STUDIES OF PRODUCTIVE TRAITS IN A NEW ZEALAND ROMNEY FLOCK: THE EFFECT OF SOME ENVIRONMENTAL FACTORS, HERITABILITIES AND REPEATABILITIES

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I INTRODUCTION

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Three traits of dual purpose sheep such as the New Zealand Romney are of paramount importance in contributing directly to income. These are reproductive ability and wool production of the ewe flock and the growth rate of the lamb produced. Investigations of methods of genetic improvement of these traits is important, since such improvement is more permanent than that caused by environmental modification or the use of hormones. Improvement of productive traits through genetic means may be brought about (1) by exploiting the differences between groups of animals which have been genetically distinct for some time (breeds, strains, studs or inbred lines) or (2) by exploiting the difference between individual animals within a flock. The first method involves crossbreeding, which may change production through the introduction of superior genes or through complex interactions between genes (heterosis and epistasis). Rae (1952) reviewed the field of crossbreeding and looked at grading up existing breeds, combining crossbreeding with selection to form new breeds and exploiting hybrid vigour (heterosis). With the N.Z. Romney this practice is in fact being carried out by some farmers who are crossing with the Cheviot (to obtain an animal for a harsh environment) or Border Leicester (for a more favourable environment). In some cases these crossbred animals so produced have been interbred and selected to form the two new breeds Perendale and Coopworth respectively. For many reasons many farmers prefer not to cross their flocks with animals of another breed and it is then necessary to use the second method, i.e. to select within the farmers flock, if any genetic improvement is to be acheived. This study is aimed at studying factors of importance to within flock selection.

Characters may be influenced by environmental factors which may be grouped in two classes, external environment and internal environment. The external environmental factors are all those that are likely to affect the mean value of production of a whole flock. Examples are the effect of region, property and management, climate and disease. Internal factors are those which affect individuals but not the whole flock. These include the animal's sex, maternal effect (age of dam), type of birth, inbreeding and other such factors. As this study is dealing with selection within the flock then only the internal environmental factors need be studied. The exception to this is when records of a character are being looked at over a number of years. In each year the climate, etc. affecting the flock is different and so the year factor must be considered. Internal factors may influence estimates of heritability and repeatability (also correlations which are not dealt with in this study). Environmental factors therefore may obscure genetic differences between individuals. In genetic studies we wish to understand the relative influence of environment and genotype on various characters so it is important to estimate the size of the effects of these factors. Such estimates can then be used as correction terms so that genetic comparisons can be made with greater accurracy.

Repeatabilities and heritabilities give indications of the expected size of gains in characters that selection will make within a selected generation of sheep and over succeeding generations of sheep respectively. Repeatability measures the extent to which differences between individuals depend on genetic and permanent environmental effects. If repeatability is high then animals will rank consistently from record to record; so elimination of low producers will raise the lifetime average of the flock. Heritability measures the proportion of the variation between individuals which arises from genes acting additively; it estimates, therefore, the proportion of the parents' superiority which will, on the average, be passed on to the offspring.

This study attempts to look at important aspects of the main traits; reproductive ability, wool production and growth rate of the lamb produced. The heritability has been calculated for weaning weight which is a measure of the growth rate of the lamb to weaning. Both heritability and repeatability are calculated for weight of lamb weaned which is a measure including both the growth rate of the lamb to weaning and an estimate of the ewes reproductive ability. Other estimates of the ewes reproductive ability studied are: the number of lambs born per ewe mated and present at lambing; the number of lambs alive at their second day of age per ewe mated and present at lambing; the number of lambs weaned per ewe mated and present at lambing; barrenness (number lambing per ewe mated and present at lambing); number of multiple births per ewe mated and present at lambing and the number of triplet births per ewe mated and present at lambing. Heritability estimates have been calculated for each of these measures of reproductive ability and repeatabilities over four lambing seasons have been calculated for the first three. Some authors call the measure of the number of ewes lambing per ewe mated and lambing "fertility" instead of "barrenness" as it has been called in this study. Also "prolificacy" is the name sometimes given to the number of lambs born per ewe lambing. The remaining character that has been studied is hogget greasy fleece weight for which the heritability has been calculated. For all these characters estimates of the magnitude of certain environmental factors are assessed.

Assessment of these parameters is carried out on a randomly bred flock kept, at Massey University, which is supposed to be representive of the N.Z. Romney: the dominant sheep breed of New Zealand. After the review of literature the flock upon which this study has been based has been described before the method of analysis and results have been set out.

II. REVIEW OF LITERATURE

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A. WEANING WEIGHT

1. Environmental effects

(i) The magnitude of environmental effects

Estimates, from the literature, of the magnitude of the environmental effects of weaning weight are given in Table 1. When age of dam effect is considered as only two groups (2-year-olds and mature ewes) then it can be seen that the weaning weights of lambs from mature ewes are significantly heavier than those from 2-year-old ewes (Hazel and Terrill, 1945a and 1946a). Results by Donald and McLean (1935) and Nelson and Venkatachalam (1949) further support these findings. Donald and McLean using data from the English Leicester breed, found that lambs from older ewes were 10.05 lb heavier than those from 2-tooth ewes (77.05 and 67.00 lb). The corresponding result from the Southdowns was 3.93 lb advantage to the mature ewes (68.99 anf 65.06 lb). These results were based on only 66 and 57 records for the English Leicester and Southdown respectively. Nelson and Venkatachalam, on studying five breeds, found, on average, that the weaning weight of lambs from mature ewes were five percent heavier than those from 2-year-olds.

