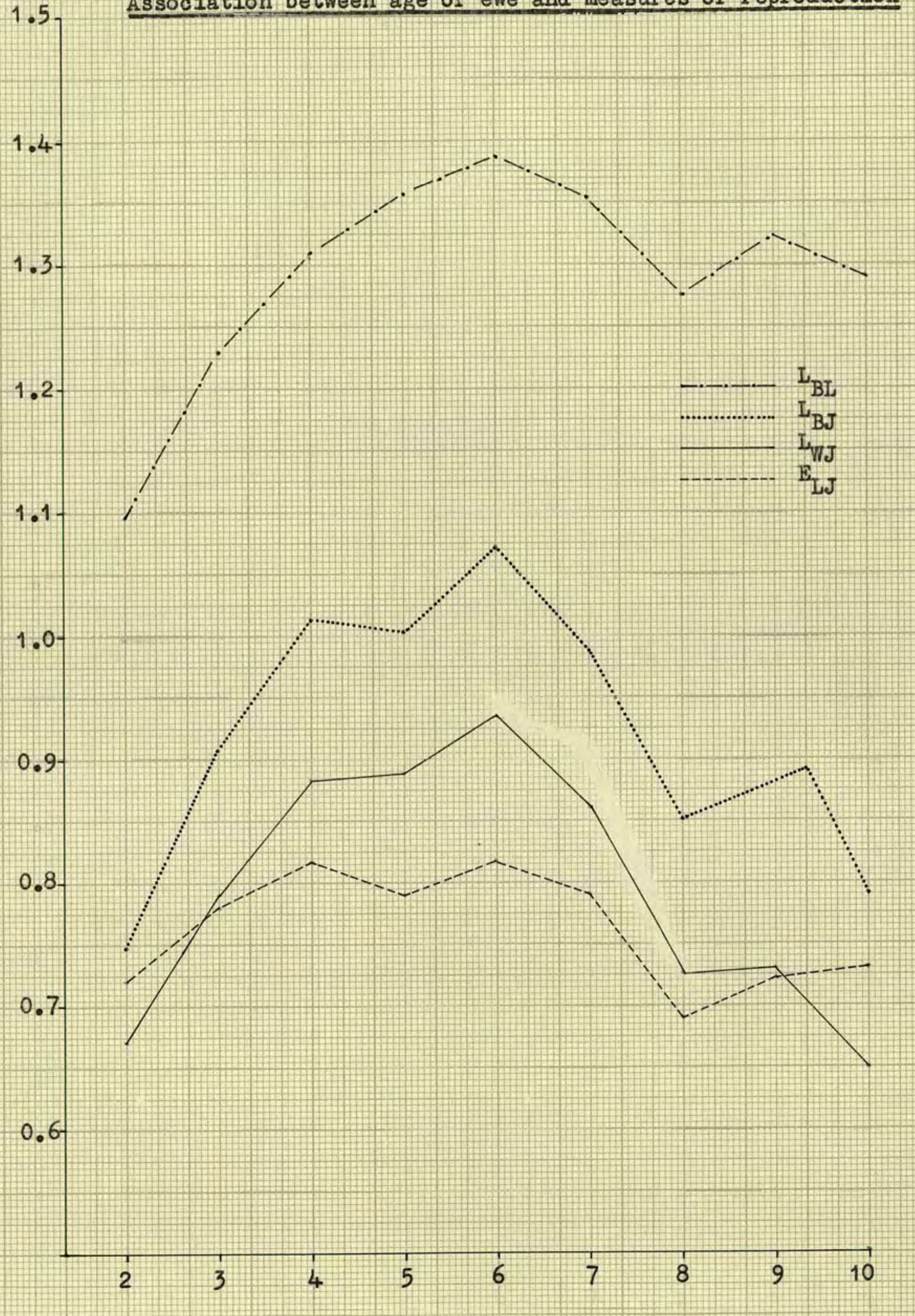
The data utilised in these analyses are binomially distributed or are both discrete and fall into a small number of classes. As the calculation of the standard errors of least squares deviations requires that the data be normally distributed, the accuracy of such estimates included here is questionable, as is the validity of significance tests which are based on estimates of the standard errors. In addition, the least squares analysis of ewe reproductive performance is not entirely adequate, as the total number of matings mainly consisted of repeat observations on the individual ewes. In such circumstances, the observations on an individual ewe are correlated to the extent that the character being investigated is repeatable (r) and the estimate of the error variance (6_e^2) is biased downwards by an amount $r6_e^2$.

Results

In examining ewe reproductive performance, ewes were classified according to nine age groups, from 2 to 10 years of age and over at the time of lambing. The effects of age of ewe, flock and year were adjudged significant for all characters examined, E_{LJ}, L_{BJ}, L_{BL}, E_{ML}, L_{WJ}, L_{WL} (Table 2.4.2). The least squares deviations for different age groups of ewes, and their standard errors, are given in Table 2.4.3 and the deviations plus overall means for all characters other than E_{ML} are presented graphically in Figure 2.4.1. The pattern of association with age was similar for all characters, with an increase from first lambing, when the ewes were two years of age, to a maximum around six years of age, followed by a decline.

Figure 2.4.1

Association between age of ewe and measures of reproduction



Age of ewe at lambing (years)

Table 2.4.2

Summary of the analyses of variance for measures of ewe reproductive performance.

All years, nine ages of ewe

Source of Variation	Degrees of Freedom	Mean Squares			Degrees of Freedom	Mean Squares		
		Ewes lambing of those joined	Lambs born per ewe joined	Lambs weaned per ewe joined		Lambs born per lambing ewe	Ewes with multiple births	Lambs weaned per lambing ewe
Flocks	9	3.104	7.758	8.050	9	6.496	5.953	5.907
Years	18	2.835	14.885	8.589	18	6.638	6.016	3.094
Age of Ewe	8	3.408	24.869	18.143	8	14.482	13.181	9.841
Residual	17038	.180	.469	.450	12113	.196	.181	.285

For example, the number of lambs born per ewe joined rose from 0.75 at 2 years of age, to 1.07 at 6 years, and fell again to 0.79 when the ewes were 10 years of age or older. Corresponding figures for lambs weaned per ewe joined were 0.67, 0.94 and 0.65.

When the data obtained in the period 1962 to 1969 were examined, ewes were classed into seven age groups, from 2 years to 8 years of age and over at lambing. Again age of ewe effects were significant for all six characters examined, and the pattern of association with age of ewe was essentially the same as observed when all data were analysed (Table 2.4.4).

There were no significant differences between single and twin ewes in any measure of reproductive performance (Table 2.4.5). A higher proportion of single ewes lambed (71.8 v. 69.7 per cent) while, for each ewe joined, twin born ewes produced more lambs at both birth (90.4 v. 88.1 per cent) and weaning (76.7 v. 74.2 per cent) (Table 2.4.6). On average twin ewes also had a higher number of lambs per lambing ewe (135.1 v. 131.1 per cent). The birth type x age of ewe term was significant for this character (Table 2.4.5, $P < .05$) and single born ewes were superior at both 2 and 7 years of age (Table 2.4.7).

Using the information collected from all lambings, 1951 to 1969 inclusive, the overall mean for lamb survival to weaning was 87.0 per cent. Year of birth of the lamb, sex and type of birth of the lamb accounted for a significant proportion of the variation ($P < .05$), but age of ewe and the interaction between the sex and the type of birth of the lamb did not (Table 2.4.8). Estimates of the overall mean for lamb survival plus the least squares deviations for

Table 2.4.3

Association between age of ewe and reproductive performance.
Fitted constants, their standard errors, and overall means

1. Nine age groups of ewes

Age of Ewe at lambing (years)	No. of lambing ewes per ewe joined (E_{LJ})		No. of lambs born per ewe joined (L_{BJ})		No. of lambs weaned per ewe joined (L_{WJ})		No. of lambs born per ewe lambing (L_{BL})		No. of lambing ewes with multiple births (E_{ML})		No. of lambs weaned per lambing ewe (L_{WL})	
	lsd	s.e.	lsd	s.e.	lsd	s.e.	lsd	s.e.	lsd	s.e.	lsd	s.e.
2	-.031	.009	-.170	.014	-.126	.014	-.197	.011	-.188	.011	-.137	.014
3	.027	.009	-.009	.014	.008	.014	-.060	.011	-.052	.011	-.030	.014
4	.066	.009	.096	.015	.096	.014	.020	.011	.024	.011	.037	.014
5	.040	.009	.085	.015	.093	.015	.065	.012	.064	.011	.086	.014
6	.067	.010	.154	.016	.140	.016	.097	.012	.090	.011	.096	.015
7	.036	.013	.071	.021	.069	.021	.061	.017	.054	.016	.066	.020
8	-.061	.018	-.070	.029	-.069	.028	-.015	.024	-.012	.023	-.029	.028
9	-.028	.023	-.031	.037	-.065	.036	.031	.029	.026	.028	-.030	.035
10 and over	-.116	.031	-.128	.050	-.145	.049	-.002	.042	-.005	.040	-.060	.050
Overall mean	.753	.003	.919	.005	.796	.005	1.292	.004	0.285	.004	1.119	.005
Proportion of the total variation accounted for by the model (R^2)	.031		.064		.047		.116		.115		.056	

Table 2.4.4

Association between age of ewe and reproductive performance. Fitted constants, their standard errors, and overall means

3. Seven age groups of ewes, years 1962-1969

Age of Ewe at lambing (years)	Deviations from overall means and their standard errors for:											
	No. lambing ewes per ewe joined (E_{LJ})		No. lambs born per ewe joined (L_{BJ})		No. lambs weaned per ewe joined (L_{WJ})		No. lambs born per lambing ewe (L_{BL})		No. lambing ewes with multiple births (E_{ML})		No. lambs weaned per lambing ewe (L_{WL})	
	lsd	s.e.	lsd	s.e.	lsd	s.e.	lsd	s.e.	lsd	s.e.	lsd	s.e.
2	-.042	.012	-.265	.020	-.202	.020	-.290	.016	-.278	.015	-.213	.019
3	-.020	.012	-.107	.020	-.085	.020	-.100	.016	-.091	.015	-.077	.019
4	.046	.012	.078	.021	.081	.020	.021	.016	.028	.015	.038	.019
5	.030	.013	.097	.021	.104	.021	.091	.010	.090	.016	.106	.020
6	.037	.013	.146	.023	.128	.023	.122	.017	.108	.017	.111	.021
7	.042	.024	.180	.040	.139	.040	.142	.030	.119	.028	.103	.036
8	-.092	.035	-.128	.060	-.165	.059	.013	.046	.025	.044	-.068	.056
Overall mean	.747	.005	1.030	.009	.878	.008	1.393	.007	.381	.006	1.188	.008
Proportion of the total variation accounted for by the model (R^2)	.034		.068		.049		.111		.111		.056	

age of ewe, sex and type of birth of the lamb are given in Table 2.4.9. Estimates of survival of single and twin born lambs were 88.0 and 83.6 per cent respectively; the figures for ram and ewe survival were 84.6 and 87.0 per cent respectively. While the effect of age of ewe was not significant, five year old ewes weaned the highest proportion of their lambs, and survival of lambs from the oldest ewes (8 to 10 years of age) was the poorest.

Table 2.4.5

Summary of the analyses of type of birth effects on ewe reproductive performance

Source of Variation	d.f.	Mean Squares			d.f.	Mean Squares		
		E_{LJ}	L_{BJ}	L_{WJ}		L_{BL}	E_{ML}	L_{WL}
Years	16	2.48*	12.42*	6.50*	16	4.49*	4.09*	1.99*
Flocks	9	2.58*	6.47*	6.70*	9	4.32*	3.87*	3.63*
Age of Ewe	8	2.31*	21.26*	15.43*	8	13.99*	12.66*	9.95
Type of Birth	1	0.18	0.23	0.26	1	0.36	0.23	0.24
Age of Ewe x Type of Birth	8	0.29	0.84	0.74	8	0.55*	0.42*	0.52
Residual	13434	0.18	0.49	0.47	9536	0.21	0.19	0.30

Essentially the same results as these were obtained when the analyses were restricted to data collected from 1962 to 1969, over which period the overall mean survival was 86.0 per cent. Again five year old ewes weaned the highest proportion of their lambs, and the oldest age group of ewes, 8 years of age and older, the lowest proportion (Table 2.4.9).

Of all ewe lambs born, 79.9 per cent of singles and 75.1 per cent of twins survived to hogget shearing (Table 2.4.11, $P < .05$). This difference was due almost entirely to the superior survival of single born ewes between birth and weaning as the difference between singles and twins after weaning were small (88.6 v. 88.0 per cent) and not statistically significant. Age of ewe effects on ewe lamb survival to the age of hogget shearing were not significant when expressed as a percentage of either ewe lambs born or weaned.

Table 2.4.6

Estimates of lambing performance of single and twin born ewes

	Character				
	E_{LJ}	L_{BJ}	L_{WJ}	L_{BL}	L_{WL}
Singles	.718	.881	.742	1.311	1.103
Twins	.697	.904	.767	1.351	1.137
Superiority of twins (%) $\frac{T-S}{S} \times 100$	-2.9	2.6	3.4	3.1	3.1

Age of ewe effects were not significant for any of the four sex x type of birth classes of lambs, or when the sexes were pooled and data on the single and twin born lambs were examined (Table 2.4.10). In the twin lamb study, there was a slight tendency for survival to be highest for lambs whose dams were in the intermediate age groups. While age of ewe effects accounted for twice the total variation in twin as in single lamb survival (0.2 v. 0.1 per cent), in both analyses the effect was trivially small. For all ages of ewe, the survival of single lambs was superior to that of twins.

Discussion

In estimating age of ewe effects on both ewe reproductive performance and lamb survival, data were drawn from genetically distinct flocks. In all of these analyses, flock effects were significant and flock means for some of the characters examined are given in Table 2.4.12. The extent to which these flock differences are genetic will be considered later in this thesis. For the moment it will be assumed that neither selection, nor the fact that flocks were mated at different times of the year has biased the relative performance of ewes of different ages.

For the period 1951 to 1969, the average numbers of lambs born and lambs weaned per ewe joined in this population were respectively .919 and .796. An estimated 75.3 per cent of all matings resulted in a ewe lambing. Of these, 27.8 per cent of ewes produced twin lambs, 0.7 per cent triplets, and there was one set of quadruplets.

The pattern of association between age of ewe and both L_{BJ} and L_{WJ} was similar to that previously reported in the literature (see Table 2.2.3 , page 68), with the peak for both characters occurring at six years of age. Only when ewes were ten years of age did they wean as few lambs as did the maidens. The same pattern of association with age was observed for E_{LJ} and L_{BL}, with the peak performance again when the ewes were six years old. On the other hand, age of ewe effects on lamb survival were small as regards their effect on total variation for lamb survival, and maiden and old ewes

Table 2.4.7

Means for the type of birth x age of ewes subclasses for lambs born per ewe lambing (L_{BL})

	Age of Ewe (years)								
	2	3	4	5	6	7	8	9	10
Singles	1.117	1.243	1.332	1.366	1.398	1.431	1.319	1.305	1.285
Twins	1.095	1.279	1.360	1.434	1.483	1.339	1.341	1.423	1.407
Superiority of twins (%) $\frac{T-S}{S} \times 100$	-2.0	2.9	2.1	5.0	6.1	-6.4	1.7	9.0	9.5

were only slightly inferior to ewes of intermediate age in their ability to rear their lambs.

Twin born ewes gave birth to 2.3 per cent more lambs than did single born ewes, and weaned 3.4 per cent more lambs. Results such as these emphasise the importance of increasing the incidence of twinning in Merino flocks. The superiority of the twin born ewes was achieved despite the fact that fewer of them lambed. While the twins produced on average larger litters, this was not so at all ages. The superiority of the single born ewes at first lambing is not surprising, as they are usually heavier at first mating (Dun and Grewal, 1963; Lax and Brown, 1967) and body weight at mating and the incidence of twins at first lambing have been found to be positively correlated in other Merino flocks (see for example, Lax and Brown, 1968). When data on the Random flock ewes were examined, singles were three per cent heavier at hogget shearing (81.5 v. 79.0 lb.), and the phenotypic correlation between the body weight and the incidence of twins at first lambing was .14. Calculated as a regression within each birth type, for every 10 lb. increase in body weight, L_{BL} increased by .03 lambs per lambing ewe. The relative improvement with age in the performance of the twins, at least up to the fifth lambing, may simply reflect the gradual decline in the importance of this maternal handicap that the twins suffer, or it could have a genetic explanation. It is not clear why singles should then be superior at the sixth lambing.

Some comment is necessary on possible bias in these measures of ewe reproductive performance. The obvious contributors to bias were the relatively infrequent mothering of lambs and ewes over the period 1951 to 1961, and the 5.9 per cent of all lambing ewes were recorded having lost their lambs before mothering (see Table 1.1.2, page 12). The first of these factors would act to underestimate performance at birth (L_{BJ}, L_{BL}, E_{ML}) for any ewe losing lambs between birth and mothering, but still having at least one live lamb at mothering. The 'lambed and lost' category is simply the limiting form of this problem of underestimation, where a ewe has lost all of her lambs by mothering. In underestimating the number of lambs at birth, lamb losses to weaning are also underestimated. It is not clear to what extent such factors could bias the age group comparisons for characters such as L_{BL} and L_{WB}. However, they will not influence either the overall performance of the population for L_{WJ}, or the relative age groups of ewes for this character.

Table 2.4.8

Summary of analysis of variance of factors affecting lamb survival to weaning

Source of Variation	All Years		1962-1969	
	d.f.	Mean Squares	d.f.	Mean Squares
Years	18	.399*	7	.465*
Flocks	9	.306*	9	.284*
Lambing	8	.180	6	.190
Sex	1	2.135*	1	1.901*
Type of Birth	1	6.041*	1	2.060*
Sex x Type of Birth	1	.196	1	.353
Residual	14556	.112	7134	.119

* $P < .05$

Lamb losses between birth and weaning were estimated at 13 per cent for the period 1951 to 1969, and 14 per cent from 1962 to 1969. As was pointed out in the previous paragraph, both figures are underestimates of mortality. If we ignore the possibility that the litter size of ewes with lambs at mothering is underestimated, then revised estimates of lamb mortality can be obtained from the incidence of 'lambed and lost' ewes in the two periods and different age groups, and by assuming that they produced litters of the same size as the average for ewes of their age. Estimates of lamb mortality were then 17.5 per cent for the whole period covered, and 14.8 per cent for the years 1962 to 1969. Using the estimate of 82.5 per cent survival between birth and weaning, and allowing for the superior survival of ewe lambs to weaning (Table 2.4.9) then the re-estimated proportion of ewe lambs surviving from birth to hogget shearing was 74.7 per cent.

The superior survival of single lambs compared with twins in this study, and of ewe lambs compared with rams, has been observed in all other studies with the Merino where such comparisons have been made (see Table 2.2.5, page 71). The sex difference of approximately three per cent is representative of all these investigations. On the other hand, the relative survival of singles and twins has been quite variable, and the figure reported here, of 3.4 per cent for the period 1962 to 1969, is much lower than obtained elsewhere (Turner and Dolling, 1965; Mullaney and Brown, 1969).

The percentage deviation technique (Turner and Dolling, 1965) has been used to assess the relative contribution of the components

Table 2.4.9

Factors affecting lamb survival to weaning: Fitted constants plus the overall mean with standard errors of the constants

Factor	All Years		1962-1969	
	Fitted constant + overall mean	Standard error of constant	Fitted constant + overall mean	Standard error of constant
Age of ewe at lambing				
2	.868	.008	.866	.011
3	.866	.007	.850	.010
4	.870	.007	.868	.010
5	.883	.008	.876	.010
6	.865	.008	.862	.011
7	.869	.011	.854	.019
8	.853	.015	.790	.027
9	.835	.019		
10	.815	.023		
Type of Birth:				
Single	.880	.003	.870	.004
Twin	.836	.003	.834	.004
Sex:				
Male	.846	.003	.836	.004
Female	.871	.003	.869	.004
Overall Mean	.870	.003	.860	.004
Proportion of the total variation accounted for by the model (R^2)	.012		.015	

Table 2.4.10

Association between age of ewe and survival rate to weaning of lambs of different types:

1. Years 1951 to 1969; Nine age groups of ewes

Age of Ewe at lambing (years)	Fitted constant plus overall mean for:					
	$S_{WB.R}$	$S_{WB.E}$	S_{WB}	$T_{WB.R}$	$T_{WB.E}$	T_{WB}
2	.878	.904	.890	.794	.873	.833
3	.880	.893	.886	.846	.846	.847
4	.872	.916	.894	.885	.838	.847
5	.877	.922	.900	.849	.877	.863
6	.853	.893	.873	.846	.859	.852
7	.846	.905	.877	.835	.872	.853
8	.860	.894	.877	.844	.816	.831
9	.824	.920	.873	.733	.851	.792
10 and over	.819	.897	.858	.718	.778	.748
Overall mean	.873	.905	.889	.835	.854	.845
2. Years 1962 to 1969; Six age groups of ewes						
2	.860	.910	.885	.799	.866	.832
3	.862	.868	.865	.840	.827	.833
4	.858	.920	.889	.860	.837	.848
5	.858	.913	.885	.856	.862	.859
6	.822	.902	.862	.828	.879	.853
7 and over	.863	.871	.867	.768	.841	.804
Overall mean	.857	.904	.880	.833	.853	.840

to age group differences in ewe reproductive performance. The age groups chosen for comparison were 2, 6 and 10 year old ewes, as they represented the extremes in terms of both age and performance. The deviations presented in Table 2.4.13 are from the overall means. The six year old ewes were above the mean in both E_{LJ} and L_{BL}, and these components contributed almost equally to the superiority of this age group in L_{BJ} and L_{WJ}. At the other extreme of performance, the 2 and 10 year old ewes performed similarly for L_{WJ} but for rather different reasons. The poor performance of the two year old ewes was because they produced few twins. The ten year old ewes were most noticeably below average in the proportion of ewes lambing and, to a lesser extent, in lamb survival. Compared with the two year old ewes, the poorer survival of lambs from 10 year old ewes was apparent both for single and twin born lambs, and was not simply a reflection of the higher proportion of twins produced by the older group of ewes. In general, these results are similar to those reported for the Cunnamulla flocks of Merinos by Turner and Dolling (1965).

In addition to these percentage deviation comparisons, the percentage of the total variation accounted for by age of ewe effects has been used as a measure of the contribution that the components make to the variation in reproductive performance over all age groups. Age of ewe effects had the greatest influence on the variation in L_{BL} (4.3 per cent) and considerably less on either E_{LJ} or L_{WB} (0.9 and 0.2 per cent respectively).

It should be pointed out that the proportion of the total variation accounted for by any of these models was small, of the order

Table 2.4.11

Influence of age of dam and type of birth on the survival rate of ewe lambs to hogget shearing: least squares deviations plus overall mean and standard errors of the deviations

Factor	Analyses					
	1. Survival rate of ewe lambs as a percentage of all lambs born		2. Survival rate of ewe lambs as a percentage of all ewe lambs born		3. Survival rate of ewe lambs as a percentage of all ewe lambs weaned	
	Deviation + Overall Mean	Standard Error	Deviation + Overall Mean	Standard Error	Deviation + Overall Mean	Standard Error
Age of ewe at lambing (years)						
2	.409	.011	.775	.014	.877	.011
3	.397	.011	.762	.013	.874	.010
4	.415	.011	.782	.013	.891	.010
5	.409	.011	.813	.014	.897	.011
6	.405	.012	.773	.014	.881	.011
7	.422	.016	.772	.018	.870	.015
8	.421	.021	.782	.025	.911	.020
9	.366	.027	.773	.033	.865	.026
10	.380	.032	.743	.039	.879	.032
Type of birth:						
Single			.799	.005	.886	.004
Twin			.751	.005	.880	.004
Overall Mean	.402	.004	.789	.005	.892	.004

of one per cent for lamb survival and varying from 3 to 12 per cent for ewe reproductive performance. Similar results to these were obtained by De Haas and Dunlop (1969) and Mullaney and Brown (1969; 1970) and De Haas and Dunlop suggested that this is due, at least in part, to the coarseness of measurement implicit in a binomial classification.

Finally it is necessary to return to a topic introduced in the previous Section. There it was reported that for a particular lambing, the average performance of all ewes alive at that lambing was less than the average for ewes which also survived to have a subsequent lambing. This could be described as a directional effect of natural selection. In the same flock, it was customary, over at least half of the period under investigation, to cull ewes considered to be incapable of rearing another lamb. The effect of both forms of selection would be to bias upwards the relative performance at later lambings. The extent of this bias would depend on the repeatability of the character and, in the culling programme, the accuracy with which potentially poor producers could be identified. In both models of selection, it would also be expected that the average performance of ewes which survived to have some later lambing would be above average at all previous lambings. This trend was, in fact, observed in a comparison of ewes born sufficiently early to have had the opportunity for at least five lambings (Table 2.4.14). In other words, estimates of age trends obtained from such ewes would be biased in such a way that the relative performance of the later and most productive ages would be overestimated.

Table 2.4.12

Flock means for various measures of ewe reproductive performance.

From analyses over all years, nine age groups of ewes

Flock	Character			
	Ewes lambing of those joined (E_{LJ})	Lambs born per ewe joined (L_{BJ})	Lambs born per lambing ewe (L_{BL})	Lambs weaned per lambing ewe (L_{WJ})
March mated flock				
Random	.769	1.007	1.375	.878
Weaning Wt. Plus	.713	.923	1.373	.794
Weaning Wt. Minus	.696	.927	1.399	.783
Folds Plus	.636	.762	1.291	.637
Folds Minus	.744	.974	1.356	.858
April mated flock				
Random	.759	.905	1.232	.764
Fleece Plus	.710	.840	1.244	.698
Fleece Minus	.786	.895	1.194	.773
Crimps Plus	.758	.876	1.220	.762
Crimps Minus	.746	.920	1.311	.768

Table 2.4.13

Contribution of components to age of ewe differences in L_{BJ} and L_{WJ}

1. Lambs born per ewe joined				
Age of Ewe at lambing (years)	Percentage deviation from the Mean in:			
	L_{BJ}	E_{LJ}	L_{BL}	
2	-15.9	- 4.1 (21.1)†	-15.3 (78.9)	
6	+16.8	+ 8.9 (54.3)	+ 7.5 (45.7)	
10	-13.9	-15.4 (98.7)	- 0.2 (1.3)	
Overall Mean	.919	.753	1.292	
2. Lambs weaned per ewe joined				
	L_{WJ}	E_{LJ}	L_{BL}	L_{WB}
2	-15.8	- 4.1 (20.9)	-15.3 (78.1)	-0.2 (1.0)
6	+17.6	+ 8.9 (56.3)	+ 7.5 (47.5)	-0.6 (-3.8)
10	-18.2	-15.4 (71.0)	- 0.2 (0.9)	-6.3 (29.1)
Overall Mean	.796	.753	1.292	.870

† Figures in brackets indicate the proportion of the deviation in L_{BJ} or L_{WJ} which can be attributed to that component.

Table 2.4.14

The effect of differential ewe wastage on the association between reproductive performance and age of ewe ≠

Estimates of least squares deviations plus the overall mean, and standard errors of the deviations

Lambs born per ewe joined	All ewes had five lambings		No restriction on number of lambings	
	lsd + u	s.e.	lsd + u	s.e.
Age of ewe at lambing (years)				
2	.771	.015	.741	.013
3	.938	.015	.914	.013
4	1.021	.015	.993	.013
5	.978	.015	.962	.014
6	1.077	.015	1.077	.014
Overall mean (u)	.970	.008	.940	.007

Lambs weaned per ewe joined	All ewes had five lambings		No restriction on number of lambings	
	lsd + u	s.e.	lsd + u	s.e.
Age of ewe at lambing (years)				
2	.680	.015	.648	.013
3	.817	.015	.788	.013
4	.879	.015	.854	.013
5	.867	.015	.845	.014
6	.923	.015	.924	.014
Overall mean (u)	.844	.007	.814	.007

≠ All ewes were born in the years 1951 to 1963.

SECTION 2.5 THE SCOPE FOR CULLING IN THE TRANGIE POPULATION

The information presented on age specific rates of both ewe wastage and reproductive performance can now be used to estimate the overall reproductive performance of this Merino population, and the relevant results are summarised in Table 2.5.1. In adjusting ewe losses between lambings (Table 2.3.3) to losses between matings (Table 2.5.1) it has been assumed that losses are equally frequent before and after lambing. The same assumption also enables estimates of ewe reproductive performance to be related to ewes joined and not ewes joined and alive at lambing (Table 2.4.3). Wastage between first mating and first lambing has been taken as half the wastage between the first and second lambing.

The Trangie population could be maintained by retaining ewes in the breeding flocks for only three years (Table 2.5.2). For flocks of from 3 to 7 age groups, seven being the largest number of age groups considered here, both the innate capacity for increase and the net reproduction rate rose as additional age groups were retained. For a flock of seven age groups, the population could grow at the rate of 159 per thousand per year, or, alternatively, 53 per cent of hogget ewes could be culled.

Compared with the three age groups necessary for the self-reproduction of the Trangie flock, the population described by Moule (1971) required seven age groups and the Cunnamulla population (Turner and Young, 1969) four. However, the Cunnamulla flock was superior to the Trangie flock in both N.R.R. and r_m if at least six age groups were kept.

One consequence of selecting ewes already in the breeding flock is that the age structure of the flock must be altered if both its size and the number of age groups are to remain constant. For instance, to cull ewes after third lambing, it is also necessary to join more ewes at the first two matings. As a simple example in which natural wastage is ignored, each age group in a flock of five age groups would constitute 20 per cent of the total numbers. To cull 50 per cent of ewes after the third lambing, the proportions in the five age groups would then be 25, 25, 25, 12½ and 12½ per cent. When natural wastage is taken into account, the increase in numbers joined at the early matings would be greater to allow for the same percentage of ewes to be culled after third lambing.

As Yalcin and Bichard (1964) pointed out, altering the age structure by increasing the proportion of young ewes in the flock often results in lowering overall flock reproductive performance. The magnitude of any such possible effects will be considered later in conjunction with responses to selection to specified levels of culling.

As to the scope for selection after ewes have entered the breeding flock, the maximum amounts of culling possible after the first or second lambings in a flock of seven age groups of ewes are respectively 62 and 76 per cent of ewes of that age. These figures correspond to 24 and 26 per cent respectively of all ewes in the breeding flock. Of course, after the third lambing all ewes could be culled, as by that time each ewe will, on average, have replaced herself. However, culling all ewes after the third lambing would mean that there would be no artificial selection based on that lambing record. In deciding on a culling policy to improve ewe reproductive performance, it would clearly be important to estimate not only the expected overall improvement in flock performance but also the relative response and hence the relative future performance of the different age groups of ewes.

Information can be gleaned from Table 2.5.1 and 2.5.2 on the effect of altering the age structure of the flock on the generation length. Increasing the number of age groups may increase the amount of selection which is possible, but it need not lead to the most rapid response. Calculations have been made of the ratio of the standardised selection differential to generation length for a flock in which selection is among hogget ewes and in which two systems of ram usage are possible (Table 2.5.3). For both systems of ram selection, the ratio is at a maximum when six or seven age groups of ewes are maintained. With appropriate estimates of heritability, it would be possible to translate these ratios into expected genetic progress.

The effects of altering the age structure on flock productivity can be seen in Table 2.5.4. As in the Cunnamulla flock, increasing the number of age groups up to seven would lead to an increase in the numbers of weaner rams and of surplus hogget ewes available for disposal. On the other hand, there would be fewer cast for age ewes and these would be older when cast. As Townsley and Schroder (1964) have pointed out, any decision on an optimal flock structure is essentially an economic one, taking into account both the quantity and value of saleable items produced. It would obviously be necessary to consider age of ewe effects on wool production and quality (Brown et. al., 1966) when attempting to determine an optimal age structure for a Merino population such as this. Finally, it should be appreciated that the foregoing discussion relates to a flock which is not undergoing selection for such production characters; selection introduces a considerable number of complications into such deliberations (see Turner, Brown and Ford, 1968).

Table 2.5.1

Values used in the calculation of overall means of reproduction

Age interval between joinings (years)	Pivotal age	Death rate (d_x)	Probability of survival to beginning of age interval (l_x)	Ewe lambs reaching age of first mating as percentage of ewes joined (M_x)	$l_x m_x$	$x l_x m_x$
1½ - 2½	2	0.042	1.000	0.300	0.300	0.600
2½ - 3½	3	0.044	0.958	0.354	0.339	1.017
3½ - 4½	4	0.051	0.916	0.411	0.376	1.504
4½ - 5½	5	0.070	0.869	0.400	0.345	1.725
5½ - 6½	6	0.112	0.808	0.417	0.337	2.022
6½ - 7½	7	0.197	0.718	0.322	0.231	1.617
7½ - 8½	8	0.255	0.577	0.321	0.185	1.480

Table 2.5.2

Overall measures of reproduction for flocks of various age structures

Measure of performance	Flock Structure				
	Ewes of 3 ages (2-4 years)	Ewes of 4 ages (2-5 years)	Ewes of 5 ages (2-6 years)	Ewes of 6 ages (2-7 years)	Ewes of 7 ages (2-8 years)
Net reproduction rate (N.R.R.)	1.015	1.360	1.697	1.928	2.113
Generation length (T)	3.075	3.563	4.047	4.401	4.716
Number of hogget ewes selected - as proportion of number available (1/N.R.R.)	.985	.735	.588	.519	.473
Number of hogget ewes which can be culled as proportion of those available (N.R.R. - 1)/N.R.R.	.015	.265	.412	.481	.527
Innate capacity for increase (r_m)	.005	.086	.131	.149	.159

Table 2.5.3

The relationship between the amount of selection which can be applied and the generation length for flocks of different age structures, where selection is only among hogget ewes

Number of age groups of ewes	Number of replacement ewes required (and available)	Standardised selection intensity (S.S.I.)	Rams used once at two years of age		Rams used twice at two and three years of age	
			Generation length (G.L.)	Ratio of $\frac{S.S.I.}{G.L.}$	Generation length (G.L.)	Ratio of $\frac{S.S.I.}{G.L.}$
Three (ewes 2-4 years)	348 (353)	.038	2.59	.015	2.79	.014
Four (ewes 2-5 years)	267 (364)	.445	2.78	.160	3.03	.147
Five (ewes 2-6 years)	220 (374)	.662	3.02	.219	3.27	.202
Six (ewes 2-7 years)	190 (366)	.768	3.20	.240	3.45	.223
Seven (ewes 2-8 years)	171 (362)	.810	3.36	.241	3.61	.224

Table 2.5.4

The effect of altering flock structure on flock performance

Number of age groups of ewes	Number of $1\frac{1}{2}$ year old ewes produced	Number of $1\frac{1}{2}$ year old ewes for disposal	Number of ram weaners produced	Number of cast for age ewes produced (age at casting)
Three (ewes 2-4 years)	353	5	384	311 (4 years plus)
Four (ewes 2-5 years	364	97	395	226 (5 years plus)
Five (ewes 2-6 years)	374	154	405	169 (6 years plus)
Six (ewes 2-7 years)	366	176	405	126 (7 years plus)
Seven (ewes 2-8 years)	362	191	397	86 (8 years plus)

SECTION 2.6 THE RESPONSE TO SELECTION FOR INCREASED REPRODUCTIVE PERFORMANCE - A REVIEW

Having demonstrated that the opportunity exists for ewe culling in the Trangie population, the aim now is to assess the response which might be achieved to selection for increased reproductive performance. As is customary, this will be considered both as response in the current flock and response in future generations. The first is determined by the repeatability of the character, the correlation between records obtained at different lambings on the same ewe and, more particularly, the extent to which early records can be used to predict subsequent performance. Response in future generations is determined by the heritability of the character at particular lambings, and by the genetic correlation between performance at different lambings.

Repeatability of Ewe Reproductive Performance

Estimates of the repeatability of reproductive performance have been obtained either as the intra-class correlation or as the regression of subsequent on initial performance. This latter method was proposed by Lush (1956). Ewes are classified as having produced 0, 1, 2 etc. lambs at a particular lambing, and the performance at some later lambing is then calculated for each of these classes of ewes. In addition to providing information from which the repeatability of performance can be estimated, it also allows a check on the linearity of the relationship between initial and subsequent performance. Linearity is assumed when, for instance, intra-class correlation estimates are used to predict gains from selection.

The repeatability of ewe fertility has been estimated for a large number of breeds (Reeve and Robertson, 1953; Turner, 1969a, b) and correlation estimates are summarised in Table 2.6.1. In general, estimates for L_{BJ} and L_{WJ} have been low although quite often the estimates were statistically significant. Where estimates are available for both characters in the same study (Young, Turner and Dolling, 1963; Purser, 1965; Inskeep, Barr and Cunningham, 1967; Kennedy, 1967; Yalcin and Bichard, 1964), there was no consistent trend in their relative magnitude. Regression estimates of the repeatability of L_{BJ} and L_{WJ} have generally been of similar magnitude to intra-class correlation estimates, although where both have been obtained from the same body of data, the regression estimates have consistently been higher (Purser, 1965; Hallgrimsson, 1966).

When the components of L_{WJ} and L_{BJ} are examined, the highest average set of repeatability estimates have been obtained for L_{BL} and E_{ML} (Table 2.6.1). However, only rarely have estimates for the different components come from the same study. Where they have (Purser, 1965), the repeatability of L_{BL} was higher than for E_{LJ}, and also higher than for the composite characters L_{BJ} and L_{WJ}.

The relationship between initial and subsequent performance has been calculated for a large number of flocks (see Turner, 1969a, b) and results obtained for the Australian Merino are summarised in Table 2.6.2. In almost all such studies, the two have been found to be positively related, the only exception being for the tendency of ewes to lamb (E_{LJ}) in a Rambouillet flock examined by Shelton and Menzies (1970).

Table 2.6.1

Repeatability estimates for ewe reproductive performance and its components, as estimated by intra-class correlation

Characteristic	Breed	Ages of observation (years)	Estimate	Authors
Lambs weaned per ewe joined L_{WJ}	Australian Merino	2 - 7	0.08	Young, Turner and Dolling (1963)
	Scottish Blackface	2 - 5	0.01	Purser (1965)
	Welsh Mountain	2 - 3	0.07	
	Various	2 - 4	0.13	Inskeep, Barr and Cunningham (1967)
	Australian Merino (Trangie flock)	2 - 5	0.04	Kennedy (1967)
Lambs born per ewe joined L_{BJ}	Various (Columbia & British breeds)	2 - 4	0.05	Desai and Winters (1951)
	Texel	not stated	0.09	Sharafeldin (1960)
	Australian Merino	2 - 7	0.05	Young, Turner and Dolling (1963)
	Scottish Blackface	2 - 5	0.07	Purser (1965)
	Welsh Mountain	2 - 3	0.10	
	Various	2 - 4	0.11	Inskeep, Barr and Cunningham (1967)
	Australian Merino (Trangie flock)	2 - 5	0.07	Kennedy (1967)
Failure to lamb E_{LJ}	Scottish Blackface	2 - 5	0.09	Purser (1965)
	Welsh Mountain	2 - 3	0.08	
Lambs born per ewe lambing L_{BL}	Shropshire	2 - 3	0.15	Johansson and Hansson (1943)
	Cheviot	2 - 3	0.17	
	Landrace	2 - 3	0.19	
	Rahmani	2 - 7	0.06	Karam (1957)
	BL x Cheviot	2 - 8	0.04 to 0.12	Yalcin and Bichard (1964)
	Scottish Blackface	2 - 5	0.19	Purser (1965)
	Welsh Mountain	2 - 3	0.24	
Lambing ewes with multiple births E_{ML}	Shropshire	2 - 5	0.09	Rendel (1956)
	Cheviot	2 - 5	0.15	
	Landrace	2 - 5	0.06	
	Oxford Down	2 - 5	0.08	
Lambs weaned per ewe lambing L_{WL}	BL x Cheviot	2 - 8	0 to 0.08	Yalcin and Bichard (1964)
	Scottish Blackface	2 - 5	0.07	Purser (1965)
	Welsh Mountain	2 - 3	0.10	

Turner (1969a, p. 547) has concluded that the relationship between initial and subsequent performance for either L_{BJ} or L_{WJ} is not linear. In other words the difference between ewes producing 0 v. 1 lambs is not the same as the difference between ewes producing 2 v. 1 lambs. Such an assessment is true in the sense that the differences are rarely exactly equal, but in neither the results obtained for Merino flocks (Table 2.6.2) nor those for all breeds (Turner, 1969a, b) is there any consistent trend in the relative magnitude of such differences.

In any particular study, deviations from linearity are important for a number of reasons. Firstly, if the relationship between initial and subsequent performance is monotonic, then deviations from linearity would not alter the choice of ewes to cull if reproductive performance was the only character being considered. However, where multiple trait selection is being practised, deviations from linearity could alter the amount of selection pressure allocated to improving reproductive performance. Secondly, deviations from linearity can influence the precision with which initial performance had to be recorded. For instance, if almost maximal gains could be achieved by culling ewes which failed to lamb, then it may be considered unnecessary to record the actual number of lambs produced by lambing ewes. Such considerations could have an important bearing on the feasibility of applying selection programmes on commercial properties, and would have to be assessed along with information on the scope for culling in the population.

Table 2.6.2

The relationship between early and subsequent performance in the Australian Merino

Character	Author	Initial Performance		Subsequent Performance		
		Age (years)	Class	Age	Actual performance	Difference from previous class
Lambs weaned per ewe joined L_{WJ}	Young, Turner & Dolling (1963)	2-4 (single lambing)	0 1 2	Average performance 3-7 years	Not available	+0.07 +0.17
Lambs born per ewe joined L_{BJ}	Young, Turner & Dolling, (1963)	2-4 (single lambing)	0 1 2	Average performance 3-7 years	Not available	+0.08 +0.16
	Dun (1961) (Trangie flock)	Mixed (single lambing)	0 1 2	One year later	0.76 1.28 1.43	+0.45 +0.15
	Pattie (pers. comm.) (Trangie flock)†	2	0 1 2	Average performance 3-5 years	0.77 1.12 1.30	+0.35 +0.18

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† Cited by Turner (1969a, b).

No consistent association has been observed between the magnitude of the repeatability estimate for a character at two lambings and the number of years separating the observations (Purser, 1965; Hallgrimsson, 1966). In addition, no general pattern has emerged when the predictive value of individual lambings has been compared (Young, Turner and Dolling, 1963; Purser, 1965; Hallgrimsson, 1966; Shelton and Menzies, 1970). For instance, Purser found that among pairs of consecutive lambings, L_{BL} at first lambing was the poorest predictor of L_{BL} at the following lambing, while Shelton and Menzies found early records to be the best predictors of this character. On the other hand, they found that the ability to predict whether a ewe would lamb in the following year increased with age. In early years, the relationship between E_{LJ} in successive years was actually negative.

If the repeatability is the same over all lambings, then the repeatability of the mean of n records ($t_{\bar{n}}$) is given by:

$$t_{\bar{n}} = \frac{nt}{1 + (n - 1)t} \qquad \text{(Lush, 1945)}$$

Thus for the mean of 2 or 3 lambings, the repeatability of, say, L_{BL} would be increased by:

$$\frac{t(1 - t)}{1 + t} \quad \text{and} \quad \frac{2t(1 - t)}{1 + 2t}$$

respectively over that for an individual lambing. While selection on pooled records has been discussed (e.g. Turner, 1969a, b) there is little direct information on their value. Turner (1966) found that ewes dry at their first two lambings were more likely to be dry, and give poorer results for L_{BJ}, at subsequent lambings. Results presented by both Johansson and Hansson (1943) and Karam (1957) indicate that the predictive value of pooled records is higher but in neither case can these estimates be directly compared with those for appropriate individual records.

Shelton and Menzies (1970) estimated the repeatability of both E_{LJ} and L_{BL} in two genetically similar flocks of Rambouillet maintained at different locations, and found that the magnitude of the estimates were positively related to the level of expression of the two characters. In a study not previously mentioned, Barrett and May (1958) concluded from contingency tables that there was no association between early and subsequent performance for L_{BJ} in a flock which contained few twins. Both of these results could be interpreted as suggesting that environmental factors, nutritional or possibly related to specific management practices at mating or lambing, can influence the correlation between a ewe's performance in different years.

Little is known of the effect that selection for increased reproductive performance might have on the scope for further improvements in current flock production. However, the estimate of 0.31 for the repeatability for L_{BJ} reported by Turner (1966)* for her high

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* It has been assumed that these estimates are not on selected records, but on unselected records in populations where previous cohorts have been subject to selection.

fertility flock is considerably higher than reported for other Merino flocks. Again the results reported by Wallace (1964, Tables 15 and 16)* for both E_{LJ} and L_{BJ} do not indicate any decline in repeatability as a result of selection.

The gain that can be obtained in current flock performances is usually calculated as pd, where p is the proportion culled and d the difference in future production between those culled and those retained (Turner, 1969a). Culling of dry ewes is the procedure usually considered and predicted gains for various populations are given in Table 2.6.3. In general the improvement to be expected is not great, although gains of from 7 to 9 per cent suggested for the Trangie population (Dun, 1961; Pattie, 1968) would certainly be worthwhile. However, it is perhaps rather surprising that, for the Merino populations so far mentioned, no consideration has been given to the need to alter flock structure in order to practise selection on ewe lambing performance, and the effect that this might have on flock performance (Yalcin and Bichard, 1964).

Responses in Future Generations

The heritability of ewe reproductive performance

Considerable attention has been given to methods of estimating the heritability of various measures of ewe reproductive performance. For both L_{BJ} and L_{WJ} half-sib correlation methods have in general been preferred. The difficulty in using daughter-dam methods lies in the fact that only dry ewes who at some other lambing, produce a daughter can be included, so that estimates obtained could be biased. Young, Turner and Dolling (1963) have pointed out that half-sib estimates could

Table 2.6.3

Gain in subsequent performance L_{BJ} through culling ewes which fail to lamb in various Australian Merino flocks

Flock	Subsequent performance	Proportion culled (p)	Difference in subsequent performance (lambs born) between culled and selected (d)	Gain in L_{BJ}
Turner (1966)	Average for			
Flock 1	3-6 years	0.20	0.025	0.005
Flock 2	3-6 years	0.20	0.297	0.059
Trangie flock				
Dun (1961)[‡]	One year later	0.13	0.540	0.070
Pattie (1968)	Average for			
	3-6 years	0.24	0.388	0.093

[‡] In all but this flock, culling was on performance at first lambing, two years of age; Dun considered the effect of culling at any lambing from the first to the sixth.

also be biased as all sires are from a selected group of ewes, those that produced at least one lamb, a male.

In their review of literature, Reeve and Robertson (1953) concluded that the estimates of heritability of ewe reproductive performance were low. Since then, numerous estimates have been published for a wide range of breeds, and the conclusion reached by Reeve and Robertson would still seem to be true, at least for L_{BJ} and L_{WJ} (see Table 2.6.4). Where estimates were given for both of these characters, the heritability of L_{BJ} has consistently been higher (Young, Turner and Dolling, 1963; Purser, 1965; Kennedy, 1967). Comparatively little information is available on the components of either overall measure of performance. In the only study in which estimates were obtained, Purser (1965) found the heritability of L_{BL} to be greater than for E_{LJ}, in which there was effectively no genetic variation. Turner (1966) also presented evidence to suggest that the heritability of E_{LJ} was low, but this was obtained from daughter-dam analysis.

Young, Turner and Dolling (1963) found that the heritability of L_{BJ} was considerably higher at second than at first lambing, although the estimates did not differ significantly. Purser (1965) also demonstrated an increase in the heritability of L_{BL} with age, a trend not shown by E_{LJ}, and only slightly by L_{BJ}. On the other hand, Hallgrimsson (1966) found no such trend.

Where it has been investigated, the heritability of records pooled over a number of lambings has been found to be higher than for the individual component pairs of lambings (Hallgrimsson, 1966;

Table 2.6.4

Heritability estimates for L_{WJ} and L_{BJ} and their components

Characteristic	Breed	Age of observation (years)	Estimate	Authors
Lambs weaned per ewe joined L_{WJ}	Australian Merino	2 3 2 + 3	0.03 0.15 0.09	Young, Turner and Dolling (1963)
	Australian Merino	2	0.06	Kennedy (1967)
	Scottish Blackface Welsh Mountain	2 - 6 2 - 4	0.00 0.03	Purser (1965)
	Rambouillet	Lifetime	0.22	Shelton and Menzies (1968)
Lambs born per ewe joined L_{BJ}	Columbia and British breeds	2 - 4 (average of no. of lambings)	0.07	Desai and Winters (1951)
	Texel	not stated	0.03 to 0.17	Sharafeldin (1960)
	Australian Merino	2 3 2 + 3	0.02 0.35	Young, Turner and Dolling (1963)
	Australian Merino	2	0.20	Kennedy (1967)
	Scottish Blackface Welsh Mountain	2 - 6 2 - 4	-0.01 0.07	Purser (1965)
	Icelandic	Four age groups	0.12 to 0.19	Hallgrimsson (1966)
	Romney	1	0.05	Ch'ang and Rae (1970)

Lambs born per ewe lambing L_{BL}	Cheviot	2	0.04	Johansson and Hansson (1943)
	Oxford Down	Sum of lambings (2-6 years)	0.17	
	Shropshire		0.26	
	Cheviot		0.18	
	Scottish Blackface	2 - 6	0.14	Purser (1965)
	Welsh Mountain	2 - 4	0.16	
	American Rambouillet and crosses	Mixed	0.21	Vakil et al (1968)
Ewes failing to lamb per ewe joined E_{LJ}	Scottish Blackface	2 - 6	-0.03	Purser (1967)
	Welsh Mountain	2 - 4	0.03	
Ewes with multiple births E_{ML}	Ossimi	not given	0.04	Ragab and Asker (1954)
	Crossbred	2	0.08	Sidwell (1956)
		Mature	0.22	
	Navajo	2	0.40	
		Mature	0.12	
	Rahmani	2 - 7	0.08	Karam (1957)
	Hampshire	2 - 5	0.14	Mechling and Carter (1969)
	Rambouillet (average of two flocks)	2 - 8	0.12	Shelton and Menzies (1970)
Lambs weaned per lambing ewe L_{WL}	Scottish Blackface	2 - 6	0.05	Purser (1965)
	Welsh Mountain	2 - 4	0.05	

Kangasniemi and Timon, 1967), although not always so (Young, Turner and Dolling, 1963; Ch'ang and Rae, 1970). If it is assumed that the heritability and repeatability (t) for all lambings are the same, and that the genetic correlation between performance at different lambings is one, then the heritability for average performance over a number (n) of lambings is given by:

$$h^2_{\bar{n}} = \frac{nh^2}{1 + t(n - 1)} \qquad \text{(Berge, 1934)}$$

Unfortunately it is not clear to what extent the assumptions required for such a prediction to hold are, in fact, true, but at least in the studies of Young, Turner and Dolling (1963) and Ch'ang and Rae (1972) there is either evidence or it can be inferred that at least some of them are not.

Finally, a number of studies should be mentioned in which alternative methods of analysis have been employed, which were considered more appropriate for such binomially distributed characters as E_{LJ} and E_{ML}. Rendel (1956) used the analyses suggested by Lush, Lamoreaux and Hazel (1948) and by Robertson and Lerner (1949) to re-examine the data on E_{ML} first presented by Johansson and Hansson (1943). The estimates of heritability obtained by the methods of Lush, Lamoreaux and Hazel, and Robertson and Lerner were similar, .13 and .10, and both corresponded closely to the estimate of .10 for L_{BL} obtained by Johansson and Hansson.