Where the above mature category is divided up into single ages, or group of ages, a pattern of rising lamb weaning weight with increasing age of dam can be seen, and if the ewes are kept long enough these reach a peak and then fall off with further increase in

Table 1: Estimates of environmental effects on weaning weight

Breed	Hampshire	Oxford Suffolk Cheviot	Dorset	Hampshire Shropshire Corriedale	Navajo X	New Zealand Romney			Corriedale Columbia Targhee	Romnelet	Rambouillet
							(ewe lambs)				
							(inter)	(red)			
No records	723	1169	485	810	1506	2655	691	691	1082	1532	2133
Mean		68.2	63.2	71.0 55.2 61.8	59.4	53.2	55.7	55.5	73.0	64.2	69.0
Std Deviation					9.8	7.8	7.6	7.7	10.3		8.5
Av weaning age		120			139	104			120		124
Birth and rearing type											
Single-Twn	8.19	12.32	7.89	8.29	11.2	10.24	9.5	9.3	11.7	12.56	9.2
Single-TrS	2.60	2.79	7.15	5.38	2.9	6.68	2.3	2.9	5.1	2.77	2.5
Sex of lamb											
Ram-ewe	6.18	4.66	4.38	3.30	4.4	3.05			10.8		8.3
Reg on age at weaning			0.27	0.13	0.37	0.28	0.26	0.26	0.45	0.36	0.41
Reg on % inbreeding									-0.302	-0.375	
Reference	(1)	(2)	(3)	(4)	(5)	(6)	(7)	(7)	(8)	(9)	(10)

continued overleaf ...

Table 1: Continuation. <u>Effect of age of dam</u>

Measure	Value (Ref)	Measure	Value (Ref)
Oxford, Suffolk and Cheviot: (2)		Navajo X: (5)	
2-year-old	-0.40	4 to 7yr - 2yr	3.50
3yr	1.54	- 3yr	0.20
4yr	3.08	- 8 to 11yr	3.10
5yr	1.72		
6yr	-0.42	N.Z. Romney: (6)	
7yr	-5.5	5yr - 2yr	4.75
		- 3yr	1.98
N.Z. Romney (inter) (red): (7)		- 4yr	0.33
4 to 5yr - 2yr 3.0	4.5		
		Corriedale, Columbia & Targhee: (8)	
- 3yr 0.9	0.9	Mature - 2yr	8.7
Romnelets. (9)			
		Rambouillet. (10)	
3 to 5yr - 2yr	2.69	Mature - 2yr	6.1
- 6+yr	1.03		

References: 1. Smith and Lidvall (1964); 2. Holtman and Bernard (1969); 3. and 4. Blackwell and Henderson (1955); 5. Sidwell and Grandstaff (1949); 6. Ch'ang and Rae (1961); 7. Ch'ang (1967); 8. Hazel and Terrill (1946a); 9. Vesely and Slen (1961); 10. Hazel and Terrill (1945a) age of dam. This is best seen in the results of Holtmann and Bernard (1969) whose ewes reached a peak at four years and declined thereafter. Another very similar result was that obtained by Felts, Chapman and Pope (1957) using data obtained from 32 farm flocks. They got values of -14.26, 0.08, 4.23, 4.57, 3.73, 2.00 and -0.34 lb deviation from the overall mean for the age of dam effect increasing from 1 to 7 years. Again the peak is at 4 years which corresponds to the 4 to 7 year and 3 to 5 year group peaks of Sidwell and Grandstaff (1949) and Vesely and Slen (1961) respectively. The fact that Ch'ang and Rae's (1961) estimates are still rising, although to a lessening extent, at 5 years shows that the peak is not necessarily fixed at 4 years of age. Blackwell and Henderson (1955), commenting on their results from grouped Corriedale, Hampshire and Shropshire ewes, noted that the effect of age of dam on weaning weight of lambs was curvilinear, reaching a maximum at approximately 5 years of age.

Some of the disadvantage suffered by the lambs from the younger ewes is likely to be due to a lower initial milk yield of these ewes. (For further discussion see below.)

As well as the results from type of birth and rearing effect given in Table 1 results by Nelson and Venkatachalam (1949), Karam, Chapman and Pope (1953) and Felts, Chapman and Pope (1957) also contain relevant information, although the first two did not consider twins reared singly. Nelson and Venkatachalam, on studying five breeds, found, on average, that the weaning weight of single lambs was 17 percent heavier than twins. Karam, et al., studying the lambs of grade ewes mated to Shropshire rams, found amongst ewe lambs 145 singles averaged 64.1 lb and 152 twins averaged 56.8 lb, and amongst wethers 145 singles averaged 67.6 lb and 151 twins averaged 59.3 lbs

- differences in favour of the singles of 7.3 and 8.3 lbs respectively. Felts, et al., using data obtained from 32 farm flocks, found pooled type of birth effects were 7.9, -2.3, 1.9, 2.8, -7.1 and -3.2 lbs for male singles, male twins, male twins reared as singles, female singles, female twins and female twins raised as singles respectively.

In all these cases, it can be seen that single lambs are heaviest at weaning and twins raised to weaning as twins have the lightest weight - a difference which is in the range of 3 to 7 lb. Twins reared as singles, in all cases, lie between the weights of the other two groups. Observations reported by Barnicoat, et al., (1949), on the N.Z. Romney, suggest that the greater weight of single lambs at weaning can be explained partly by their higher birth weight and partly by their higher milk intake. That lambs born twins but reared singly are heavier than twin-reared lambs is likely to be due, largely, to the greater amount of milk available to the twins reared singly. But, the fact that twins reared singly are lighter than singles at weaning, shows that twinning is detrimental to subsequent growth, even when post-natal conditions are otherwise similar.

Table 1 shows that the male lamb (ram or wether) reaches a heavier weight at weaning than its ewe lamb counterpart. In the results, given in the table, this advantage to the male ranges from 3.0 to 10.8 lb. Further results by Donald and McLean, (1935), on the English Leicester and Southdown; Nelson and Venkatachalam (1949); Karam, et al., (1953), using the Shropshire, and Felts, et al., (1957) all support the finding that male lambs wean at significantly higher weights than ewe lambs. Donald and McLean do note in their English Leicester 2-tooths that ram and ewe lamb offspring show very little difference, but this is only on the results of 23 animals.