A maximum likelihood approach was adopted by Young, Turner and Dolling (1963) in order to check the relative magnitude of estimates obtained for L_{BJ} at different lambings by normal analysis of variance methods. While they claimed that quite good agreement was obtained, it should be pointed out that to obtain solutions in their likelihood iteration procedures, it was necessary to pool data over years and this would render the heritability estimates liable to bias.

Genetic correlation between measures of ewe reproductive performance

Heritability estimates can be used to predict response to selection in the same character at the corresponding lambing. To predict response in other characters at the same lambing, or in any character at some other lambing, estimates of genetic correlations are required. Few such estimates are available. Purser (1965) gave a figure of 0.5 for the genetic correlation between litter size at birth (L_{BL}) and litter size at weaning (L_{WL}) for the same lambing, indicating that selection for one would lead to correlated changes in the other.

Observed Response to Selection for Increased Reproductive Performance

There are two reports of the effect of selecting for increased incidence of multiple births. In New Zealand, Wallace (1958, 1964) selected for high and low incidence of twins among Romneys, and also maintained a control flock. Selection among ram and ewe replacements was on the basis of their dam's performance, and a further selection was practised among the ewes after three lambings. Turner (1969a) has estimated that the divergence in L_{BJ} between the high and low twinning lines at .011 lambs per year.

Turner (1969a, b) herself reported an annual response of .023 in L_{BJ} between Merino flocks also selected for either high or low incidence of twinning. Selection here was primarily among rams, on the basis of their dam's and grand-dam's performance, although in later years, ewes had been selected both before and after they entered the breeding flock. While the selection criteria differed slightly between the two experiments, the more rapid response in the Merinos was probably due to the fact that single born Romneys produced more twin offspring than did single born ewes. In other words, selection of twin born Romney replacements would in itself be likely to lower flock performance. Twin born Merino ewes produced more lambs than did single born ewes.

In both of these experiments, there was some evidence that selection for an increased incidence of multiple births reduced the incidence of dry ewes as well as increasing the proportion of twins (Wallace, 1964; Turner, 1966).

SECTION 2.7 THE REPEATABILITY OF EWE REPRODUCTIVE PERFORMANCE IN THE TRANGIE FLOCK

Estimates have been obtained for three measures of ewe reproductive performance, the tendency for ewes to lamb (E_{LJ}), the number of lambs born (L_{BJ}) and the number of lambs weaned (L_{WJ}), all expressed relative to the number of ewes joined and alive at lambing. Data were drawn from ewes born in the base population between 1947 and 1951, and in the selection and Random flocks between 1951 and 1967. Some ewes, approximately 150, included in this latter category were born in the Random flocks but were, in fact, mated outside any of the flocks mentioned in this thesis. Matings considered were from 1951 to 1969. Initially, no restriction was placed on the number of records a ewe must have for inclusion so that some ewes, notably those born in 1967, could have had only one lambing. A maximum of 10 records was available on any one ewe. Lambing and weaning records generally fell into three classes, 0, 1 or 2, although 0.7 per cent of all matings resulted in ewes producing triplets or quadruplets.

Methods of Analysis

Repeatability was initially estimated as the intra-class correlation (t) from a hierarchical analysis of variance. Separate analyses were conducted for each flock and the effects considered in each nested analysis were year of birth of the ewe, variation between ewes born in the same year, and variation between records for any ewe (Young, Turner and Dolling, 1963). No attempt was made to correct in any other way for between year effects as it was felt that a repeatability estimate obtained by the method outlined above would be more appropriate to apply in practice. Degrees of freedom and sums of squares were then pooled over flocks (Young, Turner and Dolling, 1960) to obtain a single estimate of t for each character. These pooled estimates were virtually identical to those obtained by weighting intra-class correlations obtained for each flock by the inverse of their sampling variances. By this method of analysis, two sets of estimates were obtained; the first covering lambings from the first to the fifth, and the second, lambings from the first to the tenth. These involved the use of respectively 15564 and 17147 records on 4173 and 4207 ewes. Ewes with only one record would contribute to the between ewe sums of squares but not to the within ewe term.

Approximate standard errors were calculated from the formula proposed by Swiger _et. al._ (1964):

$$V_t = \frac{2(N-1)(1-t)^2(1+(K-1)t)^2}{K^2(N-S)(S-1)}$$

Using the same form of analysis, repeatability estimates were then calculated for all pairs of lambings between the first and the fifth. In these analyses, a ewe had records for both lambings being correlated and, with equal numbers of records per ewe (two), the above formula for the sampling variance of t closely approximates that suggested by Fisher (1946). Again degrees of freedom and sums of squares were pooled over flocks.

Repeatability of L_{BJ} was also estimated by the regression method suggested by Lush (1956) and presented in detail by Turner and Young (1969). In this, the regression of subsequent or initial performance is the estimate of repeatability. Here, ewes have been classified on their performance at some specified initial lambing and least squares estimates have then been obtained for performance at the subsequent lambing. The following model was used in these least squares analyses:

$$X_{ijkl} = u + Y_i + B_j + L_k + B_{jk} + e_{ijkl}$$

where X_{ijkl} = an individual observation on subsequent performance

u = overall mean

Y_i = an effect due to the i^{th} year of birth of the ewe

B_j = an effect due to the j^{th} flock

L_k = an effect due to the k^{th} initial lambing performance (0, 1 or 2)

BK_{jk} = the first order interaction between flock and initial lambing performance, and

e_{ijkl} = a random error term.

Data were drawn from the first to the seventh lambings and estimates of subsequent performance were obtained for L_{BJ} and L_{WJ} both at individual lambings and also for records pooled over a number of lambings.

In addition to this major set of analyses, least squares methods were also used to pose further questions regarding the relationship between initial and subsequent performance. In each of these investigations a representative set of lambings between the first and the fifth was used. The major difference in the model employed was that the interaction term was deleted as in none of the previous analyses did the interaction between flock and initial performance account for a significant proportion of the variation.

Firstly, the value of a more detailed description of initial performance was examined. In this, ewes were allocated into one of the following categories:

(i) Ewe dry

(ii) Ewe 'lambed and lost'

(iii) Gave birth to 1 lamb, 0 lambs weaned

(iv) " " " 1 lamb, 1 lamb weaned

(v) " " " 2 lambs, 0 lambs weaned

(vi) " " " 2 lambs, 1 lamb weaned

(vii) " " " 2 lambs, 2 lambs weaned

Secondly, the predictive value of records pooled over a number of lambings was investigated.

Finally, an attempt was made to examine the repeatability of ewe reproductive performance after the cohort had already been subject to selection for L_{BJ}. For instance, the regression of third on second lambing performance was estimated after ewes without lambs at first lambing had been culled. The major aim of these analyses was to assess to what extent estimates obtained from an unselected population, such as that examined in the major set of analyses, were appropriate for a population undergoing selection for increased reproductive performance.

Table 2.7.1

Estimates of repeatability of reproductive performance together with their standard errors

	Lambings 1 to 10			Lambings 1 to 5		
Flock	E_{LJ}	L_{BJ}	L_{WJ}	E_{LJ}	L_{BJ}	L_{WJ}
March Random	.138 (.021)	.127 (.021)	.141 (.021)	.124 (.022)	.122 (.022)	.139 (.022)
Wean Wt. Plus	.113 (.020)	.122 (.020)	.114 (.020)	.102 (.026)	.114 (.026)	.110 (.026)
Wean Wt. Minus	.119 (.020)	.154 (.019)	.172 (.022)	.131 (.022)	.161 (.022)	.169 (.022)
Fold Plus	.129 (.026)	.113 (.026)	.117 (.026)	.124 (.028)	.113 (.028)	.118 (.028)
Fold Minus	.133 (.024)	.123 (.024)	.133 (.024)	.132 (.026)	.120 (.026)	.133 (.026)
April Random	.144 (.024)	.148 (.024)	.163 (.024)	.137 (.027)	.141 (.027)	.164 (.027)
Fleece Plus	.166 (.025)	.149 (.025)	.163 (.025)	.166 (.028)	.147 (.028)	.166 (.028)
Fleece Minus	.151 (.025)	.126 (.025)	.118 (.025)	.148 (.028)	.127 (.028)	.142 (.028)
Crimp Plus	.169 (.020)	.120 (.020)	.158 (.020)	.188 (.028)	.118 (.027)	.157 (.027)
Crimp Minus	.144 (.025)	.155 (.025)	.115 (.025)	.140 (.033)	.142 (.033)	.103 (.033)
Pooled Analysis	.135 (.007)	.129 (.006)	.135 (.007)	.133 (.008)	.126 (.008)	.134 (.008)

Table 2.7.2

Intra-class correlation estimates of the repeatability of both L_{BJ} and L_{WJ}

	Previous lambing			
	1	2	3	4
	1. Lambs born per ewe joined (L_{BJ})			
Subsequent lambing				
2	.084 (.018)			
3	.062 (.019)	.107 (.019)		
4	.067 (.020)	.096 (.020)	.169 (.019)	
5	.059 (.022)	.022 (.022)	.082 (.020)	.161 (.019)
	2. Lambs weaned per ewe joined (L_{WJ})			
2	.127 (.018)			
3	.084 (.019)	.104 (.019)		
4	.083 (.020)	.101 (.020)	.188 (.019)	
5	.093 (.022)	.061 (.022)	.082 (.020)	.165 (.019)

As has already been pointed out, the distribution of the data into a small number of discrete classes presents difficulties both in the calculation of standard errors and in the application of significance tests designed for normally distributed variates. While the calculated sampling variances can only be considered approximate, standard errors have been included for want of more appropriate estimates.

Results

Estimates of the repeatability of E_{LJ}, L_{BJ} and L_{WJ}, both separately for each flock and pooled over flocks, are given in Table 2.7.1. The pooled estimates obtained in the two sets of data (lambings 1-5 and lambings 1-10) are essentially the same for all three characters. When the estimates for the individual flocks were examined, again there was remarkable consistency, as within either set of analyses (lambings 1-5 or 1-10) the individual flock estimates for all three characters did not differ significantly, nor did the estimates for any one character differ between sets of data.

In Table 2.7.2 are listed the pooled estimates for L_{BJ} and L_{WJ} when estimated for individual pairs of lambings. Both sets of estimates were adjudged to be significantly heterogeneous ($P <.05$) when a Chi-square value was estimated as:

$$\text{Chi-square} = \Sigma w_i t_i^2 - \frac{(\Sigma w_i t_i)^2}{\Sigma w_i}$$

where the t_i are estimates for individual pairs of lambings, and

w_i = the inverse of the sampling variance for the individual estimates

The Chi-square values for L_{BJ} and L_{WJ} were respectively, 37.16 and 37.38, for a test with 8 (n-2) degrees of freedom.

When the estimates in Table 2.7.2 were pooled according to the number of years between lambings, the intra-class correlation was higher for adjacent than for non-adjacent records (Table 2.7.3).

Table 2.7.3

Intra-class correlation estimates of the repeatability of both LBEJ and LWEJ for pairs of lambings, grouped according to the number of years between records being correlated

	LBEJ	LWEJ
One lambing apart (1,2; 2,3; 3,4; 4,5)	.137 (.009)	.146 (.009)
Two lambings apart (1,3; 2,4; 3,5)	.080 (.011)	.088 (.011)
Three lambings apart (1,4; 2,5)	.059 (.015)	.088 (.015)
Four lambing apart (1,5)	.059 (.022)	.093 (.022)

However, among the estimates between adjacent pairs of lambings there was also significant heterogeneity for L_{BJ} (Chi-square = 14.8, 2 d.f., $P < .05$), and for both L_{BJ} and L_{WJ} the correlations were lowest for records obtained at the earlier lambings.

The number of ewes involved in the study of the relationship between initial and subsequent performance are given in Table 2.7.4. For records up to the fifth lambing, initial and subsequent performance were directly and positively related (Table 2.7.5). This was not always so when the sixth or seventh lambings were included in the analyses, but, in these calculations, the numbers of ewes involved were much reduced (see Table 2.7.4) and the standard errors of the least squares means were correspondingly higher. For lambings 1 to 5, the difference in L_{BJ} at the subsequent lambing for ewes initially producing 0 v. 1 or 1 v. 2 were similar in magnitude and the weighted * averages of these differences were respectively .179 and .191. Corresponding figures for lambings 1 to 7 were .167 and .187.

Repeatability estimates, calculated from the least squares means in Table 2.7.5 are given in Table 2.7.6. The average estimates

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* Weights used were $\frac{n_0 n_1}{n_0+n_1}$ for the differences between ewes producing 0 v. 1 lambs, and $\frac{n_1 n_2}{n_1+n_2}$ for ewes producing 1 v. 2 lambs where n_0, n_1, and n_2 are respectively the numbers of ewes producing 0, 1 and 2 lambs.

for lambings 1 to 5 and 1 to 7 were respectively .185 and .155. The heterogeneity observed among the intra-class correlation estimates was again apparent (Chi-squares, 19 d.f., 822.9 (L_{BJ}), 818.6 (L_{WJ}), both $P < .05$). Repeatability declined as the time between lambings increased (Table 2.7.7), and for both L_{BJ} and L_{WJ} the regression of repeatability on time between lambings was significant. In addition, repeatability estimates between L_{BJ} records one or two lambings apart, and for L_{WJ} records in adjacent lambings, were significantly heterogeneous according to the Chi-square test outlined above. In all three instances, the lowest repeatability estimates were for early lambings, as was also found with the intra-class correlation estimates between adjacent lambings.

The value of employing a more detailed description of initial lambing performance was investigated by estimating least squares means at the succeeding lambings. For the four such analyses conducted, between the first and the fifth lambing, applying a more detailed description of initial performance increased the proportion of the total variation in L_{BJ} and L_{WJ} accounted for by the model; for L_{BJ} the average change was from 9.5 (3 lambing classes) to 10.0 (7 classes) per cent of the total variation in L_{BJ}, with corresponding values of 8.1 and 8.7 per cent of the variation in L_{WJ}. Unfortunately, the numbers of ewes in some of the categories in the refined classification were small (Table 2.7.8), and this reduced the value of many of the comparisons which could have been made among the least squares means. Averaged over the four analyses, ewes classed as 'lambed and lost' gave birth to and weaned 16 per cent more lambs at the following lambing than did dry ewes.

When L_{BJ} records were pooled over the first two or three lambings, initial and subsequent performance were, in general, directly related (Table 2.7.9). The only exception was when three records were pooled, where ewes which had produced six lambs subsequently gave birth to fewer lambs than those ewes which had previously produced five lambs. However, the number of ewes producing 6 lambs was small. Repeatability estimates calculated from these least squares means are given in Table 2.7.10. Pooling L_{BJ} records over a number of lambings improved the ability to predict subsequent performance, relative to the average estimates involving the individual component lambings. At the same time, the use of the pooled regression coefficients would still underestimate the effect of culling ewes without lambs at either two or three lambings, as the difference in subsequent performance between ewes producing 0 v. 1 lambs was greater than expected if the relationship between early and subsequent performance was linear. For instance, referring again to the least squares means in Table 2.7.9, the difference in L_{BJ} at the third lambing between ewes producing 0 v. 1 lamb at the first and second lambings was .253 when, if the relationship between initial and subsequent performance was linear, the expected difference (one quarter of difference between ewes producing 0 v. 4) is .141. Similarly, the difference between ewes producing 0 v. 1 lambs at the first three lambings was .287 in L_{BJ} at the fifth lambing, when the expected difference would be .127.

In three of the four situations examined, selection reduced the repeatability of L_{BJ} between later lambings (Table 2.7.11). At the same time, the general effect was also to reduce the difference in subsequent performance between ewes producing 1 v. 0 lambs relative to the difference between ewes producing 2 v. 1 lambs. The exception in both cases was the prediction of third from second lambing performance.

Discussion

The intra-class correlation estimates of the repeatability of L_{BJ} and L_{WJ} in this study are higher than corresponding estimates obtained by Kennedy (1967) for another sample of the Trangie flock, and by Young, Turner and Dolling (1963) for the Cunnamulla flock of Merinos. However, the regression estimates obtained by Kennedy (1967) are similar to those reported here. In the present investigation, no differences were found between the estimates for L_{BJ} and for L_{WJ}, nor between these estimates and the repeatability of E_{LJ} (Table 2.7.1). As in other studies (Purser, 1965; Hallgrimsson, 1966) the intra-class correlation estimates were lower than those obtained by regression. The regression estimates provide a more direct measure of the relationship between initial and subsequent performance, and of the likely consequences of culling. However, while the intra-class correlation estimates would underestimate the improvement due to culling, they are not likely to be biased by non-linearity in the relationship between initial and subsequent performance.

When repeatability estimates were obtained for individual pairs of lambings, they were found to be heterogeneous. The major factor associated with this variation was the number of years between the lambings being correlated. To a lesser extent, performance at early lambings was a poorer indicator of L_{BJ} and L_{WJ} in the following year than was performance at later lambings, a result also observed for L_{BL} by Purser (1965). Strictly speaking, the estimates on which these conclusions are based are not entirely adequate for the purpose, as the observations were not based on exactly the same ewes. Clearly, a larger number of ewes contributed to estimates between early lambings (Table 2.7.4). Some additional estimates were made of the repeatability of performance at early lambings when, in fact, the main aim was to establish the relationship involving a later lambing; (for example, lambing 2 was related to lambing 3 when the major association being investigated was between lambings 2 and 5). The estimates thus obtained were found to be generally lower than presented in Table 2.7.6, but in both sets, the relative magnitude of the estimates between the same pairs of lambings was very similar, which indicates that the findings listed above are not simply attributable to sampling.

In estimating the effect of culling on subsequent performance, a simplified version of the regression estimates of repeatability (Table 2.7.6) has been used, and this is set out in Table 2.7.12. In addition, it has been assumed that the relationship between initial and subsequent performance is perfectly linear. While culling 20 per cent of ewes is less than the maximum possible for a flock of seven age groups of ewes, it does allow for the culling of all ewes without lambings at any of the first six lambings (see Table 2.4.3, page 96), and so provides a useful basis of comparison. In addition, it is probably a reasonable level of culling for fertility in commercial flocks, where the breeder would be attempting to improve a number of economically important characters. Under these sets of conditions, culling 20 per cent of ewes at any lambing would increase the overall reproductive performance (L_{BJ}) of a flock of seven age groups of ewes (Table 2.7.13). However, the maximum gain was only 1.4 per cent, when culling was on the basis of performance at either second or third lambing. This improvement would be expected even after account had been taken of the generally adverse effect that altering age structure would have on productivity.

Because of the comparatively small gains to be achieved by this degree of culling, relatively little would be lost in the way of accuracy by assuming an overall estimate of repeatability of 18 per cent. Here the maximum improvement in flock productivity was 2.0 per cent more lambs at birth, by culling after first lambing. Gains expected following selection on second or third lambing performance were respectively 1.8 and 1.5 per cent.

Repeatability estimates for records pooled over a number of lambings were higher than corresponding estimates involving the component lambings, and in quite good agreement with the values predicted (Table 2.7.10). Assuming the relationship between initial and subsequent performance to be perfectly linear, then culling the 10 per cent of ewes without lambs after the first two lambings would increase average production over the first five lambings by 1.7 per cent. Culling 10 per cent of ewes without lambs at either first or second lambing would produce corresponding average increases of 0.8 and 1.0 per cent respectively. It has been pointed out that by assuming a linear relationship between initial and subsequent performance, improvement due to culling would be underestimated.

However, in practice, this is likely to be of little consequence as the proportion of ewes which did not produce a lamb at her first two years in the breeding flock was only 10 per cent, and this would, of course, decline as further records were pooled.

The analyses summarised in Table 2.7.8 indicated that ewes classed as having 'lambed and lost' their lamb before mothering were superior to dry ewes in subsequent performance. In practice, making such a distinction is likely to have little effect on expected response. For instance, replacing the least squares means for ewes with '0' lambs (Table 2.7.5) with those for dry ewes (Table 2.7.8) increased the repeatability estimate between adjacent pairs of lambings by at most eight per cent (.242 v. .224, regression of fourth lambing on third). Further, culling all dry ewes (taken as 18 per cent) as opposed to the same number of all ewes without lambs, of which there were 22 per cent at third lambing, increased the expected improvement at the following lambing from 5.3 to 6.1 per cent.

So far in this discussion, culling has been seen as a once-and-for-all operation, with ewes being culled on an individual or pooled record. If ewes were culled at various stages throughout their lifetime in the breeding flock, a number of factors are affected. Selection on performance at early lambings will reduce the proportion of ewes without lambs at later lambings, and so in that sense reduce the scope for culling dry ewes at the later lambings. More importantly, as shown in Table 2.7.11, prior selection reduces the expected gains from culling dry ewes at later lambings. Robertson (1966) predicted that the culling of first lactation dairy heifers, based largely on milk yield, would reduce the genetic regression of milk yields at later pairs of lactations. Here, where repeatability has been estimated as a phenotypic regression, selection on early lambing performance might also be expected to reduce repeatability estimates for subsequent pairs of lambings to the extent that repeatability included a component attributable to genetic regression.

Finally, it should be pointed out that culling ewes with '0' lambs at mothering will increase the average survival of the remaining ewes in that cohort (see Table 2.3.6, page 83) and so the gains due to culling would be expected to be higher than those cited in this Section. However, improving ewe survival in this way would have a negligible effect on the value of culling to increase current flock production, small though these gains seem likely to be.

Table 2.7.4

Relationship between L_{BJ} at initial lambing and both L_{BJ} and L_{WJ} at subsequent lambing.

Numbers of animals in each category at the initial lambing

Initial lambing	Lambing class	Subsequent lambing					
		2	3	4	5	6	7
1	0	1019	911	782	588	265	123
	1	1898	1723	1553	1238	509	267
	2	267	239	220	169	58	17
	Total	3184	2873	2525	1995	832	407
2	0		796	681	494	208	101
	1		1658	1520	1203	560	314
	2		515	480	368	135	43
	Total		2969	2681	2065	903	458
3	0			641	493	217	116
	1			1442	1162	567	316
	2			719	563	193	77
	Total			2802	2218	977	509
4	0				642	287	154
	1				1022	519	291
	2				568	171	64
	Total				2232	977	509
5	0					235	131
	1					500	271
	2					227	93
	Total					962	495
6	0						149
	1						263
	2						85
	Total						498

Table 2.7.5

Relationship between L_{BJ} at initial lambing and L_{BJ} at subsequent lambing

Estimates of least squares means and standard errors

Initial lambing	Lambing class	Subsequent lambing					
		2	3	4	5	6	7
1	0	.776 (.022)	.785 (.024)	.834 (.026)	.841 (.030)	1.015 (.046)	.750 (.069)
	1	.940 (.021)	.946 (.022)	1.024 (.023)	1.001 (.027)	1.385 (.042)	.825 (.064)
	2	1.136 (.034)	1.132 (.038)	1.205 (.036)	1.146 (.041)	1.178 (.067)	.959 (.111)
2	0		.809 (.021)	.828 (.023)	.860 (.028)	1.017 (.041)	.734 (.058)
	1		1.037 (.010)	.985 (.020)	.957 (.025)	1.058 (.035)	.842 (.049)
	2		1.172 (.028)	1.206 (.026)	1.165 (.038)	1.022 (.048)	.982 (.074)
3	0			.746 (.024)	.785 (.028)	.939 (.040)	.666 (.050)
	1			.970 (.022)	.961 (.025)	.994 (.037)	.760 (.041)
	2			1.196 (.027)	1.173 (.036)	1.096 (.057)	.958 (.056)
4	0				.743 (.027)	.858 (.042)	.613 (.049)
	1				.979 (.025)	1.022 (.037)	.786 (.044)
	2				1.201 (.038)	1.181 (.055)	.977 (.060)
5	0					.738 (.041)	.624 (.168)
	1					1.016 (.036)	.763 (.164)
	2					1.212 (.056)	.931 (.170)
6	0						.594 (.169)
	1						.853 (.167)
	2						.909 (.172)

Table 2.7.6

Repeatability of the L_{BJ} as estimated by regression and the value of L_{BJ} as a predictor of L_{WJ} at subsequent lambings

Standard errors in brackets

Subsequent lambing	Previous Lambing					
	1	2	3	4	5	6
	1. Lambs born per ewe joined (L_{BJ})					
2	.167 (.015)					
3	.148 (.006)	.189 (.045)				
4	.188 (.004)	.185 (.027)	.225 (.001)			
5	.156 (.007)	.146 (.055)	.194 (.017)	.229 (.007)		
6	.102 (.032)	.009 (.038)	.077 (.024)	.162 (.003)	.237 (.057)	
7	.085 (.021)	.118 (.056)	.138 (.052)	.180 (.009)	.151 (.014)	.175 (.100)
	2. Lambs weaned per ewe joined (L_{WJ})					
2	.177 (.015)					
3	.157 (.019)	.173 (.020)				
4	.164 (.007)	.164 (.007)	.217 (.020)			
5	.139 (.008)	.137 (.032)	.152 (.015)	.220 (.036)		
6	.098 (.015)	.075 (.013)	.068 (.047)	.153 (.004)	.221 (.001)	
7	.042 (.040)	.082 (.056)	.110 (.040)	.148 (.031)	.128 (.020)	.158 (.080)

Table 2.7.7

Regression estimates of repeatability, pooled according to the number of lambings between records

	Weighted[1] average	Unweighted average
Lambs born per ewe joined		
Records one lambing apart	.225	.204
" two " "	.160	.168
" three " "	.184	.148
" four " "	.151	.101
" five " "	.106	.110
" six " "	.085	.085
Regression coefficient (change in average repeatability per additional lambing separating records)	-.026* (.004)†	-.023* (.005)†
Lambs weaned per ewe joined		
Records one lambing apart	.221	.194
" two " "	.155	.151
" three " "	.160	.129
" four " "	.121	.108
" five " "	.097	.090
" six " "	.042	.042
Regression coefficient	-.032* (.004)†	-.028* (.004)†

† Standard error of regression coefficient

* Regression coefficient differs significantly from zero

[1] Weights used were the inverse of the sampling variances

Table 2.7.8

Effect of refining the classification for performance at the initial lambing

Least squares means and their standard errors for ewes in different categories

Initial lambing	Class	Number of ewes	Subsequent Lambing		
				Lambs born L_{BJ}	Lambs weaned L_{WJ}
First	Ewe dry	908	Second lambing	.761 (.038)	.640 (.038)
	Ewe lambed and lost	111		.876 (.064)	.749 (.063)
	1 lamb born, 0 reared	197		.941 (.052)	.765 (.051)
	1 lamb born, 1 reared	1701		.939 (.036)	.831 (.035)
	2 lambs born, 0 reared	12		1.096 (.166)	.620 (.163)
	2 lambs born, 1 reared	64		1.115 (.078)	.901 (.077)
	2 lambs born, 2 reared	191		1.203 (.052)	1.095 (.052)
Second	Ewe dry	728	Third	.779 (.035)	.666 (.034)
	Ewe lambed and lost	97		.963 (.066)	.870 (.065)
	1 lamb born, 0 reared	181		.934 (.051)	.755 (.050)
	1 lamb born, 1 reared	1534		1.049 (.031)	.905 (.030)
	2 lambs born, 0 reared	25		1.311 (.121)	.879 (.119)
	2 lambs born, 1 reared	114		1.232 (.061)	1.086 (.060)
	2 lambs born, 2 reared	415		1.142 (.039)	1.034 (.039)

Table 2.7.8 (contd.)