Table 1 shows values for the regression of weaning weight on age of lamb at weaning and the regression of weaning weight on percent inbreeding. The high values for the latter indicate that inbreeding has a very detrimental effect on weaning weight. This reflects the combined effect of inbreeding in both the dam and the offspring, since the more highly inbred ewes generally have lambs with greater than average inbreeding.

(ii) Interactions between main environmental effects

The absence of interaction between the main classifications allows the estimates of the effects to be used as additive correction factors. For example, if ram lambs differ from the average by x, and twin lambs by y, then twin rams are assumed to differ by x + y. Consequently knowledge of the occurrence of interaction is important in assessing the usefulness of the estimates of the environmental effects as correction factors.

Ch'ang and Rae (1961), dealing with the N.Z. Romney, found that first-order interactions between year, age of dam, birth rank and sex were statistically non-significant. This agreed with the findings of Hazel and Terrill (1945a), that the interaction between the different factors (sex, groups, years, age of dam, type of birth and rearing, percent inbreeding and age of lamb at weaning) were either non-significant or small as compared with the variation within classes. Felts, et al., (1957) assumed, because a "significant" interaction between age of dam and type of birth for 120-day weight was only found in 3 to 74 flock-years, it was unimportantly small or non-existent. Ch'ang (1967) using weaning weights from 691 lambs found a significant interaction between age of dam and type of birth and rearing. This interaction implied that the sub-class means were dependent not only on the main effects, four classes of age of dam and three classes of type of birth and rearing, but also on a joint effect between the elements of these two main effects. The evidence gained, when assessing the significance of this interaction (by comparing the Error Mean Squares calculated according to the "interaction" and "reduced" models --a 58.2 and 58.9 respectively) suggest that the extent of departure from linearity between age of dam and type of birth and rearing has only a negligible practical significance. In view of this interaction, two sets of environmental effects are presented in Table 1 for comparision. The corresponding values of the main effects show close agreement between the two sets of estimates thus providing further evidence that the observed significant interaction does not represent a serious departure from additivity.

(iii) Partitioning the components of variance

Hazel and Terrill (1945a) and Ch'ang and Rae (1961) partitioned the components of variance (Table 2) and found that the environmental effects accounted for 49.5 and 58.1 percent of the total variance respectively. In both cases, type of birth and rearing was found to be the most important source of variation. These two figures agree with the figure of 56 percent, for the variance in weaning weight due to measurable environmental factors, obtained by Sidwell and Grandstaff (1949) on the records of 1506 Navajo cross lambs.

Table 2: Partitioning the variance components

Breed of Sheep	Rambouillet		N.Z. Romney	
Source of Variance	d.f.	% total var.	d.f.	% total var.
Years	1	0.0	6	2.0
Age of Dam	1	3.1	3	2.1
Birth & Rearing Type	2	12.2	2	45.5
Sex of Lamb	1	8.9	1	3.2
Age at Weaning	1	5.1	1	5.3
% Inbreeding	1	6.4		
Error	2174	50.5	2641	41.9
Reference (See Table 1)	(10)		(6)	

2. Estimates of heritability and repeatability

In general, the estimates of heritability of weaning weight fall within the range of 0.05 to 0.45 with only a few estimates outside these limits. A review appears in Table 3. Rae (1956), in reviewing heritability estimates for weaning weight, noted that in the fine wool breeds, such as the Merino and Rambouillet, the heritability value appeared higher than the value for the meat breeds. It was suggested that in the meat breeds greater emphasis had probably been placed on selection for increased weaning weight than on the fine-wool breeds and possibly this has resulted in reduction of the genetic variability present. Table 3 contains many estimates published after 1956. On studying these, it can be seen that although there are some high estimates for fine wool breeds there are also other estimates of the same order as the meat breeds. The estimates available for the N.Z. Romney range from 0.23 to 0.35.

Table 3: Estimates of the heritability of weaning weight

Estimate	Breed	Remarks	Ref.
0.45	Aust. Merino(R)	430 d.f., dam offspring corr.	(1)
0.45	——— (E)	465 d.f., dam offspring corr.	(1)
0.10	———	166 d.f. (sires) PHS.	(1)
0.15	——— (R)	35 sires PHS.(Paternal half-sib)	(2)
0.16	——— (E)	80 sires PHS.	(2)
0.32	——— (R)	377 pairs, dam offspring corr.	(2)
0.28	——— (E)	436 pairs, dam offspring corr.	(2)
0.27	Rambouillet	2183 lambs, PHS.	(3)
0.34	———	892 pairs, dam offspring reg.	(3)
0.30	———	2183 lambs, 892 pairs, av. 2 methods	(3)
0.22	———	83 sires, offsping mean & sire reg.	(4)
0.56	Rambouillet & X	1281 pairs, dam offspring corr.	(5)
0.41	———	105 pairs, mid-parent offspring reg.	(5)
0.27	———	19 pairs, sire offspring reg.	(5)
0.77	———	123 pairs, dam offspring reg.	(5)
0.59	Corriedale	Full sib corr.	(6)
0.21	Columbia	PHS.	(6)
0.40	Targhee type	32 sires, PHS.	(7)
0.19	———	61 sires, PHS.	(7)
0.12	Fine wooled	559 lambs, 40 sires, offspring on sire reg.	(8)
0.06	———	599 lambs, 40 sires, PHS.	(8)
0.17	———	1711 lambs, 99 sires, 789dam offspring pairs, av. 2 methods.	(9)
0.28	Romnlet	694 dam offspring pairs.	(10)
0.35	N.Z. Romney	1441 lambs, 482 dams offspring reg.	(11)
0.30	———	d.f. 39 sires PHS.	(12)
0.23	———	518 d.f. dam offspring reg.	(12)
0.34	Shropshire	33 sires, 593 lambs, PHS.	(13)
.08-.12	———	110 dam offspring pairs.	(14)
.04-.06	Southdown	77 dam offspring pairs	(14)
0.10	Ossimi	202 dam offspring pairs - 4 months.	(15)
0.29	———	165 dam offspring pairs - 6 months.	(15)