Third	Ewe dry	540	Fourth	0.708 (.037)	0.594 (.036)
	Ewe lambed and lost	101		0.941 (.068)	0.748 (.067)
	1 lamb born, 0 reared	153		0.851 (.056)	0.712 (.055)
	1 lamb born, 1 reared	1289		0.982 (.031)	0.873 (.031)
	2 lambs born, 0 reared	28		0.696 (.119)	0.491 (.116)
	2 lambs born, 1 reared	153		1.134 (.056)	0.983 (.055)
	2 lambs born, 2 reared	539		1.236 (.038)	1.103 (.037)
Fourth	Ewe dry	548	Fifth	0.752 (.041)	0.605 (.040)
	Ewe lambed and lost	94		0.693 (.073)	0.557 (.071)
	1 lamb born, 0 reared	93		0.855 (.072)	0.745 (.070)
	1 lamb born, 1 reared	929		0.991 (.037)	0.864 (.036)
	2 lambs born, 0 reared	21		1.241 (.140)	0.829 (.137)
	2 lambs born, 1 reared	102		1.182 (.069)	0.973 (.068)
	2 lambs born, 2 reared	448		1.209 (.043)	1.057 (.042)

Table 2.7.9

The relationship between records pooled over a number of lambings and subsequent performance

Overall mean plus least squares deviation and standard error of deviation

Initial lambings	Combined initial performance	Subsequent performance					Subsequent performance				
		Number of ewes (proportion)	L_{BJ} (3)		L_{WJ} (3)		Number of ewes (proportion)	L_{BJ} (3-5)		L_{WJ} (3-5)	
			u + lsd	s.e.	u + lsd	s.e.		u + lsd	s.e.	u + lsd	s.e.
First + Second	0	325 (11.3)	0.664	0.036	0.549	.035	182 (9.1)	2.376	.096	1.955	.094
	1	848 (29.5)	0.917	.026	0.799	.026	584 (29.2)	2.744	.067	2.402	.066
	2	1195 (41.6)	1.073	.024	0.926	.024	872 (43.7)	3.154	.061	2.748	.060
	3	400 (13.9)	1.201	.033	1.045	.032	284 (14.2)	3.536	.082	3.052	.081
	4	104 (3.7)	1.230	.057	1.090	.056	73 (3.8)	3.751	.141	3.293	.139
			L_{BJ} (5)		L_{WJ} (5)			L_{BJ} (4-5)		L_{WJ} (4-5)	
First + Second + Third	0	60 (3.0)	0.443	.084	0.299	.083	60 (3.0)	0.840	.125	0.587	.124
	1	257 (13.0)	0.730	.047	0.642	.046	257 (13.0)	1.452	.070	1.282	.069
	2	488 (24.7)	0.892	.039	0.744	.038	488 (24.7)	1.793	.058	1.551	.058
	3	657 (33.2)	0.991	.036	0.858	.035	657 (33.2)	1.990	.053	1.759	.053
	4	341 (17.3)	1.110	.042	0.937	.042	341 (17.3)	2.283	.063	1.998	.063
	5	136 (6.9)	1.208	.059	1.066	.059	136 (6.9)	2.462	.089	2.104	.088
	6	37 (1.9)	1.155	.104	0.978	.104	37 (1.9)	2.297	.156	2.081	.156

Table 2.7.10

The repeatability of L_{BJ} estimated for pooled records by regression methods

Predictive value of lambings	Subsequent performance	Repeatability (standard error)	Expected repeatability from component repeatability estimates‡
Average of First + Second	Third	.318 (.068)	.271
Average of First + Second	Fifth	.250 (.022)	.262
Average of First + Second	Sum of Third to Fifth lambings	.760 (.026)	.603
Average of First, Second + Third	Fifth	.369 (.066)	.373
Average of First + Second + Third	Sum of Fourth and Fifth	.780 (.153)	.608

‡ Estimated from the repeatability estimates in Table 2.7.7 and the relationship that

$$t_{(\bar{n})} = \frac{nt}{1 + (n - 1)t}$$

, where t here is the average estimate of the subsequent on each of the previous lambings.

Table 2.7.11

Effect of culling on the relationship between subsequent production records

Repeatability estimates and their standard errors

Initial lambing	Culling system	Subsequent production			
		L_{BJ} (3)	L_{BJ} (3-5)	L_{WJ} (3)	L_{WJ} (3-5)
Second	Nil	.154 (.027)	.431 (.120)	.136 (.043)	.396 (.071)
	All ewes with 0 lambs at first lambing	.146 (.002)	.376 (.183)	.118 (.046)	.303 (.060)
	All dry ewes at first lambing	.147 (.030)	.369 (.139)	.117 (.073)	.302 (.121)
Third		L_{BJ} (5)	L_{BJ} (4-5)	L_{WJ} (5)	L_{WJ} (4-5)
	Nil	.194 (.017)	.405 (.015)	.152 (.015)	.351 (.002)
	All ewes with 0 lambs at first lambing	.161 (.026)	.357 (.062)	.120 (.032)	.298 (.033)
	All ewes with 0 lambs at second lambing	.182 (.030)	.337 (.018)	.140 (.035)	.283 (.014)
	All ewes with 0 lambs at both first and second lambing	.116 (.051)	.305 (.064)	.127 (.052)	.265 (.053)

Table 2.7.12

Values for the repeatability of L_{BJ} to be used in calculating gains which can be achieved by culling on performance at individual lambings

Subsequent lambing	Initial Lambing					
	1	2	3	4	5	6
2	.17					
3	.15	.19				
4	.15	.17	.22			
5	.11	.15	.17	.22		
6	.11	.11	.15	.17	.22	
7	.08	.11	.11	.15	.17	.22

Table 2.7.13

The expected improvement in reproductive performance for a flock of seven age groups of ewes, by culling 20 per cent of ewes on performance at individual lambings

	Lambing at which culling is to operate					
	First	Second	Third	Fourth	Fifth	Sixth
Expected change due to altering flock structure (%)	-0.8	-0.9	-0.7	-0.4	+0.0	+0.2
Improvement due to culling, flock structure alterations accounted for (%)	+1.2	+1.4	+1.4	+1.0	+1.1	+0.9

SECTION 2.8 THE HERITABILITY OF EWE REPRODUCTIVE PERFORMANCE AND THE GENETIC CORRELATION BETWEEN DIFFERENT MEASURES OF REPRODUCTIVE PERFORMANCE IN THE TRANGIE FLOCK

Methods of Analysis and Results

The heritability of ewe reproductive performance has been estimated by two general methods, half-sib correlation and the regression of daughter's performance on dam's, and this Section has been sub-divided accordingly. Estimates of genetic correlations are included at the end of this Section.

Half-sib Analyses

Major analysis

Information was obtained on a total of 3224 ewes, born in the selection and control flocks between 1951 and 1967. Data on the base population ewes could not be included as information on parentage was not available.

Heritability estimates were obtained on performance at each of the first five lambings. The following measures of performance were examined, E_{LJ}, L_{BJ}, L_{BL}, E_{ML}, L_{WJ} and L_{WL}. The proportion of triplet and quadruplet births was small (0.7 per cent) and the estimates for L_{BL} and E_{ML} were essentially the same so that often the estimates for E_{ML} have not been included in the tables.

Heritability was estimated from the intra-class correlation, which was obtained from a hierarchical analysis of variance. The levels considered in the analyses were flocks, years within flocks, sires within years within flocks and variation between daughters of individual sires. Standard errors were calculated as four times the standard error of the intra-class correlation, the formula for which is given by Swiger <u>et</u>. <u>al</u>. (1964). The distribution of family sizes for characters measured in relation to ewes joined and alive at lambing (E_{LJ}, L_{BJ} and L_{WJ}) is given in Table 2.8.1. The corresponding distribution for characters measured in relation to ewes lambing (L_{BL}, E_{ML} and L_{WL}) is similar although the average family sizes are lower.

Some pairs of full-sib families were included in the half-sib analyses. In the data examined by offspring-parent methods, and which are essentially the same as those examined here, approximately five per cent of daughters were full-sibs. From these estimates, an approximate measure of the degree of genetic relationship (r) among the 'half-sib' ewes was obtained using the following simplification of a formula given by Rendel (1956):

$$r = .25 \left(1 + \frac{2}{K(K-1)} \right) a + .25 \ (N - a)$$

where K = average number of daughters per sire (from Table 2.8.1)

N = total number of sires and

a = number of sires contributing a pair of full-sib daughters.

Assuming that sires contributed a maximum of one pair of full-sibs, r was estimated as $.\overset{2}{\cancel{0}}65$, and it was not felt necessary to make any corrections to the heritability estimates obtained assuming that r was equal to 0.25.

Estimates of heritability of ewe reproductive performance, calculated separately for each of the first five lambings, are given

Table 2.8.1

Distribution of half-sib family sizes in data used to estimate heritability of the following measures of reproductive performance

E_{LJ}, L_{BJ}, L_{WJ}

Family size	Lambing				
	1	2	3	4	5
1	177	166	156	158	156
2	166	157	156	141	137
3	136	136	126	117	127
4	110	101	104	86	65
5	85	73	61	47	40
6	52	52	39	42	27
7	39	39	38	27	16
8	33	31	22	19	13
9	12	9	9	7	5
10	10	10	12	10	3
11	10	8	5	4	1
12	2	1	1	1	1
13	4	5	2	1	2
14	1	0	0	1	0
15	0	0	1	0	0
16	0	0	0	0	0
17	0	1	0	0	0
18	0	0	0	0	0
19	0	0	0	0	0
20	1	1	1	0	0
Total number of half-sib families	837	790	733	661	593
Average family size	3.65	3.64	3.51	3.34	2.99

in Table 2.8.2. In general, the standard errors were large relative to the heritability estimates, and only two estimates, E_{LJ} and L_{BJ} at the third lambing, differed significantly from zero. The estimates for L_{BJ} and L_{WJ} were similar at all lambings other than the third, where the heritability of L_{BJ} was higher. There was no consistent difference in the order of the estimates for E_{LJ} and L_{BL}. Estimates for L_{BL} and L_{WL} were similar at all lambings other than the third, where the heritability of L_{BL} was higher.

The heritability of E_{LJ}, L_{BJ} and L_{WJ} increased from the first to the third lambing and then declined to effectively zero. On the other hand, the heritability of L_{BL} was highest at first lambing (.22).

The individual components of variance in these analyses are given in Table 2.8.3. The between sire component followed the patterns outlined above for the heritability estimates for the various characters. For L_{BJ} and L_{WJ}, the phenotypic variance increased from the first to the fifth lambing. Over all of the analyses, the between year variation accounted for a higher average proportion of the total variation than did between flock effects, 5.9 per cent as opposed to 1.1 per cent.

Restricted Analyses

For each of these analyses, an F value was calculated as the ratio of the between to within sire mean squares. The ratio in each case was close to unity, some values were negative, and the maximum value was 1.20. Robertson (1962) has pointed out that where the F

Table 2.8.2

Estimates of the heritability of ewe reproductive performance at each of the first five lambings

Standard errors of estimates in brackets

1. All data

Character	Lambing 1	 2	 3	 4	 5
Ewes lambing of those joined (E_{LJ})	-.011 (.074)	.111 (.081)	.234 (.089)	-.008 (.092)	.021 (.116)
Lambs born per ewe joined (L_{BJ})	.008 (.076)	.068 (.080)	.170 (.088)	-.011 (.093)	.006 (.116)
Lambs born per lambing ewe (L_{BL})	.222 (.116)	-.026 (.111)	.056 (.115)	.061 (.139)	-.076 (.157)
Lambs weaned per ewe joined (L_{WJ})	-.014 (.074)	.063 (.080)	.094 (.086)	.017 (.094)	-.006 (.116)
Lambs weaned per ewe lambing (L_{WL})	.046 (.114)	.032 (.112)	-.014 (.114)	.050 (.139)	-.015 (.158)

Table 2.8.3

Estimates of the variance components in the hierarchical analyses of variance

	Lambing				
	1	2	3	4	5
Ewes lambing of those joined (E_{LJ})					
σ_e^2 (residual)	.1870	.1654	.1553	.1718	.1595
σ_s^2 (between sires)	.0000	.0047	.0096	.0000	.0008
σ_y^2 (between years)	.0187	.0172	.0044	.0223	.0104
σ_f^2 (between flocks)	.0023	.0083	.0000	.0000	.0000
σ_p^2 (phenotypic variance) †	.2080	.1956	.1693	.1941	.1707
Lambs born per ewe joined (L_{BJ})					
σ_e^2	.3287	.4352	.4890	.5463	.5878
σ_s^2	.0007	.0076	.0216	.0000	.0008
σ_y^2	.0237	.0356	.0374	.0710	.0409
σ_f^2	.0063	.0059	.0030	.0000	.0000
σ_p^2	.3594	.4843	.5510	.6173	.6295

† Phenotypic variance estimated as $\sigma_e^2 + \sigma_s^2 + \sigma_y^2 + \sigma_f^2$

Lambs weaned per ewe joined (L_{WJ})					
σ^2_e	.3286	.4232	.4877	.5221	.5589
σ^2_s	.0000	.0068	.0117	.0022	.0000
σ^2_y	.0138	.0256	.0228	.0651	.0270
σ^2_f	.0069	.0067	.0052	.0000	.0012
σ^2_p	.3493	.4623	.5274	.5894	.5871
Lambs born per lambing ewe (L_{BL})					
σ^2_e	.1041	.1997	.2254	.2351	.2838
σ^2_s	.0061	.0000	.0032	.0036	.0000
σ^2_y	.0025	.0072	.0177	.0277	.0132
σ^2_f	.0025	.0042	.0058	.0040	.0027
σ^2_p	.1152	.2111	.2521	.2704	.2997
Lambs weaned per lambing ewe (L_{WL})					
σ^2_e	.1903	.2890	.3312	.3383	.3790
σ^2_s	.0022	.0023	.0000	.0043	.0000
σ^2_y	.0165	.0021	.0091	.0170	.0064
σ^2_f	.0000	.0049	.0066	.0028	.0058
σ^2_p	.2090	.2983	.3469	.3624	.3912

value is close to unity, the between sires component of variance has a sampling variance ($1 + C^2$) times that where the data were balanced for family size, C being the coefficient of variation of family size, which in these analyses varied from 65 to 73 per cent. He further suggested that with low F values the exclusion of groups below half the average size will reduce the sampling variance of the estimate of the between sires component. Accordingly, all families of less than three daughters were deleted. This increased the average family size from 3.1 to 4.7 and reduced the average coefficient of variation of family size from 70 to 42 per cent. The heritability analyses were then repeated.

In general, the standard errors of the heritability estimates were only slightly less than those calculated in the previous set of analyses (Table 2.8.4) and the heritability estimates were higher than those obtained when all data were included. Now five estimates differed significantly from zero; L_{BL} at lambing 1, E_{LJ} at lambing 2 and E_{LJ}, L_{BJ} and L_{WJ} at lambing 3. Again the estimates for L_{BJ} and L_{WJ} were similar. The heritability estimates for E_{LJ}, L_{BJ} and L_{WJ} were highest at the third lambing, although the decline at subsequent lambings was not so marked as in the previous set of analyses (Table 2.8.2).

The Heritability of Pooled Lambing Records.

The heritability was then estimated for L_{BJ} and L_{WJ} records pooled over a number of years. All data were considered for inclusion and the records were pooled as follows: lambings 1 + 2, 1 + 2 + 3, 1 + 2 + 3 + 4 and 1 + 2 + 3 + 4 + 5. In the same analyses,

Table 2.8.4

Estimates of the heritability of ewe reproductive performance at each of the first five lambings

Standard errors of estimates in parenthesis

2. Only sires with at least three daughters

Character	Lambing 1	 2	 3	 4	 5
Ewes lambing of those joined (E_{LJ})	.029 (.068)	.174 (.076)	.234 (.089)	.107 (.091)	.050 (.111)
Lambs born per ewe joined (L_{BJ})	.017 (.068)	.051 (.072)	.261 (.088)	.049 (.088)	.119 (.115)
Lambs born per lambing ewe (L_{BL})	.270 (.120)	-.037 (.098)	.200 (.120)	.133 (.140)	.055 (.163)
Lambs weaned per ewe joined (L_{WJ})	-.029 (.065)	.054 (.072)	.201 (.086)	.052 (.087)	.171 (.118)
Lambs weaned per lambing ewe (L_{WL})	-.016 (.101)	.037 (.103)	.064 (.112)	.104 (.138)	.133 (.169)

Table 2.8.5

The heritability of lambs born per ewe joined for records pooled over lambings

Standard errors in brackets

All data available used in analyses

Heritability estimated for lambing(s)	Lambings included in analysis			
	Lambings 1 + 2	Lambings 1, 2 + 3	Lambings 1, 2, 3 + 4	Lambings 1, 2, 3, 4 + 5
1	.008 (.080)	-.033 (.085)	-.054 (.095)	-.024 (.118)
2	.080 (.082)	-.006 (.086)	-.047 (.095)	-.162 (.119)
3		.163 (.085)	.092 (.098)	-.061 (.116)
4			-.025 (.096)	-.081 (.117)
5				-.016 (.118)
1 + 2	.068 (.082)	-.016 (.086)	-.033 (.095)	-.112 (.116)
1 + 2 + 3		.092 (.089)	.052 (.097)	-.042 (.118)
1 + 2 + 3 + 4			.033 (.097)	-.042 (.118)
1 + 2 + 3 + 4 + 5				-.023 (.118)

the heritability was also estimated for L_{BJ} and L_{WJ} at the individual component lambings.

The heritability for L_{BJ} records pooled over 2, 3 and 4 lambings were respectively 7, 9 and 3 per cent (Table 2.8.5). In each analysis, the value for the pooled record was lower than for one of the component records. It is also apparent that as records were pooled, the heritability of L_{BJ} at the individual lambings declined. For example, the heritability of L_{BJ} at lambing 2 was 0.08 when ewes with first and second lambing records were included, but zero when the ewes also had to survive to third lambing. Similarly, for lambing 3, the heritability of L_{BJ} was 0.16 when ewes with three lambing records were included, 0.09 if only survivors to fourth lambing were included and zero if ewes had to have records for the first five lambings. When records on the first five lambings were required, the heritability of L_{BJ} was zero both for the pooled and for the individual lambing records.

The heritability of L_{WJ} records pooled over years followed the same general pattern as observed for L_{BJ} in that the heritability of performance at individual lambings declined as additional records were required for a ewe to be included in the analysis (Table 2.8.6). However, the heritability of pooled L_{WJ} records was sometimes higher than comparable records for L_{BJ}, and also higher than the heritability of L_{WJ} at individual component lambings.

In comparing these estimates for all ewes with those for ewes that survived to a subsequent lambing (Tables 2.8.5., 2.8.6), it cannot be concluded that the differences observed are not attributable

Table 2.8.6

The heritability of lambs weaned per ewe joined for records pooled over lambings

Standard errors of estimates in brackets

All data available used in analyses

Heritability estimated for lambing(s)	Lambings included in analysis			
	Lambings 1 + 2	Lambings 1, 2 + 3	Lambings 1, 2, 3 + 4	Lambings 1, 2, 3, 4 + 5
1	.009 (.080)	-.052 (.085)	-.028 (.095)	-.001 (.119)
2	.068 (.078)	-.022 (.086)	-.047 (.095)	-.100 (.117)
3		.080 (.088)	.034 (.097)	-.082 (.119)
4			-.013 (.096)	-.057 (.119)
5				.005 (.119)
1 + 2	.053 (.081)	-.016 (.091)	.015 (.097)	.015 (.118)
1 + 2 + 3		.086 (.089)	.093 (.098)	.001 (.119)
1 + 2 + 3 + 4			.067 (.098)	-.001 (.118)
1 + 2 + 3 + 4 + 5				.016 (.118)

to sampling, as data from additional years were included in the first-mentioned of these analyses. In order to make more appropriate comparisons, the heritability of L_{BJ} and L_{WJ} at third lambing have been estimated for ewes born sufficiently early in the period under observation to have had a fifth lambing by 1969, but without requiring that they, in fact, survived to have this later lambing. A comparison of these estimates with those obtained earlier when it was required that the ewes survived to fifth lambing provides a direct check of the importance of the survival requirement. Similarly, estimates of L_{BJ} and L_{WJ} at second lambing were computed for ewes born sufficiently early to have a third lambing, without requiring that they did so.

In these comparisons (Table 2.8.7) the same trends were observed as were apparent in Tables 2.8.5 and 2.8.6, although they were not quite so marked; the heritability of lambing performance for ewes that survive to some later lambing was lower than the corresponding estimates for all ewes.

Estimates of the between sire and residual components of variance, and of the phenotypic variance of L_{BJ} and L_{WJ} were estimated in the analyses listed in Tables 2.8.5, 2.8.6. and 2.8.7. The between sire component of variance varied in a similar fashion to that reported for the heritability. In addition, the sum of the between and within sire components of variance, an estimate of the phenotypic variance within flock x year cells, also declined. For instance, in the analysis listed in Table 2.8.7, this estimate of the phenotypic variance was, on average, two per cent higher in the "all ewe" analyses than it was when it was required that ewes survive to a subsequent lambing.

Table 2.8.7

The heritability of L_{BJ} and L_{WJ} for ewes that survived to subsequent lambings as well as for all ewes born in the same years

	Lambs born per ewe joined	Lambs weaned per ewe joined
(a) Heritability for second lambing		
Ewes that survived to third lambing	-.006 (.086)	-.022 (.086)
All comparable ewes	.027 (.081)	.046 (.081)
(b) Heritability for third lambing		
Ewes that survived to fifth lambing	-.061 (.116)	-.082 (.119)
All comparable ewes	.116 (.088)	.086 (.088)

Heritability of Binomially Distributed Traits

A number of alternative methods of analysis have been investigated for the tendency of ewes to lamb (E_{LJ}), and the number of lambing ewes with multiple births (E_{ML}).

The first of these methods was proposed by Robertson and Lerner (1949) and is a form of Chi-square heterogeneity test. It was employed on records at each of the first five lambings, and families of less than three daughters were excluded from the analyses. The estimates obtained could then be directly compared with those in Table 2.8.4, although given the frequencies of E_{LJ} and E_{ML} in the population, there should perhaps have been more stringent requirements before families were included in the Chi-square analysis (Cochran, 1954).

Given the number of family groups involved here, the modification to the expected value of Chi-square suggested by Cochran (1936) was not applied. Standard errors of the heritability estimates have been calculated as if heritability was estimated as the intra-class correlation (see Robertson and Lerner, 1949).

The estimates obtained for E_{LJ} and E_{ML} were, on average, little different from those obtained in the hierarchical analysis of variance (Table 2.8.8). For both characters, the two methods of analysis were in agreement as to the lambing with the highest heritability, although the largest discrepancy between the two sets of estimates was for E_{ML} at first lambing.

The two other methods of analysis which were considered are maximum likelihood approaches. The first was suggested by Robertson (1951) and the second by Tallis (1962) and this latter method was also employed by Young, Turner and Dolling (1963) to estimate the heritability of ewe fertility traits at different lambings. In both methods of analysis, maximum likelihood solutions were only obtained after the data were pooled, in this instance, pooled over years with flocks being examined separately. Unfortunately, pooling over years is likely to bias upwards the heritability estimates (see Table 2.8.3), and the magnitude of this bias was not the same for both characters and lambings. For instance, from the components of variance estimated in the original hierarchical analyses of variance, the heritability of E_{LJ} at first and third lambing respectively would be expected to be .36 and .34, when in Table 2.8.4 they are respectively three and 23 per cent. Pooling over flocks would have

Table 2.8.8

The heritability of E_{LJ} and E_{ML} as estimated by the Chi-square heterogeneity method

Method of Analysis	Lambing 1	 2	 3	 4	 5
	1. Ewes lambing of those joined (E_{LJ})				
Chi-square heterogeneity	-.058 (.067)	.046 (.074)	.161 (.080)	-.017 (.089)	-.006 (.100)
Intra-class correlation ‡	.029 (.068)	.174 (.076)	.234 (.079)	.107 (.091)	.050 (.111)
	2. Lambing ewes with multiple births (E_{ML})				
Chi-square heterogeneity	.473 (.128)	.044 (.100)	.254 (.120)	.002 (.138)	.017 (.170)
Intra-class correlation ‡	.270 (.120)	-.035 (.098)	.202 (.120)	.117 (.139)	.072 (.170)

‡ From Table 2.8.4

produced less drastic changes. Nevertheless, it was decided not to pursue these analyses any further as the effort and expense involved in the required computations did not seem to be justified if biased estimates of heritability were the expected outcome.