Continued overleaf

Table 3: Continuation

Estimate	Breed	Remarks	Refs.
0.29	Down breeds	365 lambs, 21 sires.	(16)
0.07	Various breeds	784 dam offspring pairs.	(17)
0.29	------	348 pairs, dam offspring reg.	(18)
0.42	------	PHS.	(18)
0.35	------	Weighted av. of 2 methods.	(18)
0.21	------	233 dam offspring pairs.	(19)
0.02	------	402 dam offspring pairs.	(20)
0.15	Unnamed breeds	Data from 32 flocks.	(21)

References: 1. Young, *et al.* (1965); 2. Pattie (1964); 3. Hazel and Terrill (1945b); 4. Shelton (1959); 5. Warwick and Cartwright (1957) 6. Botkin (1964); 7. Osman and Bradford (1965); 8. Nolan, *et al.* (1969); 9. Hazel and Terrill (1946b); 10. Vesely and Slen (1961); 11. Ch'ang and Rae (1961); 12. Ch'ang (1967); 13. Karam, *et al.* (1953); 14. Ensminger, *et al.* (1943); 15. Ragab, *et al.* (1953); 16. Boyd and Woolfolk (1964); 17. Blackwell and Henderson (1955); 18. Nelson and Venkatachalam (1949); 19. Cockerham (1949); 20. Butcher, *et al.* (1964); 21. Felts, *et al.* (1957).

Sidwell and Grandstaff (1949) found a repeatability of 0.217 for weaning weight of lambs from the same ewe, when studying the offspring of Navajo ewes mated to a variety of rams. Felts, *et al.* (1957) attained a repeatability of 0.313, when studying 32 farm flocks.

3. Summary

The environmental factors, age of dam, type of birth and rearing, sex of lamb, date of birth and year of birth all have significant effects on weaning weight. The heritability of weaning weight, at 0.05 to 0,45, indicates that once the environmental factors have been corrected for then reasonable gains from selection can be expected.

B. HOGGET GREASY FLEECE WEIGHT

1. Environmental effects

(i) The magnitude of environmental effects

Table 4 contains a summary of the effect of environmental factors on hogget greasy fleece weight. Once again, as with weaning weight, the type of birth and rearing has the effect of causing single born hoggets to produce heavier fleeces than twins, while twins raised as singles are intermediate. A further example, in the N.Z. Romney breed, is given by Wright and Stevens (1953) who, on analysing 211 hoggets, found that singles averaged 0.24 lb heavier than twins.

(ii) Partitioning the components of variance

If the environmental component of variance is partitioned the importance of each factor can be seen. Table 5 demonstrates this and shows that, on average, the year effect is the most important source of variation with the others (age of dam, type of birth and rearing, age at shearing and percent inbreeding) all varying from less than 2 to 8 percent.

2. Estimates of heritability and repeatability

Estimates for the heritability and repeatability of hogget greasy fleece weight are given in Table 6 and 7. In general, the estimates of heritability fall in the range 0.25 to 0.65 with the majority 0.3 to 0.5. While the earlier estimates for the N.Z. Romney were far lower than for most other breeds (in the range

Table 4: Estimates of environmental effects on hogget greasy fleece weight

Breed	Rambouillet		Targhee		Columbia		Navijo & X		N.Z. Romney
Sex	ewe	ram	ewe	ram	ewe	ram	ewe	ewe	ewe
No records	932	499	290	213	406	359	917	1075	801
Mean	8.30	11.64	7.95	10.83	8.72	12.07	7.44	5.48	8.04
Std. dev.	1.09	1.48	1.23	1.59	1.51	1.84	1.32		
Av age at shearing	406d				402d	404d	11-12m	11m	13-14m
Type of birth and rearing									
Single-twin	.81	.43	.85	.62	1.03	.81	.90	.76	.37
Single-TrS	.37	.2[illegible]	.63	.04	.58	.47	.18	.38	.14
Reg on age at shearing	.026	.040	.061	.077	.058	.047	.03	.022	.02
Reg on % inbreeding	-.019	-.057	-.032	-.023	-.022	-.013			
Age of dam									
Mature - 2yr	.58	.40	.43	.36	1.04	.92	.20		
2-year								5.22	7.76
3-year								5.46	8.10
4-to 6-year								5.63	8.26
7+ year								5.61	
References;	(1)	(2)	(3)	(4)	(3)	(4)	(5)	(6)	(7)

References: 1. Hazel and Terrill (1946c); 2. Terrill, Sidwell and Hazel (1943b); 3. ------- (1947); 4. ------ (1948a); 5. Price, Sidwell and Grandstaff (1953); 6. Hall, *et al.* (1964); 7. Tripathy (1966)

d = days m = months

Table 5: Partitioning the variance components

Breed	Rambouillet				Targhee				Columbia				Navajo & X		N.Z. Romney	
Sex	ewes		rams		ewes		rams		ewes		rams		ewes		ewes	
Source of variation	d.f.	%	d.f.	%	d.f.	%	d.f.	%	d.f.	%	d.f.	%	d.f.	%	d.f.	%
Years	1	a	4	24	3	14	4	30	3	16	4	38	2	2.6	6	47
Age of dam	1	3.1	1	a	1	b	1	a	1	b	1	b	1	7.7	2	1
Type of B & R	2	6.7	2	1	2	b	2	a	2	b	2	a	2	5.2	2	a
Age of dam	1	b	1	2	1	5	1	b	1	5	1	a	1	2.9	1	2
% inbreeding	1	a	1	8	1	b	1	a	1	a	1	a				
Breeding groups													12	21.0		
Error d.f.	924		489		281		203		397		349		898		789	
Variation accounted for of total	29%		39%		33%		39%		29%		45%		47%		51%	
Reference	(1)		(2)		(3)		(4)		(3)		(4)		(5)		(7)	

a = less than 2% of total variation
b = more than 2% of total variation
References: see the code for Table 4.