Offspring-parent Regression Analyses

The heritability of both L_{BJ} and L_{WJ} has been estimated by daughter-dam regression. Data were available on ewes in the base population and on their daughters born in the selection and control flocks between 1951 and 1967. The maximum number of daughter-dam pairs was for first lambing, 2417, in which there were on average 1.8 daughter records for each dam. The dam's record was repeated for each of her daughters. Sums of squares and cross products and degrees of freedom were calculated within year of birth of both dam and daughter and then pooled.

Heritability estimates for L_{BJ} and L_{WJ} at each of the first five lambings are given in Table 2.8.9. For both characters the heritability estimates for the third and the fifth lambing differed significantly from zero. The overall pattern in these estimates is generally similar to that observed in the half-sib estimates.

The major objection to heritability estimates of ewe reproductive performance obtained by daughter-dam regression is that they may be biased by dam selection. Dams in the '0' class which are included in the analysis are a select portion of all ewes that did not produce a lamb at that particular lambing, in that they did produce a daughter at some other lambing. It was considered that the most likely consequence of this form of selection would be to bias upwards the daughter's performance of ewes in the '0' class. For this reason it was decided to check on the linearity of the relationship between dam and daughter performance for L_{BJ}, using a form of genetic regression analysis akin to that employed in estimating repeatability in the previous Section. A least squares form of analysis was used to estimate daughter performance, and the following model was used:

$$X_{ijklm} = u + Y_i + YD_j + F_k + D_l + e_{ijklm}$$

where X_{ijklm} = an observation on daughter's performance for L_{BJ}

Y_i = an effect due to the i^{th} year of birth of the daughter

YD_j = an effect due to the j^{th} year of birth of the dam

F_k = an effect due to the k^{th} flock

D_l = an effect due to the l^{th} performance of the dam (0, 1 or 2 lambs), and

e_{ijklm} is a random error term

Separate analyses were conducted on the first to the fifth lambing records for L_{BJ}, the same lambing record being examined for both daughter and dam at any one time. In addition, the value of the dam's record for L_{BJ} as a predictor of L_{WJ} in the daughter was also determined.

Table 2.8.9

Heritability of L_{BJ} and L_{WJ} as estimated by daughter-dam regression

	Lambing 1	2	3	4	5
Lambs born per ewe joined	.038 (.036)	.038 (.036)	.127 (.036)	.031 (.038)	.142 (.048)
Lambs weaned per ewe joined	.040 (.036)	-.004 (.036)	.126 (.036)	.027 (.038)	.197 (.050)

The estimates of heritability obtained (Table 2.8.10) from the performance of the dam and the least squares estimate of daughter's performance are of the same order of magnitude as those obtained by more usual offspring-parent methods (Table 2.8.9). However, the relationship between daughter and dam performance was clearly not linear. At two lambings, the second and the fourth, daughters of ewes with '0' lambs at mothering produced more lambs than the daughters of ewes with 1 lamb. Over the five lambings, there was no difference in performance (L_{BJ}) between these two groups of daughters, while the daughters of the '1 lamb' dams weaned 1.3 more lambs per 100 ewes joined. Daughters of '2 lamb' dams were 7.7 per cent superior to the daughters of '1 lamb' dams in L_{BJ}.

Unbiased estimates of the heritability of twinning have been obtained for each of the first five lambings by two daughter-dam methods. The first of these could be described as a realised heritability method, the second a threshold model suggested by

Table 2.8.10

Relationship between a dam's record for L_{BJ} and her daughter's records for L_{BJ} and L_{WJ} at the corresponding lambing

Standard errors of estimates of daughter's performance given in brackets

Dam's record for L_{BJ}	Daughter's Performance				
	Lambing				
	1	2	3	4	5
	Lambs born per ewe joined				
0	0.854 (.022)	0.893 (.026)	0.896 (.027)	0.986 (.029)	0.976 (.035)
1	0.868 (.019)	0.837 (.021)	0.965 (.021)	0.947 (.024)	0.982 (.029)
2	0.906 (.026)	0.922 (.024)	1.038 (.025)	1.061 (.026)	1.058 (.031)
	Lambs weaned per ewe joined				
0	0.693 (.020)	0.812 (.025)	0.750 (.026)	0.865 (.029)	0.858 (.035)
1	0.718 (.017)	0.785 (.019)	0.858 (.020)	0.817 (.023)	0.865 (.028)
	0.716 (.024)	0.806 (.023)	0.918 (.024)	0.903 (.026)	0.961 (.031)
Heritability[‡] of L_{BJ}	0.047 (.024)	0.046 (.140)	0.160 (.044)	.098 (.154)	.094 (.034)

[‡] Estimated as twice the regression of daughter's L_{BJ} on dam's L_{BJ}

Falconer (1965) for estimating the liability to disease. In both, daughter's performance was estimated from least squares analyses, using the same model as that previously employed for L_{BJ} and L_{WJ}. Here, only dams and daughters producing 1 or 2 lambs at the corresponding lambing were included.

To estimate heritability as the response to selection among the dams, the difference in daughter performance between dams producing 1 v. 2 lambs was doubled. This response was achieved for a selection differential of one lamb, the difference between the two classes of dams. With only two groups of ewes in either generation, the sampling variance of the regression coefficient was calculated from the incidence of twins in the two groups of daughters.

In the method of analyses proposed by Falconer (1965), it is assumed that the binomially distributed trait, twinning, is determined by some underlying variate which is normally distributed. The heritability of twinning was calculated from Equation (4) in Falconer's paper, which makes due allowance for the fact that the controls in this comparison, single bearing dams, are selected in the same sense that twins are selected. Estimates of the incidence of twinning at each of the first five lambings were obtained from Table 2.3.6, page 83. The standard error of the regression coefficient was calculated by Method 2, Appendix B, in Falconer (1965).

The second of these methods of analysis was not, in fact, used for first lambing records, as the incidence of twins in the daughter and dam generations was negatively related (Table 2.8.11). For the other lambings, the threshold model gave higher estimates.

Both methods of analysis estimated that the heritability of twinning was highest at the third lambing.

Phenotypic and Genetic Correlations Between Measures of Reproductive Performance

In the hierarchical analysis of variance, phenotypic and genetic correlations have been estimated between L_{BJ} and L_{WJ} and between L_{BL} and L_{WL} at the same lambing. Estimates of the genetic correlation could not be obtained where one of the measures was not heritable (see Table 2.8.2, 2.8.4). Where estimates of the heritability were positive but close to zero, estimates have been calculated although it is not clear to what extent either they or their estimated sampling variances are reliable. Standard errors of the genetic correlations were estimated using the approximate formula suggested by Robertson (1959).

The phenotypic correlations between L_{BJ} and L_{WJ} were all in excess of .8 and were significantly higher than the phenotypic correlation between L_{BL} and L_{WL} at the corresponding lambings. The genetic correlations did not differ significantly from unity for either pair of characters.

Phenotypic correlations between either L_{BJ} or L_{WJ} at different lambings have been considered in the previous Section. It was not possible to estimate corresponding genetic correlations as in no case was the heritability positive for either L_{BJ} or L_{WJ} at different lambings.

Table 2.8.11

The incidence of twinning among daughters of single and twin producing dams, and estimates of the heritability of twinning

	Lambing				
	1	2	3	4	5
	1. Incidence of twinning in daughters (%)				
Performance of dam at corresponding lambing (E_{ML})					
One lamb	16.6	33.7	32.3	40.4	44.9
Twins	16.1	36.5	39.0	42.1	46.6
	2. Heritability of twinning				
(a) Realised heritability	-.010 (.026)	.054 (.023)	.134 (.026)	.036 (.022)	.034 (.033)
(b) Falconer's threshold model	no estimate	.086 (.089)	.219 (.085)	.054 (.094)	.053 (.106)

Table 2.8.12

Phenotypic and genetic correlations between measures of reproductive performance at the same lambing

Lambing	Phenotypic Correlations (95% confidence limits)		Genetic Correlations (Standard error of estimate)			
	L_{BJ}/L_{WJ}	L_{BL}/L_{WL}	L_{BJ}/L_{WJ}		L_{BL}/L_{WL}	
			(1)‡	(2)‡	(1)‡	(2)‡
First	.862 (.851, .869)	.592 (.558, .617)	-	-	-	-
Second	.851 (.840, .859)	.653 (.613, .675)	.888 (.191)	.868 (.240)		-
Third	.845 (.834, .854)	.658 (.578, .686)	1.117 (.121)	.940 (.031)	1.113 (.173)	-
Fourth	.862 (.849, .870)	.667 (.641, .696)	-	1.063 (.160)	1.200 (.368)	-
Fifth	.842 (.824, .854)	.671 (.641, .701)	-	1.068 (.080)	.596 (.885)	-

Estimate 1, from the analysis of all data (Table 2.8.2)

Estimate 2, from the analyses in which all sires had at least 3 daughters (Table 2.8.4)

Discussion

The heritability of ewe reproductive performance has been estimated for a heterogeneous population, heterogeneous in that 8 of the 10 flocks had been subject to continued directional selection. In such circumstances, half-sib heritability estimates in particular could be biased downwards if the characters under selection are genetically correlated with ewe reproductive performance. Differences between the flocks have already been reported for various measures of performance (see Section 2.4) and this topic will be returned to in the Part 3 of this Thesis. For the purposes of the present discussion it will be assumed that the estimates refer to an unselected population. However, it should be pointed out that Kennedy (1967) estimated the heritability of L_{BJ} and L_{WJ} at first lambing at .20 and .06 respectively for a sample of ewes from the base population and Random flocks. These values are considerably higher than those reported here and, while the two sets of estimates do not differ significantly, the possibility that the differences are due to the selection history of the flocks cannot be discounted.

The estimates obtained for L_{BJ} and L_{WJ} at the individual lambings were low (see Tables 2.8.2 and 2.8.4) with a maximum value of 0.26 for L_{BJ} at third lambing (Table 2.8.4). They are thus broadly similar to estimates obtained for other breeds (see Table 2.6.4). In the present study estimates for L_{BJ} and L_{WJ} increased from the first to the third lambing, fell at the fourth, and then behaved variably. Evidence from other studies on possible associations between heritability and age of ewe is conflicting (see Section 2.6), although

Young, Turner and Dolling (1963), also working with Merinos, reported a much more dramatic increase for L_{BJ} between first and second lambing than was obtained here. Ideally, any such observation should be based on analyses using the same body of data and not, as in Table 2.8.2 and in the other studies, where varying numbers of drops contributed to the different estimates. However, where some attempt was made to balance the data in an appropriate fashion, the heritability estimates for the earlier lambings were consistently lower than when they were considered on their own (Tables 2.8.5, 2.8.6 and 2.8.7). It seems reasonable to conclude from these Tables 2.8.2 and 2.8.4 that among the first four lambing records, heritability for both L_{BJ} and L_{WJ} is highest at the third lambing. Nevertheless, it should be appreciated that any such pattern of association may be influenced by factors which influence the probability of a ewe surviving to various lambings.

The heritability of L_{BJ} at a lambing was lower for ewes that survived to some later lambing than it was for all ewes. In addition, the phenotypic variance among surviving ewes was less. This decline in phenotypic variance would be expected from the results presented in Table 2.3.6, where it was shown that the probability of subsequent survival was related to lambing performance, such that ewes of intermediate lambing performance had the greatest chance of survival. It is tempting to attribute the pattern of declining heritability to stabilising selection on lambing performance. However, stabilising selection would not be expected to reduce the heritability of lambing performance if, for that lambing, selection acted only at the level of phenotypic expression for L_{BJ}. The heritability among survivors might be expected to be lower if there was a curvilinear genetic relationship between L_{BJ} and the likelihood of survival. Because of the small size of the half-sib family groups, it was not thought worthwhile to look for such a relationship in these data.

In previous studies the disparity between estimates for L_{BJ} and L_{WJ} has almost always been greater than reported here (Young, Turner and Dolling, 1963; Purser, 1965; Kennedy, 1967). The average estimates for L_{BJ} and L_{WJ}, obtained by weighting individual values by the inverse of the sampling variance, were respectively 5.1 and 3.1 per cent (Table 2.8.2) and 8.4 and 6.5 per cent in the analyses on the restricted body of data (Table 2.8.4). Only at the third lambing was the heritability of L_{BJ} consistently and appreciably greater. Given the similarity of the estimates of the two characters and the high genetic correlation between them at any one lambing, equivalent responses in L_{WJ} might be expected, regardless of whether selection was on L_{BJ} or L_{WJ}. The heritability of L_{BL} was also higher than for L_{WL}, with average weighted estimated over the two sets of analyses of 11 and 8 per cent. These results support the conclusion of Purser (1965) that the action of the environmental factors influencing survival was such as to 'dilute what little genetic variation is present in litter size at birth'.

Previous reports (Purser, 1965) or suggestions (Turner, 1966) that the heritability of E_{LJ} was effectively zero do not seem to apply to this population, where the weighted average estimate was 11.6 per cent (Table 2.8.4). Both in magnitude and in their pattern of change with age, the heritability estimates for E_{LJ} and L_{BJ} were similar.

Culling families of less than three daughters had comparatively little effect on the standard errors of the half-sib heritability estimates (Table 2.8.4). By increasing the average number of daughters and, as it t~~i~~urned out, also the between sire component of variance, the loss of information in the analysis of variance due to variation in family size would be reduced (Robertson, 1962). However, in the process, between 41 and 63 per cent of the sire groups were culled, so that it is not surprising that the effect on the standard errors was not greater (see Swiger, _et_. _al_., 1964). The estimates obtained in the two sets of analyses (Tables 2.8.2, 2.8.4) are not independent. In subsequent predictions of response to selection for increased reproductive performance the estimates obtained for the restricted body of data will be used if for no better reason than that they are more encouraging as to the responses which might be achieved.

These half-sib estimates will also be used in preference to offspring-parent regression estimates of heritability. While the daughters of ewes that produced twins at the corresponding lambing consistently produced more lambs than did the daughters of single bearing ewes, the daughter-dam heritability estimates are subject to bias as only a selected portion of dams in the zero lambs class are represented in the analyses, namely those ewes that produced a daughter at some other lambing. This form of dam selection is not the same as truncation selection for some normally distributed trait, so that it is not clear what form of correction to the heritability estimates would be appropriate. All that can be concluded is that the relationship between daughter and dam records which can be included in the analysis is not linear.

The half-sib and daughter-dam regression estimates of the heritability of twinning are in general agreement (Tables 2.8.2, 2.8.4 and 2.8.11), with one obvious exception, that of performance at first lambing. Here the half-sib estimate was .27 (Table 2.8.4), while the regression estimate was negative. This discrepancy may be due to the importance of different genetic components included in the two estimates (see Dickerson, 1969), but is likely to be at least partially attributable to a negative maternal handicap such as that reported by Falconer (1964) in mice. The maternal handicap in this case would be being born a twin, and the daughters of twin producing ewes would be likely to contain more twins than the daughters of single producing ewes. It has already been pointed out that twin born ewes produce fewer twins at first lambing than do singles (Table 2.4.7). The importance of this suggested maternal effect could be tested by comparing the relative performance of the daughters of single and twin producing ewes, the daughters themselves being sub-divided according to their own type of birth.

Finally, the half-sib heritability estimates for L_{BJ} at third lambing was as high or higher than repeatability estimates for L_{BJ} in which data on the third lambing were included. This situation is by no means confined to the present study (Young, Turner and Dolling, 1963; see Turner, 1969a,b, for other references). By way of explanation Bradford (1972) has invoked negative environmental effects, such that producing twins in one year could lead to a ewe being in poor body condition and hence give lower than average performance in the following year. Certainly, such effects do appear to have operated in a number of studies in which repeatability estimates have been increased by improved environmental conditions (Purser, 1965; Shelton and Menzies, 1970). In addition, Purser (1965) also suggested that the stress associated with twinning at early lambings could be responsible for the poorer predictive value of such records. However, while these findings and suggestions may be apposite, there is no reason why the repeatability between a pair of lambings may not be lower than the heritability at one of them. In the relatively simple model proposed in Appendix B , repeatability sets an upper limit not to the heritability at either lambing but to the square root of the product of the heritabilities, even when the genetic correlations between the two records is one.

SECTION 2.9 ESTIMATING THE RESPONSE TO SELECTION FOR INCREASED REPRODUCTIVE PERFORMANCE IN THE TRANGIE FLOCK ~~IN THE TRANGIE FLOCK~~

From the information presented in the previous Sections, the expected response in ewe reproductive performance can be predicted for a number of forms of selection. As already mentioned, selection can be among hogget replacements, based on their dam's performance, or among ewes already in the breeding flock based on their own lambing records. Initially these will be considered as alternative rather than as complementary programmes. In all of the subsequent calculations, half-sib estimates of the heritability of L_{BJ} will be used; from Table 2.8.4, .017 for first lambing, .051 for second, .261 for third, .049 for fourth and .119 for fifth. The flock will be assumed to be closed and of five age groups of ewes, 2 to 6 years of age. Rams are only used once, at 1½ years of age. In all of the following calculations, responses will be measured as the genetic improvement in flock reproductive performance. This should also be the same as the asymptotic rate of response in a continuing selection programme, provided of course that the genetic parameters and population structure and statistics are constant (Hinks, 1970; Hill, 1971, 1974). Using the terminology of Rendel and Robertson (1950), genetic improvement (ΔG) should be equal to:

$$\frac{I_{RR} + I_{RE} + I_{ER} + I_{EE}}{L_{RR} + L_{RE} + L_{ER} + L_{EE}}$$

where I and L refer respectively to the genetic superiority of selected parents and to generation lengths with reference to the four possible paths to improvement (in subscripts), rams to breed rams, rams to breed ewes, ewes to breed rams and ewes to breed ewes. In the following examples, the generation lengths L_{RR} and L_{RE} are both equal to 2.0 years, the average age of sires when their progeny are born. In an unselected flock of ewes, L_{ER} and L_{EE} are both equal to 4.05 (Table 2.5.2) and in the following examples are little affected by the selection procedures being examined.

In selecting hogget rams on their dam's performance, we are selecting ewes to breed rams. In the following example, it will be assumed that triplet rams are chosen from ewes having their third lambing. Given that at least one per cent of rams would probably be required at mating (Dawe et al, 1970), and the known frequency of triplets at birth in this flock, this selection pressure might not be achieved in practice, but it will suffice for the present purposes. Selection is based on the dam's third lambing as this record of L_{BJ} has the highest heritability. The genetic superiority of the selected dams will be equal to the product of the selection differential and the heritability. As response will be measured relative to a population where rams are not chosen with regard to their dam's record, the selection differential applied is equal to 3 minus the average litter size among the lambs from ewes having their third lambing. From the results in Table 2.4.3, almost equal proportions of single and twin born rams would be available for selection.

The genetic superiority of the selected ram lambs for L_{BJ} at third lambing should be equal to the average of their parents' superiority (half that of their dam's superiority in this example) or

.198 lambs. As the interest is in improving flock reproductive performance, the genetic superiority of the selected dams and their sons at other lambings would also have to be considered. To obtain this information, the genetic correlations between L_{BJ} at different lambings have been assumed to be 1, while the between sire and residual components of variance (Table 2.8.3) have been used to estimate phenotypic standard deviations. When the age structure of the breeding flocks is taken into account, the genetic superiority of the selected ewes in flock reproductive performance is equal to .176 lambs. Calculated as an annual rate of improvement (L_{ER} = 4.00, L_{EE} = 4.05), response would be expected to be .015 lambs born per ewe joined per year, or 1.55 per cent of average flock performance.

Similar calculations could be made for the improvement expected as a result of selecting hogget ewes on their dam's record. A simple version of this form of selection would be to choose twin born hogget ewes in preference to singles, without regard to the lambing at which they were born. Such a selection programme would have much to recommend it in commercial flocks, as permanent records would not be required, only the identification of either singles or twins at birth. Given the relative frequency of twins and singles at 18 months of age (Tables 2.4.3; 2.4.9), an estimated 41 per cent of ewes entering the breeding flock would be twins, if the choice was made at random. By choosing all available twins, this figure could be increased to 70 per cent. From the relative performance of singles and twins (taken from the age specific estimates of L_{BJ} for singles and twins), the average genetic superiority of the twins in flock reproductive performance is equal to .023 lambs. Hence the superiority of their dams is equal to twice this, and the expected rate of improvement is .0038 lambs per ewe joined per year, or 0.40 per cent of mean flock performance. Selection of ewes to breed both rams and ewes could be practised concurrently and the total response to selection would be expected to be simply the sum of the two independent contributions to improvement. Clearly in this example, selection of ewes to breed rams is by far the major contributor to improvement.

Where selection is among ewes already in the breeding flock, improvement due to artificial selection comes about by keeping the selected ewes for subsequent lambings. Hence, for a flock with a fixed number of age groups, selection on early lambing records would offer the greatest opportunity for passing genetic superiority to the following generation. In the following examples of this form of selection, 20 per cent of ewes will be culled after any of the first four lambings. Culling of this order would be expected to make little improvement to current flock productivity; in fact, culling 20 per cent of ewes after the fourth lambing would lower flock reproductive performance, due to the adverse effect of altering the age structure of the flock (Table 2.9.1).

After making allowance for the necessary alterations in age structure of the breeding flock, 79, 58, 36 and 17 per cent of hogget ewes are produced by selected ewes where culling was respectively after the first, second, third and fourth lambing, and all estimates of response have been modified accordingly. To bring them to a common basis of comparison, responses have been estimated for a flock of five age groups of ewes in which there is no culling. Genetic

Table 2.9.1

The effect of culling on flock reproductive performance: Twenty per cent of ewes without lambs culled after the nominated lambing

	Lambing on which culling based			
	First	Second	Third	Fourth
Effect on current flock productivity † (%)	+.62	+.66	+.52	-.02
Rate of genetic improvement † (% per year)	+.08	+.12	+.17	+.04

† Both expressed relative to performance of unselected flock

correlations between L_{BJ} at different lambings have again been assumed to be 1. In this form of selection, the genetic superiority of the selected ewes is passed equally to their ram and ewe offspring. However, from the figures in Table 2.9.1 it can be seen that the expected annual rate of improvement in flock reproductive performance is low, with a maximum value of .17 per cent per year when ewes are culled on the basis of their third lambing record.

Breeding programmes recommended for improving reproductive performance in commercial flocks normally suggest that selection should be practised among both potential hogget replacements and ewes in the breeding flock, even to the extent of culling all dry ewes after each lambing, if this is possible. It is difficult to translate estimates of phenotypic and genetic parameters on populations not subject to artificial selection, such as has been obtained here, into predictions of genetic progress in programmes where such a range of consecutive selection decisions are made. If characters associated with reproductive performance were normally distributed, then appropriate modifications to the parameter estimates might be made (Cochran, 1951; Thompson, 1973). As this is not the case, it will probably be necessary to re-estimate parameters of interest after some appropriate form of paper culling of the data in order that agreement between predictions and response can be assessed (Turner, 1969a, b).

PART 3

SECTION 3.1 THE CORRELATION BETWEEN EWE REPRODUCTIVE PERFORMANCE AND THE CHARACTERS UNDER SELECTION IN THE TRANGIE SINGLE CHARACTER SELECTION FLOCKS - A REVIEW

Estimates of genetic correlations are of interest for two major reasons within the present context of attempting to improve ewe reproductive performance. Firstly, they are necessary in order to predict the effects of such a selection programme on other production characters. Secondly, they enable an assessment of the feasibility of improving ewe reproductive performance by indirect selection. In this Thesis, the aim is simply to estimate the magnitude of phenotypic and genetic correlations, and also to examine the correlated changes in ewe fertility in the Trangie single character selection flocks. These analyses are presented in Section 3.2. Before that, available estimates of such correlations will be reviewed, an area also recently covered by Turner (1972).

Correlations between reproductive performance and fleece characters.

In discussing such relationships, it is useful to distinguish those studies in which fleece characters were recorded before first mating, from those where the measurements were made after the ewe had entered the breeding flock. The latter situation is complicated by the fact that pregnancy and lactation can influence measures of wool production (Brown *et. al.*, 1966). Then if no adjustment is made for say the effect of previous lambing performance on fleece weight, a biased estimate of the genetic relationship between that fleece record and the previous or following lambing can result. If a correction is made, it is not clear to what extent correlations estimated are between reproductive performance and the correction, rather than with the breeding value of the animal for that character. While estimates of the correlation between fertility and wool production throughout life are of considerable importance in designing improvement programmes, greater confidence can be placed in correlations where the fleece characters are recorded prior to first mating.

In general, estimates of the phenotypic correlation between ewe reproductive performance and hogget fleece weight have not been large, whether positive (Young, Turner and Dolling, 1963) or negative (Kennedy, 1967). Purser (1965) found the relationship between later fleece weights and litter size to be positive. Estimates of the genetic correlation are similarly variable although here the majority are negative (Rae and Ch'ang, 1955) and sometimes strongly so (Kennedy, 1967; Shelton and Menzies, 1968). The standard error of many of these estimates is high so that the considerable range in magnitude of these estimates is perhaps not surprising. A further complication is the low degree of genetic variation for reproductive performance. For instance, Young, Turner and Dolling (1963) found the heritability of L_{BJ} and L_{WJ} at first lambing to be low (both 0.03), while corresponding estimates at second lambing were 0.35 and 0.15. It is not clear to what extent information on genetic correlations between such traits and production characters should be weighted, if only subjectively, by information on the heritability of reproductive performance. In any event, given that the genetic correlation between fleece weight and L_{BJ} at both the first and second lambing was the same, the relative magnitude of the expected correlated changes in L_{BJ} at these two lambings as a result of selecting for clean fleece weight would be very different.

Few estimates of correlations between crimp frequency and ewe reproductive performance are available. Phenotypic correlations with crimp frequency at the hogget shearing would appear to be small (Young, Turner and Dolling, 1963; Kennedy, 1967), while the genetic correlation with L_{BJ} at first lambing was positive in both of these studies.

Two studies have been made of correlated changes in ewe reproductive performance to selection for increased fleece weight. Turner, McKay and Guinane (1973) found no consistent evidence of any change in L_{BJ} or L_{WJ}, which is in line with estimates obtained for their population by Young, Turner and Dolling (1963). Kennedy (1967) also reported that selection for increased fleece weight at Trangie (Fleece Plus v. Fleece Minus flocks) had not affected reproductive performance of 2 year old ewes, although he did estimate a high negative genetic correlation between fleece weight and these measures of fertility.

Correlations between reproductive performance and body weight.

A large number of estimates of the phenotypic association between body weight prior to mating and various measures of ewe reproductive performance are available largely because of the interest in such practices as flushing to improve lambing rates (see Moule, 1962). The present discussion will be restricted to studies in which estimates of both phenotypic and genetic correlations are available (Table 3.1.1). Again the distinction between body weights recorded prior to first mating and later weights is apposite.

In all of the studies listed in Table 3.1.1, the phenotypic and genetic correlations between body weight and reproductive performance were positive. The estimate of the genetic correlation reported by Ch'ang and Rae (1972) was such to indicate that selection for hogget body weight might produce a greater response in ewe reproductive performance, than direct selection for such characters. On the other hand, a positive genetic correlation would mean that selection for improved fertility would increase the average body weight of the population, with the consequent expected increase in maintenance requirements.

Pattie (1965b) reported that the reproductive performance of ewes in the Weaning Weight Plus and Minus flocks at Trangie was similar. If there was a positive genetic correlation between weaning weight and L_{BJ} or L_{WJ}, as in the studies mentioned above, then the Weight Plus flock would be expected to be superior. However, Pattie (1965b) also reported that prior to the use of type of birth corrections, the proportion of twins included in the two flocks differed markedly, with a higher percentage being included in the Weight Minus flock. From the results reported earlier in this Thesis on the relative reproductive performance of single and twin born ewes (see Table 2.4.6), and more generally on the inheritance of ewe reproductive performance (Section 2.8), such unequal representation of twins would counteract any positive correlation in the Trangie flock.

Table 3.1.1

Phenotypic and genetic correlations between ewe reproductive performance and body weight

Study	Body weight at:	Measure of ewe reproductive performance (lambing(s))	Phenotypic correlation	Genetic correlation
Young, Turner and Dolling (1963)	16 months (hogget)	L_{BJ} (1)	0.14	0.47
		L_{WJ} (1)	0.03	0.16
	16 months (hogget)	L_{BJ} (2)	0.12	0
		L_{WJ} (2)	0.01	0.22
Purser (1965)	Pre-mating	E_{LJ} (various)	0.23	0.44
		E_{LJ} (various)	0.25	0.78
Kennedy (1967) (Trangie flock)	16 months of age (hogget)	L_{BJ} (1)	0.07	0.20
		L_{WJ} (1)	0.06	0.06
Shelton and Menzies (1968)	weaning	L_{BJ} (various)	0.06	0.06
		L_{WJ} (various)	0.10	0.04
	yearling	L_{BJ} (various)	0.15	0.57
		L_{WJ} (various)	0.11	0.44
Ch'ang and Rae (1972)	weaning	L_{BJ} (1)	0.13	.32 to 1.27
		L_{BJ} (1+2)	0.15	.40 to .83
		L_{BJ} (1+2+3)	0.15	0 to 0.42
	hogget	L_{BJ} (1)	0.23	.72 to 1.25
		L_{BJ} (1+2)	0.22	.16 to .67
		L_{BJ} (1+2+3)	0.23	-.24 to .65

Correlations between skin fold and ewe reproductive performance.

Young, Turner and Dolling (1963) found both the phenotypic and genetic correlations to be negative, and the genetic correlation strongly so. Dun (1964) presented evidence on the poorer reproductive performance of the Folds Plus flock at Trangie, relative to the Folds Minus flock. However, subsequent work by Dun and Hamilton (1965) indicated that this difference in flock reproductive performance was due to differences in ram fertility, a topic also dealt with by McGuirk (1969) and extensively so by Fowler (1966 <u>et</u>. <u>seq</u>.).

SECTION 3.2 ESTIMATES OF PHENOTYPIC AND GENETIC CORRELATIONS BETWEEN REPRODUCTIVE PERFORMANCE AND OTHER CHARACTERS IN THE TRANGIE FLOCK

In this Section two topics are dealt with, estimates of genetic and phenotypic correlations between ewe reproductive performance and the characters under selection at Trangie, using an unselected population of ewes, and then the correlated responses in ewe reproductive performance actually observed for the single character selection flocks.

Correlations in the unselected Trangie population

The measures of ewe reproductive performance examined in these analyses were E_{LJ}, L_{BJ} and L_{WJ}, at each of the first three lambings. These were correlated with clean fleece weight, crimp frequency, age corrected weaning weight, for which the age correction was applied to weaning weight itself and not gain from birth to weaning, and the combined skin fold score for neck and side. No type of birth correction was applied to any of these characters. Estimates of genetic correlations were obtained by both half sib analysis of variance and daughter-dam regression. In each case, data were from ewes born and mated in either the March or April mated Random flocks. For the half-sib analyses, information was available on a maximum of 791 ewes, the progeny of 247 rams. At most 592 daughter-dam pairs were considered. Dam records were repeated each time a daughter was represented.

Heritability estimates for ewe reproductive performance (Table 3.2.1) were not greatly different from those reported earlier in this Thesis (Table 2.8.4, page 168). Heritability estimates for clean fleece weight, crimp frequency, weaning weight and fold score, averaged over all the estimates obtained, were respectively .25, .40, .17 and .52.

Table 3.2.1

Estimates of heritability of ewe reproductive performance in the Trangie Random flocks

	Half-sib Estimates			Daughter-dam Estimates	
	E_{LJ}	L_{BJ}	L_{WJ}	L_{BJ}	L_{WJ}
Lambing 1	.01	-.20	-.04	-.05	.05
2	.15	.09	-.07	.05	.04
3	.16	.09	-.08	.18	.22

Phenotypic correlations were small and none differed significantly from zero; the maximum deviation from zero being a correlation of .09 between E_{LJ} at third lambing and clean fleece weight. If the individual estimates are pooled, the average correlation between all measures of ewe reproductive performance and the other characters was as follows: clean fleece weight, -.02; crimp frequency, -.01; weaning weight, .0; and fold score, -.03.

In view of the heritability estimates presented in Table 3.2.1, genetic correlations were not calculated with ewe reproductive performance at first lambing, while correlations with L_{WJ} were only obtained using the daughter-dam regression method. Standard errors of the genetic correlations were calculated using the approximate method proposed by Robertson (1959) while for the daughter-dam estimates, the formula suggested by Reeve (1955) was used.

Nine of the thirty two estimates of genetic correlations differed significantly from zero (Table 3.2.2). Even so, there was considerable variation between estimates for say fleece weight and different measures of reproductive performance, especially when recorded for different lambings. Where comparable half-sib and offspring parent estimates were available, as there were for correlations involving L_{BJ}, the two estimates sometimes differed quite markedly. In view of this variation, there seems little point in dealing with individual estimates in any detail. It would appear that correlations between performance at second lambing and clean fleece weight were strongly negative, but with third lambing the correlations were small and mostly positive. With crimp frequency, it is with third lambing that the correlations are consistent and negative. While the genetic correlations with weaning weight are variable in sign, those that differ significantly from zero were positive. Correlations with fold score were all relatively low and tended to be negative.

Having indicated which genetic correlations differ significantly from zero, it should be pointed out that they had to be of the order of ± 0.7 to do so, so large were the standard errors of the individual, estimates.

One might have sufficient confidence in a correlation which differs significantly from zero to predict the direction of the change in one character to selection in the other. One would be less confident in predicting the magnitude of such a change. For this reason the estimates given in Table 3.2.2 could only be regarded as provisional for the Trangie population; for the assessment of, for example, schemes for indirectly selecting for increased reproductive performance, more precise estimates of genetic correlations would be required.

Table 3.2.2

Estimates of the genetic correlation between reproductive performance and other characters

Measure of reproductive and method of estimation	Other Character			
	Clean Fleece Weight	Crimp Frequency	Weaning Weight	Fold Score
Second Lambing				
E_{LJ} (HS)	-1.10*	.18	.26	-0.16
L_{BJ} (HS)	-1.00*	.76*	1.15*	-0.12
L_{BJ} (DD)	-0.83*	-.33	-0.38	-0.33
L_{WJ} (DD)	-0.45	-.13	-0.15	-0.31
Third Lambing				
E_{LJ} (HS)	-0.13	-.37	0.76*	0.16
L_{BJ} (HS)	0.38	-.48	0.71*	0.25
L_{BJ} (DD)	0.08	-.70*	-0.06	-0.31
L_{WJ} (DD)	0.19	-.54*	-0.27	-0.17

* $P < .05$

HS = half-sib analysis of variance

DD = daughter dam regression

Comparisons of the Selection Flocks

In Section 2.4 it was pointed out that the flocks differed in measures of ewe reproductive performance and an indication of the magnitude of these differences was given in Table 2.4.12. The aim here is to give a little more detail on this topic. It should be pointed out at the outset that any differences in flock reproductive performance could be due to differences in either ram or ewe fertility, a point well brought out in the study of the Folds selection flocks by Dun and Hamilton (1965).

The March and April mated flocks have been compared separately. For each, two groups of matings were considered. In the first of these, flocks were compared between the year in which animals born in the selection flocks were first mated (1953 or 1954) and 1961, and then for the period 1962 and 1969. The comparisons were based on the following characters, the number of ewes lambing of those joined (E_{LJ}), the number of lambs born per ewe joined (L_{BJ}) and the number of lambs weaned per ewe joined (L_{WJ}). In the first time period considered, information was included on ewes between 2 and 8 years of age (first to seventh mating); in the second only data on the first five matings were included.

The flocks were compared by least squares analysis, using the following model:

$$X_{ijkl} = u + f_i + a_j + y_k + fa_{ij} + e_{ijkl}$$

where u is the overall mean

f_i = an effect due to the i^th flock

a_j = an effect due to the j^{th} age group of ewe

y_k = an effect due to the k^{th} year of lambing

fa_{ij} = the first order interaction between flock and age of ewe, and

e_{ijkl} is a random error term.

The least squares means for the flocks are given in Table 3.2.3. There was significant variation among the March mated flocks in both time periods for all measures of performance. Differences between the Random and selection flocks cannot be attributed to selection, as the system of mating the flocks also differed, especially in the second time period. A more appropriate method of detecting the effects of selection is to compare the Plus and Minus flocks of a pair. Here the most obvious difference is between the Folds Plus and Minus flocks, with the Folds Plus flock being inferior to all of the other March mated flocks in both periods. In contrast, differences between the Weaning Weight flocks were small in both periods.

There were no significant differences among the April mated flocks in the period 1954 to 1961. In the second period they showed significant variation for E_{LJ} and L_{WJ}. However, the flock x age of ewe interaction was also significant for E_{LJ}, indicating that if correlated responses in this character had occurred, the effect was not equal for all lambings. In both periods the Fleece Minus flock was superior to the Fleece Plus; in L_{WJ} the Fleece Minus flock was superior by respectively 17.5 and 12.3 per cent. On the other hand, differences between the Crimps selection flocks were not consistent in direction, although, in period 2, the Crimps Minus flock had an overall superiority in L_{WJ} of 6.6 per cent.

Table 3.2.2

Measures of ewe reproductive performance in the March and April mated flocks

	Measure of reproductive performance		
	E_{LJ}	L_{BJ}	L_{WJ}
March mated flocks			
Period 1, 1953 - 1961			
Random	.789	.966	.864
Weaning Weight Plus	.698	.752	.664
Weaning Weight Minus	.665	.755	.661
Folds Plus	.715	.760	.677
Folds Minus	.792	.988	.895
Period 2, 1962 - 1969			
Random	.789	1.112	.982
Weaning Weight Plus	.762	1.139	.987
Weaning Weight Minus	.758	1.142	.952
Folds Plus	.610	.824	.673
Folds Minus	.743	1.028	.895
April mated flocks			
Period 1, 1954 - 1961			
Random	.726	.768	.655
Fleece Plus	.722	.720	.590
Fleece Minus	.738	.753	.693
Crimps Plus	.770	.729	.645
Crimps Minus	.754	.731	.623
Period 2, 1962 - 1969			
Random	.820	1.123	.997
Fleece Plus	.715	1.019	.813
Fleece Minus	.821	1.067	.913
Crimps Plus	.747	1.035	.854
Crimps Minus	.718	1.092	.910

Correlated responses in ewe reproductive performance

Having established that the Plus and Minus flocks of some pairs of selection flocks differ in ewe reproductive performance, the need then is to estimate the realised genetic correlation between ewe reproductive performance and the character under selection. For each of the three measures of performance, E_{LJ}, L_{BJ} and L_{WJ}, the differences between the Plus and Minus flocks were calculated each year at each of the first five lambings. Cumulated selection differentials were obtained for each flock as the average of the unscaled individual cumulated selection differentials for all ewes mated in that particular year, and then the values for the two flocks were summed.

Estimates of the realised genetic correlation (r_g) were obtained as:

$$r_g = (CR_X/i) / \sigma_X \sqrt{(h_X^2 h_Y^2)}$$

where CR_X = correlated response in reproductive performance (X)

i = the cumulated selection differential for the character under selection (character Y)

σ_X = the phenotypic standard deviation for the measure of reproductive performance (from Table 2.8.3, p. 166)

h_Y^2 = the realised heritability to 6 generations of divergent selection (Tables 1.3.7, 1.3.10, 1.3.13, 1.3.15)

and h_X^2 = the heritability for the measure of reproductive performance (Table 2.8.4).

The ratio $(CR_X/_i)$ was calculated as a regression of divergent response in reproductive performance on cumulated selection differential. A sampling variance of the realised genetic correlation was obtained in terms of the sampling variances of the components of the ratio from which it was estimated, assuming the phenotypic standard deviation of X was known without error.

Estimates of the realised genetic correlations are given in Table 3.2.4. Values have not been given for the correlated response of L_{WJ} at first lambing, as the estimate of the heritability of this character was negative (Table 2.8.4). A number of the estimates of the realised genetic correlations differed significantly from zero. Only for the Folds selection flocks was the direction of the correlations consistent for all measures of reproductive performance. The correlation between fleece weight and reproductive performance was negative for the early lambings and then variable in sign.

Unconscious selection for ewe reproductive performance in the single character selection flocks

Pattie (1965b) pointed out that the relative numbers of singles and twins chosen as replacements in the Weaning Weight selection flocks were not the same as the corresponding numbers available for selection. In the Weight Plus flock singles were chosen in preference to twins and the reverse was true in the Weight Minus flock. The reason for this directional if unconscious selection for birth type and hence for ewe reproductive performance was that the weaning weights of singles and twins were not equal and that prior to 1959 no type of birth corrections were applied to Weaning Weight before the selections

Table 3.2.4

Estimates of the realized genetic correlations between characters under selection and measures of ewe reproductive performance, and their standard errors†

Reproductive Performance	Character under selection							
	Fleece Weight		Crimp Frequency		Weaning Weight		Fold Score	
	r_g	s.e.	r_g	s.e.	r_g	s.e.	r_g	s.e.
First lambing								
E_{LJ}	-.33	.392	.52	.828	.22	.508	.18	.228
L_{BJ}	-.38	.769	-1.46	2.985	.57	1.275	-2.29	4.800
L_{WJ}	-	-	-	-	-	-	-	-
Second lambing								
E_{LJ}	-.17	.123	.09	.103	-.04	.080	-.25	.163
L_{BJ}	-.16	.128	-.43	.448	-.12	.191	-.70	.700
L_{WJ}	-.14	.129	-.26	.307	.01	.031	-.69	.603
Third lambing								
E_{LJ}	-.09	.065	.06	.049	.01	.020	-.22	.121
L_{BJ}	.10	.500	-.06	.076	.00	.005	-.24*	.074
L_{WJ}	-.04	.040	.04	.075	.00	.010	-.33*	.106
Fourth lambing								
E_{LJ}	-.14	.119	.47	.282	.00	.008	-.23	.215
L_{BJ}	-.04	.149	.28	.576	-.02	.081	-.53	.604
L_{WJ}	-.08	.140	.49	.718	.01	.102	-.40	.535
Fifth lambing								
E_{LJ}	.11	.188	.13	.186	.25	.411	-1.19	1.351
L_{BJ}	.07	.098	-.18	.168	.06	.067	-.46	.270
L_{WJ}	.01	.061	-.08	.094	-.04	.046	-.08	.205

† see text for explanation

* correlation significantly different from zero

were made.

Analyses have been conducted to estimate type of birth effects on the four characters under selection. Data from 984 hogget ewes in the March and April mated Random flocks were considered for an analysis of fleece weight and crimp data in which the effects of type of birth, age of dam and year of birth were examined in a least squares analysis. Singles produced more wool (6.40 v. 6.08 lb.) and the wool had more crimps (10.48 v. 10.26 c.p.i); type of birth accounted for respectively 1.0 and 0.3 per cent of the total variation in the two analyses.

Weaning Weights on 1533 lambs in the March Random flock were used to examine the effects of type of birth, sex, age of dam and year of birth. The weaning weights had previously been adjusted for age, on weaning weight itself and not gain from birth to weaning. Singles were 13 per cent heavier at weaning (51.1 v. 45.2 lb.) and type of birth accounted for 6.4 per cent of the total variation in the character.

In a corresponding analysis of skin fold data on 870 lambs born in the March Random flock between 1951 and 1961, three measures of fold score were considered, neck, neck and side, and neck and side and breech. Averaged over the three characters, singles were 19 per cent more wrinkled than twin born lambs and type of birth accounted for an average of 3.5 per cent of the total variation.

Clearly the characters recorded at weaning were more affected by type of birth effects than were either clean fleece weight or crimp frequency. Correspondingly, it might be expected that there would be poorer agreement between the proportion of twins available and selected in the Folds and Weaning Weight flocks. Figures for the numbers of twins available for selection and chosen for mating in the Weaning Weight flocks between 1953 and 1961 were given by Pattie (1965b). Even after type of birth corrections were applied, a higher propostion of twins were selected for the Weaning Weight Minus flock than would be expected from the numbers available (Table 3.2.5). For the Folds selection flocks, twins were preferentially selected in the Folds Minus flock, and discriminated against slightly in the Folds Plus flock; a situation that would be expected given the relative performance of singles and twins for skin fold score. No such clear cut distinctions between a pair of selection flocks were apparent for the Fleece and Crimps groups, although there was a consistent preference for singles in the Crimps Plus flock.

Discussion

The major interest in this Section is in the comparison of estimated and realised genetic correlations. The most obvious agreement was for estimates between clean fleece weight and reproductive performance. Selection for increased fleece weight would be expected to decrease performance at second lambing and to perhaps increase it slightly at third lambing, and these changes were observed. The agreement between the two sets of estimates in this instance suggests that

Table 3.2.5

The proportions of twins available for selection as hoggets and chosen for inclusion in the selection flocks

Flock	Rams		Ewes	
	% of available hoggets born twins	% of selected hoggets born twins	% of available hoggets born twins	% of selected hoggets born twins
Weaning Weight Plus [‡]	51.5	55.2	54.6	52.3
Weaning Weight Minus [‡]	53.9	63.0	52.8	54.1
Folds Plus	29.0	24.6	33.9	33.9
Folds Minus	46.5	50.7	50.7	55.6
Fleece Plus	27.8	28.8	30.1	29.6
Fleece Minus	22.3	24.4	24.2	23.8
Crimps Plus	23.1	20.3	25.9	22.3
Crimps Minus	34.2	29.1	38.7	38.9

[‡] Numbers given refer to hoggets born in years in which type of birth corrections were applied prior to selection, i.e. for matings between 1961 and 1969.

this pattern of association is real and probably worthy of study so as to elucidate a physiological mechanism for its occurrence. It was concluded earlier that performance at different lambings could not simply be regarded as different measures of the same character, in the sense that the heritability estimates differed, and this view would be strengthened if genetic correlations do behave in the way suggested for fleece weight.

The most consistent observed change in reproductive performance is in the Folds selection flocks, with the Folds Plus flock being inferior at each of the first five lambings. From the estimates given in Table 3.2.2, the changes observed in second lambing performance would be expected, and this trend would be reinforced by the selection against twins in the Folds Plus flock. However, it has already been pointed out that these differences in performance between the Folds Plus and Minus flocks have been attributed by Dun and Hamilton (1965) to differences in ram and not ewe fertility. Nevertheless, the estimates of genetic correlations, at least with performance at second lambing, along with corresponding estimates obtained by Young, Turner and Dolling (1963), suggest that selection for increased skin fold would lead to reduced ewe fertility.

The agreement between estimated and realized genetic correlations is less impressive for crimp frequency and weaning weight. As regards the latter, this is perhaps not surprising given the history of twin selection in the years up to 1961 (Pattie, 1965b), and the fact that in estimating genetic correlations, no type of birth corrections were applied to weaning weight. The pattern of selection in both the weaning weight and folds selection flocks emphasises the need for a clear understanding of the factors which account for an appreciable portion of the phenotypic variation, before selection experiments such as this commence. This is especially true as it is in the expression of correlated responses, either unexpected or which might offer a physiological explanation of the direct responses, that such flocks have proved to be perhaps most rewarding and interesting (Fowler, 1966; Williams, 1973).

The heritability estimates for ewe reproductive performance in the Random flocks (Table 3.2.1) are similar to those given in Tables 2.8.2 and 2.8.4, for which data from all 10 flocks were examined. The similarity of these estimates supports the view that the estimates given in Section 2.8 are representative of the Trangie population and the fact that they are lower than the estimates of Young, Turner and Dolling (1963) would not seem to be accounted for simply as the result of the artificial selection experiment at Trangie.

Finally, the finding of significant flock x age of ewe interactions for reproductive performance indicates another of the difficulties encountered in using data from selection flocks to estimate some parameter or statistic for the population as a whole. However, in this instance, it appears unlikely that the association between age of ewe and reproductive performance has altered to any great extent the overall relationship in the Trangie flock, if only because the relationship observed is similar to that reported elsewhere (Section 2.2).

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APPENDIX A

Table A1

Selection differentials for clean fleece weight in establishing the Fleece Plus and Fleece Minus flock

	No. chosen	Mean of selected animals	Population mean	Deviation
Fleece Plus - Rams				
Born in 1949	5	9.70	7.56	2.14
" 1950	6	13.02	10.22	2.80
Fleece Plus - Ewes				
Born in 1948	10	7.66	6.75	0.91
" 1949	6	6.68	6.97	-0.29
" 1950	64	5.18	4.75	0.43
" 1951	21	6.90	6.10	0.80
Fleece Minus - Rams				
Born in 1949	5	5.48	7.56	-2.08
" 1950	5	6.62	10.22	-3.60
Fleece Minus - Ewes				
Born in 1948	14	5.91	6.75	-0.84
" 1949	6	5.66	6.97	-1.31
" 1950	61	4.45	4.75	-0.30
" 1951	21	5.58	6.10	-0.52

Table A2

Selection differentials for crimp frequency in establishing the Crimps Plus and Minus flocks

	No. chosen	Mean of selected animals	Population mean	Deviation
Crimps Plus - Rams				
Born in 1949	5	16.60	12.40	4.20
" " 1950	5	14.00	9.55	4.45
Crimps Plus - Ewes				
Born in 1948	12	11.50	10.56	0.94
" " 1949	12	12.36	10.71	1.65
" " 1950	59	12.96	11.62	1.34
" " 1951	28	9.63	8.76	0.87
Crimps Minus - Rams				
Born in 1949	5	8.00	12.40	-4.40
" " 1950	5	7.00	9.55	-2.55
Crimps Minus - Ewes				
Born in 1948	13	9.69	10.56	-0.87
" " 1949	8	9.38	10.71	-1.33
" " 1950	61	10.33	11.62	-1.29
" " 1951	17	7.59	8.76	-1.27

Table A3

Selection differentials for age corrected weaning weight in establishing the Weight Plus and Weight Minus flocks

	No. chosen	Mean of selected animals	Population mean	Deviation
Weaning Weight Plus - Rams				
Born in 1949	5	81.40	70.9	+10.5
Weaning Weight Plus - Ewes				
Born in 1944 [†]	7	-	-	-
" " 1945 [†]	9	-	-	-
" " 1946 [†]	13	-	-	-
" " 1947	28	61.2	56.7	+4.5
" " 1948	14	50.8	45.3	+5.5
" " 1949	27	61.6	57.4	+5.2
Weaning Weight Minus - Rams				
Born in 1949	5	59.7	70.9	-11.2
Weaning Weight Minus - Ewes				
Born in 1944 [†]	3	-	-	-
" " 1945 [†]	9	-	-	-
" " 1946 [†]	13	-	-	-
" " 1947	28	48.2	56.7	-8.5
" " 1948	18	37.8	45.3	-7.5
" " 1949	28	52.5	57.4	-4.9

[†] Body weights not available for these years.