Table 6: Estimates of heritibility of hogget greasy fleece weight

Estimate	Breed	Remarks	Reference
0.39	Aust Merino	529 d.f. dam offspring pairs.	(1)
0.67	-------	17 rams, 14 d.f. PHS.	(1)
0.40	-------	Parent offspring reg.	(2)
0.44	-------	PHS.	(2)
0.42	-------	1495 d.f. dam offspring corr.	(3)
0.45	------- 15mth	1071 d.f. dam offspring corr.	(4)
0.43	------- 15mth	394 d.f. dam offspring corr.	(4)
0.32	------- 11mth	857 d.f. dam offspring corr.	(4)
0.40	Rambouillet	70 dam offspring pairs.	(5)
0.28	-------	162 dam offspring pairs.	(6)
0.66	-------	29 sires, 28 d.f. PHS.	(7)
0.52	Corriedale	68 dam offspring pairs.	(8)
0.24	-------	173 dam offspring pairs.	(5)
0.84	Targhee Type	32 sires, PHS.	(9)
0.50	-------	61 sires, PHS.	(9)
0.14	Romney x Rambouillet	213 dam offspring pairs.	(5)
0.17	N.Z. Romney	639 d.f. dam offspring pairs.	(10)
.10-.15	-------	200 dam offspring pairs.	(11)
0.31	-------	163 d.f. offspring dam reg.	(12)
0.32	-------	17 d.f. PHS.	(12)
.10-.15	-------	Extensive data.	(13)
0.43	-------	508 dam daughter pairs reg.	(14)
0.34	Navijo	867 daughter dam pairs.	(15)
0.40	Mixed breeds	233 dam offspring pairs.	(16)

References: 1. Morley (1951); 2. ------ (1955); 3. Brown and Turner (1968); 4. Young, Turner and Dolling (1960); 5. Rasmussen (1942); 6. Terrill and Hazel (1943); 7. Shelton (1959); 8. Wright and Stevens (1953); 9. Osman and Bradford (1965); 10. Rae (1950); 11. ------ (1948); 12. ------ (1958); 13. McMahon (1943); 14. Tripathy (1966); 15. Hall, et al. (1964); 16. Cockerham (1949)

0.1 to 0.2) the later results are between 0.30 and 0.35. Rae (1958), on discussing his higher results for the N.Z. Romney, commented that the accurracy of the 0.31 and 0.32 estimates was low and the difference between them and earlier results could well have been due to sampling errors.

Tripathy's (1966) result of 0.43 for the hogget fleece weight heritability is the highest to be estimated for the N.Z. Romney. When he obtained this result his comment was that it appeared to be in line with preliminary results of a selection experiment for hogget greasy fleece weight which was being carried out a Massey University (Rae, 1964).

Table 7: Estimates of repeatability of hogget greasy fleece weight

Estimate	Breed	Remarks	Reference
0.56	Rambouillet	81 ewes: 1st 3 fleeces	Rasmussen, 1942
0.56	Corriedale	196 ewes: 1st 3 fleeces	------
0.72	-------	68: hogget with mature average	Wright & Stevens, 1953
0.43	Romney X Rambouillet	232: 1st 3 fleeces	Rasmussen, 1942
0.51	N.Z. Romney	hogget with 2nd fleece	Wright & Stevens, 1953
0.44	-------	hogget with sum of 4 mature fleeces	------
0.62	-------	hogget with sum of 4 mature & hogget fl.	------

3. Summary

The above on heritability of hogget greasy fleece weight and the repeatability of greasy fleece weight indicate that the response to selection of hogget greasy fleece weight will be high (heritability

0.25 to 0.65) and that this will be carried on through the life of the ewe as the repeatability between hogget and subsequent fleece weights is high - 0.45 to 0.70. Greater accuracy of selection can be obtained if, within each year, corrections are made for the effects of age of dam, type of birth and rearing and the age of the hogget at hogget shearing.

C. REPRODUCTIVE RATE

1. Introduction

The farmer wants to raise the fertility level of his flock because he will have available a greater number of animals for sale or a greater number from which to select his replacements. In this way he can ensure a greater selection differential because the replacements make up a smaller proportion of those available for selection. Thus the farmer is really interested in the number of surviving lambs at weaning or at some subsequent profitable age.

When considering fertility in sheep, until the progeny reach a profitable age, it is important to realise that the efficiency of reproduction depends on a series of events each of which determines the upper limit of the succeeding one. Until parturition the events can be divided into three main stages:

(1) the number of ova the ewe sheds

(2) the number of ova fertilized

(3) the number of zygotes carried to term.

Following parturition the series of events can be further grouped into:

(4) the number of lambs surviving with the dam to a period after parturition

(5) the number of lambs surviving with the dam to weaning or to a subsequent profitable age.

The number of ova is a character of the dam while the number of ova fertilized may conceivably be insluenced by either the dam or the sire. The third stage could be considered to be due to the viability of the zygote but the influence of the dam and her contribution to the genotype of the zygote(s) must not be overlooked. Similarly, the fourth and fifth groupings are influenced by the dam while the viability of the zygote increases in importance as the animal gets older.

As this series of events is influenced at all stages by factors within the dam and environmental factors external to the dam, probably the best measure of the fertility of the ewe is the number of ova she sheds. This, being the first stage, does not include the viability of the young and is least affected by other factors. It is impractical for the farmer to measure the number of ova shed. It is more practical for the farmer to measure the number of lambs born or reaching a specific age alive.

All these characters mentioned are measured on the ewe. The ram has an influence in two ways - through the genes which he contributes to the offspring, and through a direct effect of his libido and semen traits.

This review sets out results from the literature of the effects of environment on certain measures of reproductive rate. Following this estimates of heritabilities and repeatabilities and progress in selection experiments for reproductive rate are given.

2. Environmental effects

(i) The magnitude of environmental effects

(a) Age of ewe effect

The age of the ewe is the most important non-genetic factor to influence repoductive rate in sheep. Table 8 contains some of the results from the literature of the influence of age of ewe on the number of ewes lambing. This character is sometimes referred to as the measure of the ewes fertility or as "barrenness". The number of ewes not lambing is always high at 2 years of age and thereafter

Table 8: The effect of age on the number of ewes barren

Breed	Age of Dam: Barrenness as a Percentage									Re.
	2	3	4	5	6	7	8	9	10	
Aust. Merino	18.1	13.6	12.4	8.3	8.3	8.5	9.8	11.9	13.5	(1)
--------	35.6	18.5	19.4	17.9	17.8	22.5	30.0	23.8	26.1	(2)
Fine wooled	22	14	12	9	13	10	13	0		(3)
--------	7.7	8.2	7.0	7.9	5.7	10.5				(4)
Corriedale	6.6	4.3	2.8	6.4	7.0	5.9				(5)
N.Z. Romney	15.6	4.3	6.5	12.5	9.4					(5)
--------	16.6	11.2	5.8	5.9	6.0					(6)
--------	25.2	13.5	11.5	10.8	7.1	10.9	7.1			(7)
Border Leicester	5.5	3.0	4.1	2.4	2.5	7.6				(5)
Southdown	6.1	4.0	7.1	3.3	9.1					(5)
Various breeds	13.1	9.2	7.5	8.4	10.2	7.8	10.0	17.8		(8)

References: 1. Turner and Dolling (1965); 2. Shelton and Menzies (1968); 3. Terrill and Stoehr (1939); 4. Vesely and Peters (1965); 5. Hart and Stevens (1952); 6. Goot (1952a); 7. Barton (1947); 8. Sidwell, Everson and Terrill (1962).

decreases with age reaching a low point at 3- to 6-years of age and then increases again. The percentage of barrenness in older ewes is usually considerably below the figure for 2-year-olds. The only exception to this pattern is the result of Vesely and Peters but the small numbers involved may be the cause of this. Results from Teodoreanu and Rusu (1959), De Haas and Dunlop (1969) and Campbell (1962) further support these findings. Teodoreanu and Rusu, with 1287 Palas Merino ewes, found the incidence of infertility was higher in younger and older ewes than in 4- to 8-year-olds. De Haas and Dunlop, using reproductive records covering 4855 ewe-years coming from five strains of Australian Merino, found in general dry ewes were at a maximum at 2 years, fell sharply at 3 years and remained relatively constant with a hint of an increase at advancing ages (6 to 7 years old). Campbell found, using approximately 3300 Rambouillet sheep, that the percentage of barren ewes was 30.0 at 2 years of age, varied between 9.8 and 12.9 for 3 to 7 years, and was 17.4 to 21.4 at 8 to 10 years. Wallace (1958) provides a further example for the N.Z. Romney. Data from three flocks selected for high and low fertility and a control showed that in general the incidence of barren ewes decreased with increasing age. The interesting feature of the study was that whereas at the 2-year-old stage the percentage of barren ewes had been higher for the high fertility flock than in either the control or low fertility flocks (16 verses 12.3 and 12.7) the reverse was the case at later ages where there were only about half as many dry ewes in the high fertility flock.

Tables 9 and 10 contain some of the information available from the literature on the age of ewe effect on reproductive rate using various types of measurement. There is a characteristic rise with the age of the ewe to a maximum usually followed by a decline. Sometimes this fall may be only slight and at other times ewes may not be kept long enough to show this trend. The only exception to the characteristic trend was that recorded by Mullaney and Brown (1969) with Australian Merinos. These animals first lambed at 3 years of age and thereafter showed a steady decline in number born per ewe joined to 9 years. The decline in the first three lambings was not as great as that recorded during the rest of the lifetime. The following are further references noting the effect of age of ewe on reproductive rate and all show the general trend of a rise followed by a decline with age of the ewe if they were kept long enough: Roberts (1921), Nikoljskii (1933), Smirnov (1935), Biegert (1938), Johansson and

Table 9: The effect of age of ewe on reproductive measures based on the number of ewes joined

Breed	Age of dam: Reproductive rate as a %									Ref.
	2	3	4	5	6	7	8	9	10	
No born per ewe joined										
Aust Merino	84	91	96	105	110	111	110	107	104	(1)
------		101	100	98	95	90	87	85		(2)
Polwarth		91	98	100	98					(2)
Corriedale	84	89	98	101	102	102				(2)
------	112	131	155	147	178	174				(3)
N.Z. Romney	128	158	163	162	171	181				(3)
Border Leicester	146	154	174	177	198	177				(3)
Wensleydale	158	167	189	183	175	172				(4)
Southdown	114	134	136	132	152					(3)
Various breeds	123	136	156	151	164	157	160	145	152	(5)
Multiple births per ewe joined										
Aust Merino	2	4	8	13	18	20	20	18	18	(1)
N.Z. Romney	19	32	40	42	42					(6)
No born alive per ewe joined										
Fine woolled	73	88	101	113	105	117	101	144		(7)
N.Z. Romney	82	112	123	127	131	124	150			(8)
No alive at docking per ewe joined										
N.Z. Romney	85	108	119	121	118					(6)
------	78	94	97	109	100	94	92	87	84	(10)
No weaned per ewe joined										
Merino	62	72	77	86	89	87	82	78	71	(1)
------		75	81	82	78	76	71	56		(2)
Polwarth		69	82	85	87					(2)
Corriedale	59	64	74	79	87	92				(2)
Various breeds	83	98	112	105	110	105	93	99		(9)
------	106	120	134	132	128	127	120	114	130	(5)