Table A4

Selection differentials for skin fold score in establishing the Folds Plus and Folds Minus flocks

	No. chosen	Mean of selected animals	Population mean	Deviation
Folds Plus - Rams				
Born in 1949	5	7.80	3.90	3.90
Folds Plus - Ewes				
Born in 1944 †	5	-	-	-
" " 1945 †	7	-	-	-
" " 1946 †	15	-	-	-
" " 1947	30	4.07	2.80	1.27
" " 1948	23	4.74	3.11	1.63
" " 1949	11	5.73	3.35	2.38
Folds Minus - Rams				
Born in 1949	5	1.20	3.90	-2.70
Folds Minus - Ewes				
Born in 1944 †	6	-	-	-
" " 1945 †	10	-	-	-
" " 1946 †	18	-	-	-
" " 1947	27	1.93	2.80	-0.87
" " 1948	21	1.81	3.11	-1.30
" " 1949	14	2.00	3.35	-1.35

† Fold scores not available for these years

Table A5

Selection differentials imposed in the Fleece Plus flock

Year	Rams			Ewes		
	Number of animals available	Number of animals chosen	Deviation	Number of animals available	Number of animals chosen	Deviation
1952	20	5	0.88	22	12	0.66
1953	29	5	1.64	32	14	0.60
1954	23	5	1.12	48	6	0.94
1955	22	5	1.34	22	8	0.92
1956	38	5	1.79	33	7	1.11
1957	29	5	0.67	24	17	0.16
1958	23	5	1.01	15	11	0.29
1959	27	5	1.99	30	20	0.21
1960	19	6	+1.55	24	16	0.37
1961	24	5	0.96	23	17	0.41
1962	39	5	1.31	37	20	0.33
1963	34	5	1.61	39	15	0.60
1964	46	5	1.55	30	13	-0.11
1965	25	5	1.58	39	25	-0.17
1966	35	6	1.09	39	12	0.41
1967	33	5	1.21	30	6	0.04

Table A6

Selection differentials imposed in the Fleece Minus flock

Year	Rams			Ewes		
	Number of animals available	Number of animals chosen	Deviation	Number of animals available	Number of animals chosen	Deviation
1952	20	5	-0.97	18	11	-0.17
1953	30	5	-1.46	36	20	-0.71
1954	34	5	-1.07	29	14	-0.38
1955	41	5	-2.28	29	9	-1.30
1956	35	5	-1.69	43	5	-1.27
1957	29	5	-1.10	32	12	-0.68
1959	24	5	-1.86	22	12	-0.72
1959	24	5	-1.49	41	18	-0.83
1960	39	5	-2.21	22	14	-0.31
1961	29	5	-1.23	33	22	-0.30
1962	28	5	-1.70	46	23	-0.81
1963	38	5	-1.33	28	20	-0.27
1964	33	6	-0.79	31	11	+0.12
1965	35	5	-1.88	35	20	-0.24
1966	35	5	-1.20	47	13	-0.48
1967	33	5	-0.79	33	10	-0.01

Table A7

Selection differentials in the Crimps Plus flock

Year	Rams			Ewes		
	Number of animals available	Number of animals chosen	Deviation	Number of animals available	Number of animals chosen	Deviation
1952	16	5	1.19	21	15	0.73
1953	25	5	3.40	27	15	1.69
1954	26	5	4.43	25	13	1.10
1955	31	5	1.88	21	12	0.81
1956	25	5	2.20	24	16	1.04
1957	23	5	2.16	25	13	1.62
1958	23	5	2.18	24	20	0.67
1959	37	5	2.72	27	18	1.51
1960	31	5	2.84	23	19	0.41
1961	28	5	2.34	26	23	0.86
1962	35	5	2.11	37	20	1.12
1963	34	5	2.97	44	29	0.39
1964	38	5	3.33	40	25	0.55
1965	37	5	2.82	54	24	1.55
1966	50	5	3.64	44	20	1.72
1967	44	5	2.62	51	18	1.40

Table A8

Selection differentials in the Crimps Minus flock

Year	Rams			Ewes		
	Number of animals available	Number of animals chosen	Deviation	Number of animals available	Number of animals chosen	Deviation
1952	16	5	-1.31	22	20	-0.02
1953	25	5	-2.50	33	32	-0.07
1954	24	5	-1.67	31	18	-1.31
1955	26	5	-1.96	28	6	-2.35
1956	34	5	-2.35	25	9	-1.26
1957	38	5	-1.83	28	11	-1.59
1958	22	5	-1.84	31	13	-1.54
1959	32	6	-2.08	38	13	-1.81
1960	21	5	-2.60	38	20	-1.52
1961	22	5	-1.45	36	30	-1.37
1962	47	5	-1.84	43	32	-0.87
1963	46	5	-1.55	44	19	-0.95
1964	39	5	-2.64	38	21	-0.88
1965	31	5	-0.97	29	24	-0.16
1966	30	5	-1.07	47	19	-1.25
1967	49	5	-2.35	42	22	-0.68

Table A9

Selection differentials imposed in the Weaning Weight Plus flock

Year	Rams			Ewes		
	Number of animals available	Number of animals chosen	Deviation	Number of animals available	Number of animals chosen	Deviation
1951	38	5	12.65	35	30	1.15
1953	30	5	11.89	29	18	2.40
1954	34	5	8.46	35	17	4.07
1955	28	5	-1.30	31	22	1.49
1956	14	5	3.07	9	6	1.28
1957	39	5	13.47	37	19	2.09
1958	36	5	19.23	44	18	8.10
1959	27	5	10.86	28	16	4.32
1960	34	5	9.69	39	25	2.90
1961	28	5	7.51	34	17	2.90
1962	42	5	10.80	48	22	5.60
1963	19	5	6.19	20	14	3.10
1964				47	42	1.27
1965	30	5	10.68	37	13	1.56

Table A10

Selection differentials imposed in the Weaning Weight Minus flock

Year	Rams			Ewes		
	Number of animals available	Number of animals chosen	Deviation	Number of animals available	Number of animals chosen	Deviation
1951	30	5	-5.62	39	35	+0.01
1953	31	5	-8.16	31	16	-2.34
1954	41	5	-14.65	48	10	-6.90
1955	33	5	-7.51	32	23	-0.33
1956	10	5	-2.96	16	12	+2.58
1957	45	5	-13.00	37	12	-4.23
1958	45	5	-14.10	40	24	-2.96
1959	21	5	-8.14	27	13	-5.53
1960	30	5	-7.10	37	23	-2.15
1961	25	5	-7.72	28	7	+0.62
1962	47	5	-10.19	52	33	-1.63
1963	18	5	-7.16	25	19	-2.07
1964				42	34	+1.09
1965	42	8	-5.80	43	8	+2.24

Table A11

Selection differentials imposed in the Folds Plus flock

Year	Rams			Ewes		
	Number of animals available	Number of animals chosen	Deviation	Number of animals available	Number of animals chosen	Deviation
1951	11	5	+1.04	39	37	-0.10
1953	18	5	+5.33	26	20	+1.13
1954	21	5	+8.48	34	21	+1.10
1955	18	5	+4.44	28	19	+0.05
1956	11	5	+4.89	9	8	+0.35
1957	30	5	+8.17	28	19	+2.43
1958	33	5	+7.33	35	29	+0.79
1959	10	5	+1.90	26	19	+2.13
1960	25	5	+6.06	26	21	+1.66
1961	18	5	+3.72	27	14	+2.66
1962	21	5	+2.57	11	11	0.00
1963	31	5	+4.02	35	28	+1.20
1964	22	5	+2.66	29	27	-0.19
1965	39	5	+5.65	32	17	+0.02
1966	5	5	+0.00	7	6	+0.97
1967	19	5	+3.06	20	20	0.00

Table A12

Selection differentials imposed in the Folds Minus flock

Year	Rams			Ewes		
	Number of animals available	Number of animals chosen	Deviation	Number of animals available	Number of animals chosen	Deviation
1951	12	5	01.23	62	46	-0.83
1953	42	5	-2.33	41	9	-2.06
1954	42	5	-3.27	42	12	-2.18
1955	42	5	-2.16	40	26	-0.50
1956	18	5	-1.34	17	14	+0.42
1957	46	5	-1.78	49	17	-1.29
1958	49	5	-3.22	59	26	-1.86
1959	35	5	-1.60	36	20	-0.71
1960	46	5	-2.75	42	26	-1.26
1961	28	5	-2.64	28	16	-0.82
1962	29	5	-2.01	31	22	-0.67
1963	46	5	-1.57	40	21	-1.03
1964	50	5	-2.10	58	25	-0.83
1965	30	5	-0.90	28	17	-0.08
1966	34	5	-1.18	38	19	-0.61
1967	41	5	-0.46	32	15	-0.69

Table A13

Fleece Weights for Rams in the April Random Flock

Year	Number	Mean	Variance	S.D.	C of V	Skewness	Kurtosis
1952	2	7.10	2.00	1.41	19.9	0.00	0.25
1953	12	8.16	1.96	1.40	17.1	-0.03	1.81
1954	35	5.39	0.41	0.64	11.9	-0.37	2.47
1955	26	7.90	2.16	1.47	18.6	-0.06	2.73
1956	33	6.66	0.76	0.87	13.1	-0.10	2.38
1957	35	7.32	0.71	0.84	11.5	-1.06	5.79
1958	23	9.00	3.48	1.87	20.7	0.29	2.27
1959	26	9.99	1.83	1.35	15.1	0.10	2.29
1960	12	8.24	1.64	1.28	15.6	0.40	1.76
1961	17	7.15	1.27	1.13	15.8	0.13	2.33
1962	42	8.48	1.21	1.10	13.0	0.35	4.18
1963	36	7.61	1.76	1.33	17.4	-0.45	2.64
1964	38	3.94	0.44	0.67	16.9	0.52	3.30
1965	27	7.37	1.19	1.09	14.8	-0.05	2.48
1966	31	6.77	1.95	1.39	20.6	-0.27	2.95
1967	30	3.56	0.37	0.61	17.0	0.16	2.42
1968	26	7.19	1.43	1.19	16.6	-0.14	2.81
TOTALS	451	7.11	1.30	1.14	16.0	-0.02	3.54

Table A14

Fleece weight records for ewes in the April Random flocks

Year	Number	Mean	Variance	SD	C of V	Skewness	Kurtosis
1952	25	6.98	0.55	0.76	10.6	0.11	2.55
1953	24	8.09	0.86	0.92	11.4	-0.12	2.19
1954	26	5.06	0.43	0.65	12.9	0.13	1.73
1955	30	7.87	0.84	0.92	11.6	0.82	3.92
1956	34	5.60	0.61	0.78	14.0	-0.12	3.32
1957	33	6.28	0.50	0.71	11.3	0.16	3.44
1958	25	6.91	0.89	0.94	13.6	-0.95	4.91
1959	42	7.70	1.02	1.01	13.1	0.30	2.47
1960	35	7.20	0.58	0.76	10.6	-0.46	2.71
1961	40	6.29	0.86	0.93	14.8	0.22	1.98
1962	41	7.57	0.89	0.94	12.4	0.26	2.60
1963	54	6.68	0.83	0.91	13.6	0.70	4.05
1964	42	4.14	0.53	0.73	17.6	-0.18	2.35
1965	41	6.83	1.01	1.00	14.7	-0.46	3.33
1966	38	5.81	0.62	0.79	13.6	0.22	2.27
1967	40	3.31	0.43	0.66	19.8	0.14	3.47
1968	43	6.77	0.83	0.91	13.4	0.30	3.52
TOTALS	596	6.42	0.73	0.86	13.3	0.11	3.28

Table A15

Fleece weights for rams in the Fleece Plus flock

Year	Number	Mean	Variance	SD	C of V	Skewness	Kurtosis
1952	20	8.62	1.17	1.08	12.6	-0.23	3.40
1953	29	8.66	1.89	1.37	15.9	-0.36	2.14
1954	23	6.40	0.77	0.88	13.7	0.18	2.81
1955	22	9.70	1.77	1.33	13.7	0.08	2.55
1956	38	7.71	1.18	1.09	14.1	0.18	2.54
1957	29	8.29	1.23	1.11	13.4	1.43	6.14
1958	23	10.85	1.63	1.28	11.8	0.20	2.25
1959	27	10.49	2.07	1.44	13.7	0.08	1.64
1960	19	9.43	2.30	1.52	16.1	-0.60	2.37
1961	24	9.38	1.18	1.09	11.6	-0.20	2.50
1962	39	9.23	1.18	1.09	11.8	-1.08	5.30
1963	34	9.27	1.04	1.02	11.0	0.19	2.54
1964	46	4.47	0.64	0.80	17.9	0.48	3.08
1965	25	8.54	3.47	1.86	21.8	-1.32	4.22
1966	35	7.73	1.83	1.35	17.5	-0.30	3.12
1967	33	3.36	0.36	0.60	17.8	0.44	3.82
1968	13	9.09	2.96	1.71	18.9	-0.38	2.37

Table A16

Fleece weight records for ewes in the Fleece Plus flock

Year	Number	Mean	Variance	SD	C of V	Skewness	Kurtosis
1952	22	7.47	1.28	1.13	15.2	-0.07	3.05
1953	32	7.65	3.22	1.80	23.5	0.23	1.53
1954	48	5.76	0.44	0.66	11.5	0.18	2.48
1955	22	8.27	0.86	0.93	11.2	-0.00	3.02
1956	33	6.05	0.79	0.89	14.7	-0.03	2.16
1957	24	7.61	1.19	1.09	14.3	0.01	2.35
1958	15	8.36	1.99	1.41	16.9	0.17	2.03
1959	30	8.45	1.32	1.15	13.6	-0.34	2.65
1960	24	8.04	0.50	0.71	8.8	-0.49	2.26
1961	23	7.81	1.33	1.15	14.8	-0.12	2.54
1962	37	8.59	0.85	0.92	10.7	0.06	3.00
1963	39	7.73	0.81	0.90	11.6	0.07	2.45
1964	30	4.81	0.30	0.54	11.3	0.44	2.03
1965	39	8.12	0.98	0.99	12.2	-0.02	2.58
1966	39	6.70	1.03	1.01	15.1	0.06	5.03
1967	30	3.53	0.48	0.69	19.6	0.44	2.29
1968	17	7.73	1.58	1.26	16.3	-0.41	3.87

Table A17

Fleece weight results for rams in the Fleece Minus flock

Year	Number	Mean	Variance	S.D.	C of V	Skewness	Kurtosis
1952	20	7.29	1.08	1.04	14.2	0.95	4.05
1953	30	7.30	1.34	1.16	15.9	0.33	2.02
1954	34	5.07	0.66	0.81	16.1	0.06	2.53
1955	41	7.88	1.93	1.39	17.6	-0.15	2.37
1956	35	5.99	1.11	1.05	17.6	-0.09	3.22
1957	29	6.22	0.71	0.85	13.6	0.35	3.98
1958	24	6.72	2.01	1.42	21.1	0.09	2.60
1959	24	7.01	1.78	1.33	19.0	0.48	2.09
1960	39	6.41	2.61	1.62	25.2	0.51	2.94
1961	29	5.61	1.02	1.01	17.9	0.13	1.89
1962	28	6.22	1.69	1.30	20.9	0.58	3.01
1963	38	4.99	1.20	1.09	21.9	0.04	3.17
1964	33	2.59	0.45	0.67	25.9	0.32	2.06
1965	35	4.62	1.29	1.14	24.6	-0.15	2.25
1966	35	4.22	0.75	0.87	20.5	0.16	2.23
1967	33	2.19	0.56	0.75	34.1	0.40	3.17
1968	39	4.14	0.84	0.92	22.1	0.28	2.78

Table A18

Fleece weight records for ewes in the Fleece Minus flock

Year	Number	Mean	Variance	SD	C of V	Skewness	Kurtosis
1952	18	6.29	0.79	0.89	14.1	-0.28	2.02
1953	36	5.85	1.78	1.33	22.8	0.43	2.89
1954	29	4.62	0.35	0.59	12.8	0.25	2.47
1955	29	6.30	1.35	1.16	18.5	-0.09	2.58
1956	43	4.97	0.54	0.73	14.7	-0.05	2.82
1957	32	5.46	0.67	0.82	15.0	-0.03	2.07
1958	22	5.18	1.05	1.03	19.8	0.45	2.98
1959	41	5.74	1.36	1.17	20.4	0.22	2.63
1960	22	5.36	1.73	1.32	24.5	0.17	2.62
1961	33	4.51	1.00	1.00	22.2	-0.32	3.90
1962	46	5.45	1.68	1.29	23.8	0.32	2.37
1963	28	4.26	0.68	0.83	19.4	-0.98	4.73
1964	31	3.31	0.35	0.59	17.9	1.37	6.03
1965	35	4.54	0.93	0.96	21.3	0.78	5.69
1966	47	3.45	0.38	0.62	18.0	0.51	2.73
1967	33	2.38	0.21	0.46	19.3	0.01	2.12
1968	42	4.28	1.54	1.24	29.0	0.62	3.45

Table A19

Crimp frequency results for rams in the April Random Flock

Year	Number	Mean	Variance	Standard Deviation	Coefficient of Variation
1952	13	11.39	3.42	1.85	16.2
1953	18	11.78	5.81	2.41	20.5
1954	21	11.29	6.50	2.55	22.6
1955	25	10.52	4.33	2.08	19.8
1956	32	11.84	2.59	1.61	13.6
1957	36	10.08	2.40	1.55	15.4
1958	26	9.89	3.72	1.93	19.5
1959	26	10.89	6.20	2.49	22.9
1960	12	11.58	5.90	2.43	21.0
1961	24	11.17	4.67	2.16	19.3
1962	40	9.48	4.24	2.06	21.7
1963	37	9.51	3.76	1.94	20.4
1964	38	12.74	6.25	2.50	19.6
1965	45	9.76	4.80	2.19	22.4
TOTALS	393	10.70	4.49	2.12	19.8

Table A20

Crimp frequency records for ewes in the April Random flock

Year	Number	Mean	Variance	SD	C of V	Skewness	Kurtosis
1952	25	11.16	1.97	1.40	12.6	-0.01	2.02
1953	24	10.38	2.24	1.50	14.4	0.05	1.93
1954	26	10.58	4.01	2.00	18.9	-0.07	2.06
1955	30	10.63	2.45	1.56	14.7	-0.03	3.14
1956	34	10.82	3.85	1.96	18.12	-0.30	2.94
1957	33	8.79	2.17	1.47	16.8	0.41	2.19
1958	26	10.23	1.46	1.21	11.8	0.61	2.16
1959	42	10.69	4.90	2.21	20.7	-0.04	2.66
1960	35	11.40	1.36	1.17	10.3	0.07	2.22
1961	40	10.50	2.92	1.71	16.3	-0.18	1.82
1962	40	10.57	2.46	1.57	14.8	0.16	2.16
1963	54	9.26	2.87	1.70	18.3	1.38	5.83
1964	42	11.88	5.08	2.25	19.0	0.17	1.94
1965	41	9.54	2.80	1.67	17.6	0.89	3.99
1966	38	9.76	2.29	1.51	15.5	-0.11	1.72
1967	40	10.38	2.45	1.56	15.1	0.52	2.65
1968	43	10.56	4.92	2.22	21.01	0.24	2.66
TOTALS	596	10.42	3.05	1.75	16.8	0.23	3.06

Table A21

Crimp frequency records for rams in the Crimps Plus flock

Year	Number	Mean	Variance	S.D.	C of V	Skewness	Kurtosis
1952	16	10.81	1.90	1.38	12.7	-0.26	2.34
1953	25	13.20	6.50	2.55	19.3	0.21	2.31
1954	26	13.27	5.56	2.36	17.8	1.01	2.61
1955	31	11.52	3.32	1.82	15.8	0.29	2.28
1956	25	12.60	2.67	1.63	13.0	-0.14	1.92
1957	23	11.04	3.23	1.80	16.3	-0.11	3.06
1958	23	11.22	3.45	1.86	16.6	-0.38	2.49
1959	37	13.68	5.61	2.37	17.3	-0.48	2.09
1960	31	13.16	4.21	2.05	15.6	-0.82	6.21
1961	28	13.46	5.00	2.24	16.6	-0.61	3.51
1962	35	12.89	2.46	1.57	12.2	-0.13	1.75
1963	34	13.03	4.45	2.11	16.2	-0.24	2.28
1964	38	16.87	5.36	2.32	13.7	-0.67	3.85
1965	37	14.38	5.91	2.43	16.9	-1.31	5.12
1966	50	14.36	4.68	2.16	15.1	0.25	2.99
1967	44	14.18	4.66	2.16	15.2	-0.93	4.45

Table A22

Crimp frequency records for ewes in the Crimp Plus flock

Year	Number	Mean	Variance	SD	C of V	Skewness	Kurtosis
1952	21	11.57	4.16	2.04	17.6	0.26	2.02
1953	27	11.93	3.53	1.88	15.8	1.07	4.96
1954	25	11.36	3.41	1.85	16.3	0.71	2.75
1955	21	12.57	4.46	2.11	16.8	0.24	2.14
1956	24	12.96	2.82	1.68	13.0	0.01	1.91
1957	25	10.76	7.02	2.65	24.6	0.12	1.83
1958	24	11.38	4.77	2.18	19.2	-0.37	2.80
1959	27	13.67	6.62	2.57	18.8	-0.31	2.50
1960	23	13.22	3.63	1.91	14.4	0.15	3.21
1961	26	13.38	3.29	1.81	13.5	0.22	3.03
1962	37	12.78	4.34	2.08	16.3	-0.53	4.13
1963	44	12.48	5.32	2.31	18.5	-0.50	2.69
1964	40	16.95	2.46	1.57	9.3	0.04	3.29
1965	54	13.80	4.09	2.02	14.7	-0.52	3.28
1966	44	15.93	5.46	2.34	14.7	-1.83	8.38
1967	51	15.57	4.41	2.10	13.5	-0.37	1.84
1968	42	15.93	4.58	2.14	13.4	-1.31	5.37

Table A23

Crimp frequency records for rams in the Crimps Minus flock

Year	Number	Mean	Variance	S.D.	C of V	Skewness	Kurtosis
1952	16	7.71	1.76	1.33	17.2	0.49	1.83
1953	25	9.83	4.84	2.20	22.4	0.53	2.63
1954	24	9.67	1.88	1.37	14.2	0.68	2.68
1955	26	7.96	2.41	1.55	19.5	0.63	2.99
1956	34	9.35	3.21	1.79	19.1	0.16	2.30
1957	38	7.03	2.84	1.68	24.0	0.52	3.33
1958	22	7.64	3.19	1.79	23.4	0.72	2.80
1959	32	8.36	3.57	1.89	22.6	0.48	2.97
1960	21	7.95	4.16	2.04	25.6	0.74	4.92
1961	22	7.45	1.84	1.36	18.2	1.00	3.40
1962	47	7.05	5.37	2.32	32.9	1.51	5.63
1963	46	6.15	1.51	1.23	20.0	-0.00	2.86
1964	39	8.64	2.03	1.42	16.5	-0.18	3.08
1965	31	5.74	0.66	0.81	14.2	0.88	3.16
1966	30	5.87	3.71	1.93	32.8	2.51	10.92
1967	49	7.42	3.79	1.95	26.2	0.63	3.49

Table A24

Crimp frequency records for ewes in the Crimp Minus flock

Year	Number	Mean	Variance	S.D.	C of V	Skewness	Kurtosis
1952	22	8.59	2.44	1.56	18.2	0.16	2.29
1953	33	9.70	4.53	2.13	22.0	0.40	2.90
1954	31	8.06	3.66	1.91	23.7	0.57	2.49
1955	33	8.85	2.88	1.70	19.2	-0.07	2.11
1956	25	8.48	2.43	1.56	18.4	0.23	2.37
1957	28	7.32	2.45	1.56	21.4	0.10	1.87
1958	31	8.77	2.45	1.56	17.8	0.01	2.04
1959	38	7.50	3.93	1.98	26.4	1.05	3.69
1960	38	8.42	4.63	2.15	25.6	0.68	2.63
1961	33	7.18	1.84	1.36	18.9	0.63	3.42
1962	43	7.16	2.57	1.60	22.4	0.72	3.37
1963	45	6.27	1.43	1.19	19.1	0.27	2.01
1964	28	8.50	2.85	1.69	19.9	0.33	2.72
1965	29	5.72	0.78	0.88	15.4	0.23	1.77
1966	47	6.36	4.06	2.02	31.7	2.99	1.38
1967	43	6.95	1.38	1.17	16.9	0.09	2.77
1968	29	7.01	6.86	2.61	37.2	1.02	5.26

Table A25

Summary of age and type of birth corrected weaning weight records for rams in the March Random flock

1. Age adjustment applied to weaning weight

Year	Number	Mean	Variance	SD	C of V	Skewness	Kurtosis
1951	13	43.69	56.35	7.51	17.18	-0.39	1.63
1953	48	46.14	53.42	7.31	15.84	-0.59	2.96
1954	48	66.87	110.31	10.50	15.71	0.19	2.73
1955	33	76.25	72.96	8.54	11.20	-0.51	2.75
1956	18	61.89	38.04	6.17	9.97	-0.17	2.01
1957	45	60.19	62.88	7.93	13.17	0.35	2.32
1958	61	66.59	74.73	8.64	12.98	-0.14	2.27
1959	30	59.87	108.47	10.41	17.40	-0.31	3.39
1960	43	52.21	58.99	7.68	14.71	0.68	4.72
1961	37	47.14	36.64	6.05	12.84	0.30	4.67
1962	55	49.37	44.45	6.67	13.50	-0.87	4.09
1963	49	58.98	64.43	8.03	13.61	-0.31	3.08
1964	41	56.24	36.50	6.04	10.74	0.43	3.52
1965	39	40.81	25.63	5.06	12.41	0.79	4.19
1966	64	53.17	53.60	7.32	13.77	0.74	5.05
1967	47	54.78	34.70	5.89	10.75	-0.29	2.23
1968	50	47.69	45.38	6.74	14.13	0.33	2.82
1969	49	43.68	74.46	8.63	19.75	-0.92	3.96
TOTALS	770	54.75	58.83	7.67	14.01	-0.08	3.64