References: 1. Turner and Dolling (1965); 2. Mullany and Brown (1969) 3. Hart and Stevens (1952); 4. Dry (1936); 5. Inskeep, *et al.*, (1967) 6. Goot (1952b); 7. Terrill and Stoehr (1939); 8. Barton (1947); 9. Sidwell, *et al.*, (1962); 10. Hickey (1960)

Table 10: The effect of age of ewe on reproductive measures based on the number of ewes lambing

Breed	Age of dam: Reproductive rate as a %									Ref.
	1	2	3	4	5	6	7	8	9	
No born per ewe lambing										
Rambouillet		108	119	127	129	129	130	128	123	(1)
Fine woolled		119	142	150	149	148	150			(2)
-------		109	116	129	134	134	139	127	150	(3)
N.Z. Romney		127	143	151	149	151	151	169	150	(4)
Lange	108	126	145	151	156	156	140	142	142	(5)
B.L. x Cheviot	128	180	187	197	196	198	195			(6)
-------		175	186	185	199	196	177			(6)
Wensleydale	181	175	179	196	188	178	177			(7)
Rahmani		112	127	135	141	135	146			(8)
Ossimi		111	118	141	117	130	145	137		(9)
Dala & Steigar	148	156	175	174	178	184				(10)
Various breeds		126	131	137	143	145	141	145		(11)
-------		132	144	150	153	154	157	149		(12)
No weaned per ewe lambing										
Fine woolled		87	104	121	118	116	103			(2)
B.L. x Cheviot	110	167	171	183	181	172	155			(6)
-------		160	175	169	171	178	168			(6)
Dala & Steigar	107	155	157	163	159	157				(10)

References: 1. Shelton and Menzies (1968); 2. Vesely and Peters (1965); 3. Terrill and Stoehr (1939); 4. Barton (1947); 5. Mason and Dassat (1954); 6. Yalcin and Bichard (1964a); 7. Dry (1936); 8. Karam (1957); 9. Ragab and Asker (1954); 10. Gjedrem (1966); 11. Sidwell, et al., (1962); 12. Valik, et al., (1968)

Hansson (1943), Desai and Winters (1951a), Wright and Stevens (1953), Wallace (1958), Belic (1958), Riches (1958), Teodoreanu and Rusu (1959) Sharafeldin (1960), Polach (1960), Bernoco (1961), Maymone and Dattilo (1962), Hulet, et al. (1962), Campbell (1962), Dhaliwal, et al.

(1963), Joustra (1964), Sannikov (1964), Polasek (1965), Ermekov and Makbuzov (1966), Fehse (1966), Bichard and Cooper (1966) Maijala (1966), Donald and Read (1967), Potanina (1967), Donald, et al. (1968), De Haas and Dunlop (1969) and Eikje (1971). These references cover a wide range of breeds and countries.

(b) Date of lambing within the lambing season

Reeve and Robertson (1953) when they reviewed the effect of the position of birth in the lambing season concluded:

> "There may well be differences between breeds and between regions in the shape of the curve for changes in fertility with season of birth, due to climatic and other factors, but it seems likely that the maximum rate of twinning will be in the middle rather than at the beginning of the lambing season".

Their review mentioned the results and conclusions of Heape (1899), Marshall (1908), Nichols (1924) and Biegert (1938) who concluded that twins tended to be born early in the season and Johansson and Hansson (1943) and Hammond Jr. (1944) who found that the peak, of lambs born per fertile service, occurred near the middle of the lambing season. Hammond Jr. found that the variation during the lambing season could be attributed to a progressive change in the number of ova shed. More recent work by Karam (1957) and Mason and Dassat (1954) confirm the trend of a mid-season peak while results by Ragab and Asker (1954), Teodoreanu and Rusu (1959) and Potanina (1967), all reporting a higher lambing percentage in the first half of the lambing season, give support to the alternative proposal. It is interesting to look back on the two possibilities attributed by Marshall and Potts (1921) to explain the observation that twin lambs were produced mainly in the early part of the lambing season. The possible causes given were (1) the ewes in the best condition would tend to come on heat and therefore to lamb first, or (2) the feed and pastures are more nutritious early in the season and causes production of more ova by the ewes bred at that time.

If a peak in the middle of the lambing season is assumed the natural situation then factors which could camouflage it are (1) the time a flock is mated may be near the peak of the sexual cycle so all the first part of the natural lambing season would be removed. The observer would then observe a early high lambing rate which would subsequently decline. (2) If a flock is mated near the beginning of the sexual cycle then presumably the ewes lambing early in the season would be the more fertile animals as the less fertile animals would take longer to conceive. The less fertile animals may begin cycling later in the season or due to a lower proportion of ova may at first be less likely to be fertilised. (3) During the mating season the nutition may greatly affect the number of ova shed by the ewe. Flushing, which is the increased level of nutition often given the ewe immediately before joining, has been found to increase multiple births and decrease barrenness (reviewed by Reeve and Robertson, 1953).

(c) Effect of the body weight of the ewe.

There is evidence available that the weight of the ewe is positively associated with the number of lambs she produces (Terrill and Stoehr, 1942, with Columbias, Corriedales and Rambouillets; Coop, 1962 with Corriedales and Romneys; Coop and Clark, 1966, with Merinos and Halfbreds and Killeen, 1967, with Border Leicester x Merinos). Cockrem (1967) does not agree with the interpretation of the data presented by Coop and Clark which discusses the influence of liveweight on reproduction. Cockrem claims that culling on liveweight would not overcome the problem of barren ewes to any great extent. Terrill and Stoehr found that ewes which were heavier in the autumn as yearlings, on the average, weaned more pounds of lamb per ewe-year during their lifetime. This advantage of the heavier ewes was due more to a higher percent of lambs weaned than to heavier weaning weights.