Table A26

Summary of age and type of birth corrected weaning weight records for ewes in the March Random flock

1. Age adjustment applied to weaning weight

Year	Number	Mean	Variance	SD	C of V	Skewness	Kurtosis
1951	46	42.54	35.92	5.99	14.09	0.04	2.90
1953	40	43.65	51.04	7.14	16.37	-0.22	2.32
1954	48	51.85	111.89	10.58	20.40	0.91	4.59
1955	35	56.41	40.92	6.40	11.34	-0.69	2.77
1956	14	57.73	44.21	6.65	11.52	0.35	1.83
1957	44	53.35	50.56	7.11	13.33	-0.07	3.08
1958	63	57.95	57.84	7.61	13.12	0.07	2.51
1959	27	57.96	80.48	8.97	15.48	0.64	2.79
1960	45	46.53	28.48	5.34	11.47	0.32	2.40
1961	64	42.08	27.48	5.24	12.46	-1.27	5.62
1962	49	44.76	27.77	5.27	11.77	-0.76	5.96
1963	53	51.89	39.24	6.26	12.07	0.13	3.03
1964	45	47.64	30.48	5.52	11.59	0.13	2.27
1965	46	37.59	22.21	4.71	12.54	-0.54	3.54
1966	54	46.41	40.24	6.34	13.67	1.02	4.91
1967	43	43.94	43.75	6.61	15.05	0.31	2.73
1968	36	42.76	49.09	7.01	16.39	-0.25	2.74
1969	26	40.38	32.18	5.67	14.05	0.37	2.53
TOTALS	778	48.11	44.68	6.68	13.89	0.27	4.38

Table A27

Summary of weaning weight records for rams and ewes in the March Random flock

2. Age correction applied to gain from birth to weaning

Year	Number	Mean	Variance	S.D.	C of V	Skewness	Kurtosis
				Rams			
1962	52	51.35	45.31	6.73	13.11	-1.15	5.37
1963	48	58.06	62.65	7.92	13.63	-0.45	3.14
1964	41	55.96	36.76	6.06	10.84	0.50	3.58
1965	37	40.42	20.77	4.56	11.27	0.90	4.62
1966	64	53.02	49.77	7.05	13.31	0.71	5.32
1967	45	54.49	36.36	6.03	11.07	-0.39	2.19
1968	50	47.12	47.91	6.92	14.69	0.24	2.81
1969	49	42.26	83.27	9.13	21.59	-0.86	3.62
TOTALS	386	50.33	49.17	7.01	13.93	-0.28	4.26
				Ewes			
1962	49	43.84	30.39	5.51	12.58	-0.85	6.41
1963	53	51.60	36.53	6.04	11.71	-0.09	2.65
1964	45	47.69	30.93	5.56	11.66	0.20	2.37
1965	44	37.10	19.93	4.46	12.03	-0.70	3.57
1966	54	47.03	33.82	5.82	12.37	0.73	4.32
1967	43	43.94	43.75	6.61	15.05	0.31	2.73
1968	36	42.40	42.35	6.51	15.35	-0.43	2.73
1969	26	39.74	30.50	5.52	13.90	0.24	2.50
TOTALS	350	44.17	33.48	5.79	13.10	-0.01	3.49

Table A28

Summary of age and type of birth corrected weaning weight records for rams in the Weaning Weight Plus flock

1. Age adjustment applied to weaning weight

Year	Number	Mean	Variance	SD	C of V	Skewness	Kurtosis
1951	38	48.28	59.33	7.70	15.95	0.01	3.26
1953	30	50.92	78.79	8.88	17.43	0.77	4.18
1954	34	68.49	70.24	8.38	12.24	0.08	2.02
1955	28	77.12	219.55	14.82	19.21	-0.67	2.65
1956	14	67.98	104.19	10.21	15.01	1.06	3.82
1957	39	63.62	108.49	10.42	16.37	-0.93	4.55
1958	36	73.10	228.14	15.10	20.66	-1.35	5.62
1959	27	68.96	112.95	10.63	15.41	-0.07	2.12
1960	34	56.54	62.54	7.91	13.99	-0.77	4.30
1961	28	52.84	67.22	8.20	15.52	-0.62	2.18
1962	42	54.36	65.99	8.12	14.94	-0.31	3.54
1963	19	64.95	27.65	5.26	8.10	-0.18	2.03
1964	54	64.90	82.65	9.09	14.01	0.11	2.44
1965	30	47.00	59.44	7.71	16.40	-0.24	2.30
1968	47	55.24	42.83	6.54	11.85	-0.29	2.62
1969	54	51.70	41.44	6.44	12.45	-0.72	4.14

2. Age adjustment applied to gain from birth to weaning

Year	Number	Mean	Variance	SD	C of V	Skewness	Kurtosis
1962	35	54.78	46.62	6.83	12.46	-1.13	4.01
1963	19	63.27	38.14	6.18	9.76	-0.23	2.14
1964	54	63.49	80.05	8.95	14.09	0.06	2.31
1965	30	45.98	52.40	7.24	15.74	-0.13	2.34
1968	47	54.37	43.56	6.60	12.14	-0.43	2.70
1969	54	50.68	44.49	6.67	13.16	-0.67	4.23

Table A29

Summary of age and type of birth corrected weaning weights for ewes in the Weaning Weight Plus flock

1. Age adjustment applied to weaning weight

Year	Number	Mean	Variance	S.D.	C of V	Skewness	Kurtosis
1951	35	42.15	69.41	8.33	19.8	0.04	2.39
1953	29	47.43	72.75	8.53	18.0	0.47	2.57
1954	35	56.49	61.94	7.87	13.9	0.05	2.92
1955	31	61.70	29.52	5.43	8.81	0.12	2.05
1956	9	56.72	39.39	6.28	11.1	-0.44	1.80
1957	37	59.75	46.13	6.79	11.4	-0.48	3.06
1958	44	64.05	107.65	10.38	16.2	-0.31	2.12
1959	28	67.08	60.97	7.81	11.6	-0.02	2.04
1960	39	52.74	62.24	7.89	15.0	0.57	2.99
1961	34	50.31	61.35	7.83	15.6	-0.64	4.11
1962	48	50.73	81.62	9.03	17.81	-0.01	4.52
1963	20	60.83	50.10	7.08	11.6	-0.05	2.19
1964	47	53.74	36.44	6.04	11.2	-0.17	2.35
1965	37	42.44	34.35	5.86	13.8	-0.22	2.61
1968	48	53.59	48.22	6.94	13.0	-0.40	3.83
1969	49	47.83	41.72	6.46	13.5	-0.02	2.95

2. Age adjustment applied to gain from birth to weaning

1962	48	48.84	67.46	8.21	16.82	-0.51	4.78
1963	20	60.68	49.05	7.00	11.5	-0.13	2.21
1964	47	53.06	36.54	6.05	11.4	-0.21	2.05
1965	37	41.46	34.02	5.83	14.1	-0.20	2.73
1968	48	52.58	43.52	6.60	12.6	-0.51	4.11
1969	49	46.85	41.26	6.42	13.7	-0.03	2.94

Table A30

Summary of age and type of birth corrected weaning weights for rams in the Weaning Weight Minus flock

1. Age adjustment applied to weaning weight

Year	Number	Mean	Variance	S.D.	C of V	Skewness	Kurtosis
1951	30	46.19	46.53	6.82	14.8	-0.29	3.38
1953	31	43.76	42.61	6.53	14.9	0.01	4.18
1954	41	61.89	114.32	10.69	17.3	-0.06	3.07
1955	33	75.13	55.72	7.46	9.9	-0.15	2.72
1956	10	62.54	48.20	6.94	11.1	-0.26	1.90
1957	45	57.97	80.80	8.99	15.5	0.42	2.97
1958	45	65.29	103.66	10.18	15.6	-0.78	5.11
1959	21	53.78	109.38	10.46	19.5	0.07	2.59
1960	30	47.16	53.11	7.29	15.5	-0.14	2.45
1961	25	44.07	39.13	6.26	14.2	-0.30	4.12
1962	47	44.69	44.52	6.67	14.9	0.25	2.13
1963	18	52.26	54.67	7.39	14.2	0.12	1.76
1964	48	50.55	46.60	6.83	13.5	0.02	2.19
1965	42	37.17	28.76	5.36	14.4	0.19	2.37
1968	50	41.02	30.47	5.52	13.5	-0.12	2.60
1969	52	35.53	32.53	5.70	16.1	-0.57	2.69

2. Age adjustment applied to gain from birth to weaning

1962	47	46.61	38.56	6.21	13.3	-0.02	2.16
1963	18	51.36	60.19	7.76	15.1	0.10	1.64
1964	48	50.9	46.23	6.80	13.6	-0.00	2.14
1965	42	36.78	24.61	4.96	13.49	0.21	2.41
1968	50	40.00	28.62	5.35	13.4	0.01	2.60
1969	52	34.77	31.37	5.60	16.1	-0.50	2.58

Table A31

Summary of age and type of birth corrected weaning weights for ewes in the Weaning Weight Minus flock

1. Age adjustment applied to weaning weight

Year	Number	Mean	Variance	S.D.	C of V	Skewness	Kurtosis
1951	39	41.12	47.17	6.87	16.7	-0.34	2.44
1953	31	41.27	39.00	6.25	15.1	-0.03	2.41
1954	48	49.34	67.40	8.21	16.64	-0.35	3.56
1955	32	56.47	38.77	6.23	11.0	-0.12	2.16
1956	16	47.39	61.97	7.87	16.61	-0.83	2.43
1957	37	49.45	49.16	7.01	14.2	-0.22	2.41
1958	40	54.84	55.10	7.42	13.5	-0.34	3.21
1959	27	52.64	76.99	8.77	16.7	0.17	2.76
1960	37	41.80	41.99	6.48	15.5	0.35	2.33
1961	28	39.17	77.64	8.81	22.5	0.19	3.16
1962	52	41.71	32.92	5.74	13.8	0.24	2.70
1963	25	47.07	37.42	6.12	13.0	-0.32	1.97
1964	42	43.50	30.76	5.55	12.8	0.10	2.46
1965	43	32.20	32.68	5.72	17.8	0.85	3.56
1968	54	41.25	27.64	5.26	12.8	0.04	2.27
1969	43	36.16	23.49	4.85	13.4	-0.36	2.79

2. Age adjustment applied to gain from birth to weaning

Year	Number	Mean	Variance	S.D.	C of V	Skewness	Kurtosis
1962	51	41.31	26.90	5.19	12.6	-0.06	3.07
1963	25	47.02	36.37	6.03	12.8	-0.35	1.90
1964	42	43.10	29.81	5.46	12.7	0.13	2.55
1965	43	31.68	31.37	5.60	17.7	0.84	3.40
1968	54	40.01	26.74	5.17	12.9	-0.14	2.07
1969	43	35.24	21.43	4.63	13.1	-0.48	3.05

Table A32

Summary of Fold Scores for rams in the March Random flock

1. Total fold score (Neck + Side + Breech)

Year	No.	Mean	Variance	S.D.	C of V	Skewness	Kurtosis
1951	12	8.25	4.93	2.22	26.9	0.26	1.15
1953	46	10.20	23.27	4.82	47.3	1.31	4.41
1954	49	9.49	27.17	5.21	54.9	1.02	3.56
1955	32	11.91	25.12	5.01	42.1	0.22	1.84
1956	16	12.00	16.93	4.12	34.3	0.48	2.21
1957	42	10.10	22.23	4.72	46.7	0.67	2.65
1958	58	12.78	23.97	4.90	38.3	0.32	1.84
1959	29	10.52	13.69	3.70	35.2	0.28	2.25
1960	40	13.55	25.69	5.07	37.4	0.06	2.12
1961	35	11.71	18.74	4.33	36.9	0.84	3.59
TOTALS	359	11.36	22.59	4.75	41.8	0.61	2.87

2. Restricted fold score (Neck + Side)

1951	12	5.00	1.45	1.21	35.0	0.57	1.58
1953	46	6.76	9.79	3.13	46.3	1.22	4.51
1954	49	6.43	12.42	3.52	54.8	0.83	3.05
1955	32	8.00	11.35	3.37	42.1	0.18	2.10
1956	16	7.88	7.72	2.78	35.3	0.52	2.16
1957	42	6.45	9.57	3.09	48.0	0.63	2.77
1958	58	8.14	10.40	3.23	39.6	0.55	2.12
1959	29	6.66	5.59	2.36	35.5	0.21	2.35
1960	40	9.15	11.67	3.42	37.3	0.07	2.13
1961	35	7.46	10.37	3.22	43.2	0.86	3.29
1962	55	9.71	14.54	3.81	39.3	0.39	2.30
1963	48	8.79	18.93	4.35	49.4	0.45	1.99
1964	34	9.26	15.53	3.94	42.5	0.11	1.62
1965	30	6.27	10.06	3.17	50.6	0.56	2.29
1966	62	9.21	16.00	4.00	43.4	0.34	1.62
1967	46	7.50	14.03	3.75	50.0	0.63	2.16
1968	50	7.06	7.45	2.73	38.7	0.81	3.35
1969	50	6.18	12.52	3.54	57.3	1.13	3.65
TOTALS	734	7.55	11.92	3.45	45.7	0.56	2.57

Table A33

Skin fold scores for ewes in the March Random flock

1. Total fold score (Neck + Side + Breech)

Year	Number	Mean	Variance	S.D.	C of V	Skewness	Kurtosis
1951	46	7.28	6.34	2.52	34.6	0.25	2.48
1953	41	8.51	23.56	4.85	57.0	1.09	3.53
1954	51	8.18	17.51	4.18	51.2	0.69	2.32
1955	37	13.30	25.71	5.07	38.14	0.18	2.06
1956	14	9.64	16.40	4.05	42.00	0.24	1.36
1957	43	8.98	13.55	3.68	41.00	0.92	3.89
1958	64	11.89	16.86	4.11	34.5	0.95	3.43
1959	28	11.00	11.78	3.43	31.2	0.30	2.63
1960	44	12.43	27.74	5.27	42.4	0.35	1.95
1961	64	12.47	20.92	4.57	36.7	0.66	3.12
TOTALS	422	10.37	18.25	4.27	41.2	0.65	3.01

2. Restricted fold score (Neck + Side)

1951	46	4.59	2.69	1.64	35.8	0.45	2.74
1953	41	5.76	10.89	3.30	57.3	1.00	3.26
1954	51	5.37	7.72	2.78	51.7	0.62	2.27
1955	37	8.51	12.20	3.49	41.0	0.33	2.11
1956	14	5.86	7.82	2.80	47.8	0.33	1.29
1957	43	5.49	5.87	2.42	44.2	1.13	4.75
1958	64	7.45	8.57	2.93	39.3	1.20	4.19
1959	28	7.25	4.49	2.12	29.2	0.56	3.34
1960	44	8.30	13.14	3.63	43.7	0.27	1.83
1961	61	7.80	10.83	3.29	42.2	0.86	3.49
1962	48	6.75	10.83	3.29	48.8	1.02	3.59
1963	52	10.46	14.21	3.77	36.0	-0.05	1.87
1964	45	8.69	11.63	3.41	39.3	0.75	2.67
1965	45	4.91	3.76	1.94	39.5	0.87	3.17
1966	52	7.17	11.17	3.34	46.6	1.08	3.35
1967	41	5.80	7.16	2.68	46.1	0.99	3.84
1968	36	7.19	8.96	2.99	41.6	1.33	4.26
1969	26	6.27	7.08	2.66	42.5	0.57	2.29
TOTALS	759	6.87	9.09	3.01	43.9	0.74	3.25

Table A34

Summary of fold scores for rams in the Folds Plus selection flock

1. Total fold score (Neck + Side + Breech)

Year	No.	Mean	Variance	S.D.	C of V	Skewness	Kurtosis
1951	11	11.36	2.86	1.69	14.9	-0.07	1.47
1953	18	12.67	31.76	5.64	44.5	0.65	1.96
1954	21	13.52	30.36	5.51	40.7	-0.08	2.24
1955	18	14.56	29.97	5.19	35.7	0.19	2.17
1956	11	15.91	64.49	8.03	50.5	0.03	1.32
1957	30	14.83	35.80	5.98	40.3	0.13	1.80
1958	33	15.27	22.58	4.75	31.1	0.14	2.02
1959	10	15.70	39.12	6.25	39.8	-0.24	2.17
1960	25	17.44	19.09	4.37	25.1	-0.29	2.44
1961	18	17.06	15.35	3.92	23.0	-0.31	2.05

2. Restricted fold score (Neck + Side)

1951	11	7.09	2.69	1.64	23.1	0.36	1.75
1953	18	8.11	14.58	3.82	47.1	0.73	2.08
1954	21	9.05	13.15	3.63	40.1	0.12	2.70
1955	18	9.83	13.09	3.62	36.8	0.01	2.22
1956	11	10.09	28.69	5.36	53.1	0.26	1.39
1957	30	9.27	16.34	4.04	43.6	0.30	1.71
1958	33	9.58	10.75	3.28	34.2	0.31	2.18
1959	10	10.10	18.32	4.28	42.4	0.08	2.20
1960	25	11.68	9.98	3.16	27.0	-0.28	2.50
1961	18	11.50	8.85	2.98	25.9	-0.32	2.08
1962	21	12.43	12.66	3.56	28.6	-0.26	1.72
1963	31	12.68	17.56	4.19	33.1	-0.91	2.67
1964	22	14.64	11.77	3.43	23.4	-0.97	2.87
1965	39	10.15	12.13	3.48	34.3	0.45	2.07
1966	5	15.60	6.30	2.51	16.1	-0.40	1.09
1967	19	14.74	13.54	3.68	25.0	-0.99	2.48
1968	34	12.50	9.05	3.01	24.1	-0.26	2.49
1969	30	14.10	9.40	3.07	21.8	-0.60	2.12

Table A35

Summary of fold scores for ewes in the Fold Plus selection flock

Year	Number	Mean	Variance	S.D.	C of V	Skewness	Kurtosis
			Total fold score (Neck + Side + Breech)				
1951	39	10.21	12.48	3.53	34.6	1.02	3.87
1953	26	10.92	28.55	5.34	48.9	0.89	2.77
1954	34	13.00	24.18	4.92	37.8	-0.29	1.99
1955	28	15.32	32.60	5.71	37.3	-0.21	1.64
1956	9	15.78	18.69	4.32	27.4	0.68	1.96
1957	29	14.52	38.04	6.17	42.5	0.02	1.98
1958	35	16.80	16.34	4.04	24.1	0.21	2.38
1959	26	17.19	19.12	4.37	25.4	-0.17	1.71
1960	26	16.58	22.89	4.78	28.9	-0.37	1.83
1961	27	14.70	24.68	4.97	33.8	-0.17	1.94
			Restricted fold score (Neck + Side + Breech)				
1951	39	6.13	6.37	2.52	34.7	0.75	3.22
1953	26	7.19	12.32	3.51	48.8	0.90	2.85
1954	34	8.44	9.65	3.11	36.8	-0.11	2.26
1955	28	10.00	15.93	3.99	39.9	-0.09	1.78
1956	9	10.22	9.94	3.15	30.9	0.61	1.77
1957	29	9.28	17.00	4.12	44.4	0.22	2.02
1958	35	10.63	9.01	3.00	28.2	0.48	2.43
1959	26	11.38	9.77	3.13	27.5	-0.10	1.85
1960	26	10.58	9.77	3.13	29.6	-0.16	1.99
1961	27	14.70	24.68	4.97	33.8	-0.17	1.94
1962	11	12.36	15.25	3.91	31.6	-0.62	1.71
1963	35	14.09	11.43	3.38	24.0	-0.73	2.28
1964	29	14.00	13.79	3.71	26.5	-1.01	2.89
1965	32	9.31	11.19	3.35	35.9	0.08	1.72
1966	7	10.86	23.81	4.88	44.9	0.01	1.03
1967	20	13.45	17.21	4.15	30.8	-0.82	2.46
1968	33	10.36	12.74	3.57	34.4	-0.41	2.35
1969	26	13.73	13.96	3.74	27.2	-1.44	4.80

Table A36

Folds scores for rams in the Folds Minus selection flock

Total fold score (Neck + Side + Breech)

Year	No.	Mean	Variance	S.D.	C of V	Skewness	Kurtosis
1951	12	4.83	3.79	1.95	40.3	1.50	4.41
1953	42	5.33	4.42	2.10	39.4	1.07	3.63
1954	42	6.67	12.47	3.53	53.0	1.14	3.78
1955	42	5.76	6.62	2.57	44.7	1.72	5.99
1956	18	5.94	4.29	2.07	34.9	1.49	4.58
1957	46	4.98	2.24	1.50	30.1	0.54	2.28
1958	49	7.02	7.60	2.76	39.3	1.42	5.65
1959	35	5.40	2.07	1.44	26.7	0.51	2.44
1960	46	6.35	4.32	2.08	32.8	0.57	2.35
1961	28	6.14	10.42	3.23	52.6	2.19	7.72

Restricted fold score (Neck + Side)

1951	12	2.92	0.81	0.90	30.9	0.83	2.92
1953	42	3.69	2.37	1.54	41.7	1.06	3.70
1954	42	4.81	5.87	2.42	50.4	0.87	3.22
1955	42	4.17	3.22	1.79	43.0	1.69	5.87
1956	18	3.83	2.15	1.47	38.2	1.75	4.93
1957	46	3.17	1.30	1.14	36.0	0.63	2.25
1958	49	4.63	3.28	1.81	39.1	1.47	5.61
1959	35	3.71	1.03	1.02	27.4	0.57	2.47
1960	46	4.41	2.60	1.61	36.6	0.70	3.07
1961	28	4.00	5.19	2.28	56.9	2.32	9.30
1962	29	4.21	6.60	2.57	61.1	1.84	5.63
1963	46	3.57	2.52	1.59	44.5	1.01	3.09
1964	50	4.10	2.83	1.68	41.0	1.08	4.12
1965	30	2.90	4.71	2.17	74.9	3.54	16.06
1966	34	3.18	1.18	1.09	34.2	0.62	2.57
1967	41	2.46	0.95	0.98	39.7	2.14	6.75
1968	31	3.00	1.27	1.13	37.5	0.95	2.94
1969	36	2.86	2.01	1.42	49.7	1.76	5.09

Table A37

Summary of fold scores for ewes in the Folds Minus selection flock

Total fold score (Neck + Side + Breech)

Year	No.	Mean	Variance	S.D.	C.of V	Skewness	Kurtosis
1951	62	5.74	4.56	2.13	37.2	1.46	6.50
1953	41	5.95	5.85	2.42	40.6	1.59	6.22
1954	42	5.60	6.69	2.59	46.2	1.39	5.18
1955	40	5.77	3.31	1.82	31.5	0.97	3.44
1956	17	4.65	1.87	1.37	29.4	0.33	1.72
1957	49	5.53	6.55	2.56	46.3	3.16	16.40
1958	59	7.17	4.97	2.23	31.1	0.80	3.23
1959	36	5.11	2.79	1.67	32.7	1.84	6.70
1960	42	5.76	6.43	2.54	44.0	2.54	10.50
1961	28	5.32	1.71	1.31	24.6	-0.10	1.67

Restricted fold score (Neck + Side)

1951	62	3.58	1.89	1.37	38.4	1.10	5.44
1953	41	4.17	3.20	1.79	42.9	1.06	4.07
1954	42	3.86	2.81	1.68	43.5	1.04	3.52
1955	40	3.92	1.40	1.19	30.2	0.95	3.20
1956	17	3.18	0.90	0.95	29.9	0.50	2.24
1957	49	3.47	3.05	1.75	50.3	2.57	12.43
1958	59	4.54	1.84	1.36	29.9	0.73	3.24
1959	36	3.33	1.43	1.20	35.9	1.61	5.51
1960	42	3.64	3.36	1.83	50.3	1.70	5.84
1961	28	3.18	0.89	0.94	29.7	-0.09	1.52
1962	31	3.03	2.97	1.72	56.8	3.17	14.92
1963	40	3.55	2.92	1.71	48.1	2.92	15.19
1964	58	3.24	1.20	1.10	33.9	0.46	2.16
1965	28	2.43	0.40	0.63	26.1	1.10	3.02
1966	38	2.61	0.95	0.97	37.4	1.34	3.43
1967	32	2.69	6.09	2.47	91.9	4.89	26.44
1968	47	2.96	1.30	1.14	38.6	1.37	4.71
1969	49	2.53	0.50	0.71	28.1	0.92	2.48

APPENDIX B

APPENDIX B

The general relationship between repeatability and heritability

The model to be investigated is as for some measure of ewe reproductive performance, measured at two separate lambings. Heritability at the two lambings may differ, while the genetic correlation between them need not be unity.

The phenotype at the two lambings, P_1 and P_2 can be expressed as follows:

$$P_1 = G_1 + C + E_1 \quad \text{and}$$

$$P_2 = G_2 + KC + E_2$$

where G and E refer respectively to genetic and environmental effects on performance. C is a permanent environmental effect which may have a scaled effect on performance (K).

If G, C and E are assumed to be independent, and if t is the repeatability of performance (phenotypic correlation between records), then:

$$t = \frac{\operatorname{cov}(G_1\ G_2) + K\sigma^2_C}{\sigma_{P1}\ \sigma_{P2}}$$

$$= \frac{r_g \sigma_{G_1}\sigma_{G_2}}{\sigma_{P_1}\sigma_{P_2}} + \frac{K\sigma_c^2}{\sigma_{P_1}\sigma_{P_2}}$$

$$= r_g h_1 h_2 + \frac{K\sigma_c^2}{\sigma_{P_1}\sigma_{P_2}}$$

Here repeatability sets an upper limit to the product of the genetic correlation between records and the square root of the product of the heritability at the two lambings. The heritability at either lambing could thus exceed the repeatability.