Sannikov (1964) and Pelasek (1965) both found the twinning incidence increased (30.1 to 59.4 percent and 2.2 to 45.3 percent respecitively) with increasing ewe weight. Similar results were found by Gjedrem (1966), with Dala and Steigar breads, measuring number born and number weaned per ewe lambing and Potanina (1967), with the Dagestan Mountain bred, measuring lambing percentage. De Haas and Dunlop (1969), on working with the Australian Merino, found a difference in premating body weight has its greatest effect in increasing multiple births. Most of this comes from a decrease in single births with a lesser contribution from a reduction in barren ewes. They estimated an additional 0.37 percent increase in multiply births per pound of body weight increase. Coop and Hayman (1962) estimated 0.46 percent additional twin births per pound of increased body weight in the Corriedale breed.

(d) Year effect

Ragab and Asker (1954), Karam (1957), Sharafeldin (1960), Sidwell, et al. (1962), Vesely and Peters (1965) and Valik, et al. (1968) all found that the year of lambing had a significant effect on various measures of reproductive rate. The breeds referred to were Ossimi, Rahmani, Texel and groups of five, four and five breeds respectively. Goot (1952b) found, for the N.Z. Romney, that the difference between years was highly significant for number tailed per ewe mated and was significant for the number of multiple births per ewe mated.

3. Partitioning the components of variance

Goot (1952a and b), Dunlop (1963), Vesely and Peters (1965) and De Haas and Dunlop (1968) have given estimates for the partitioning of the components of variance for measures of reproductive rate. Table 11 presents the results of Dunlop and De Haas and Dunlop.

Table 11: Partitioning the variance components for measures of reproductive rate in Australian Merinos

Variance due to	No born / ewe mated		No weaned / ewe mated		Dry ewes	Single births	Multi births
	young	base	young	base			
Locations	1.4	1.5	4.1	1.2	0	1.2	1.9
Years	0.1	0.7	0	0	0	0	0
Strains	0.6	0.6	0.4	0.5	0.4	0.4	0
Loc x age	-	-	-	-	0.7	1.6	2.5
Loc x yrs	6.1[a]	4.3[c]	4.9[b]	8.5[d]	7.2	3.2	0.6
Loc x str	1.2	0.7	0.3	0.3	1.3	1.4	0.5
Str x yrs	0	0	0.6	0.4	-	-	-
Loc x str x yr	1.5	0.7	1.3	0.5	-	-	-
Error	89.2	91.5	88.3	88.6	90.5	92.2	94.5
References	(1)	(1)	(1)	(1)	(2)	(2)	(2)

a - significant in 1 of 3 age groups
b - significant in 2 of 3 age groups
c - significant at 1% level
d - significant at 0.1% level

References: 1. Dunlop (1963); 2. De Haas and Dunlop (1968)

Both Dunlop and De Haas and Dunlop commented that the most striking feature was the extremely large size of the error variance

Table 12: Partitioning the variance components for measures of reproductive rate in N.Z. Romneys

Variance due to	Barrenness	No tailed / ewe mated	No multi birth / ewe mated
Year	10.74		
Age	43.11	72.3	66.8
Stud			3.7
Year x age	11.42	10.5	6.1
Year x stud	7.06	6.6	3.8
Age x stud x year	27.66	10.6	19.6
References: Coot	1952a	1952b	1952b

and the small amount of variation controlled by main effects and interactions. They felt it likely that the large error term was due in part to the rather coarse units in which values are measured. As a result of the large error variance, other classes of variation are necessarily small when expressed as fractions of the total. The results of Vesely and Peters, who studied four breeds, were in general agreement with the above. They used ewes lambing per ewes mated (fertility), lambs born per ewes lambing (prolificacy), lambs weaned per ewe mated and weight of lambs weaned per ewe mated as their measures of reproductive ability. Year effects were significant ($P < 0.01$) for all measures. 2-year-old ewes were inferior ($P < 0.01$) to middle aged ewes in all traits but fertility. However all factors together (year, age of dam, sex, type of birth and breed) represented 2, 9, 4 and 6 percent of the total variability of fertility, prolificacy, number of lambs weaned and weight of lambs weaned per ewe mated respectively. These figures give error variances of 98, 91, 96 and 94 percent respectively which are even higher than those given for the Australian Merino. Goot when he partitioned the variance components for the N.Z. Romney did not consider the error terms so his percentages were based on the total variance less the error term. The results are given in Table 12.

In both measures the age of dam is of major importance amongst the environmental effects.

4. Estimates of repeatability and heritability

Instead of measuring the heritability of reproductive rate many authors have compared the number of lambs born by single- and multiple-born ewes. Various estimates obtained have been reviewed by Reeve and Robertson (1953), Clarke (1963) and Turner (1969). Multiple-born ewes have generally produced more lambs than single-born ewes though the differences are not great. Two additional references which further support the superiority of the multiple-born ewes are Dun and Grewal (1963) and Sannikov (1964). As this thesis does not calculate any comparable values for the flock being considered the discussion of the effect of birth rank of the dam will be carried no further.

(i) Repeatability

The repeatability of fertility refers to the consistency of the reproductive performance of the same ewe at different lambings. On using the intra-class correlation method the estimates are normally low.

Clarke (1963) and Turner (1969) have reviewed the literature of repeatability of reproductive ability. In the following review the various measures of reproductive ability are arranged in a similar order to that used above for looking at the effect of age of dam.

(a) Barrenness (ewes failing to lamb)

Purser (1965) found that the repeatability of barren ewes per ewe joined was low for both the Scottish Blackface and Welsh Mountain breeds: 0.09 and 0.08 respectively. The Scottish Blackface were aged from 2- to 6-years and the Welsh Mountain from 2- to 4-years of age. Shelton (1969) estimated the repeatability in two flocks of fine wool sheep to be 0.04 with an actual negative value in one flock.

(b) Number born per ewe joined

Turner, et al., (1953), Young, et al., (1963) and Kennedy (1967) all give results for the Australian Merino. Turner, et al., with a flock of medium Peppin Merinos calculated a repeatability of 0.30 over four successive years for ewes aged from 7- to 10-years. Young, et al., obtained repeatability estimates for three flocks, for ewes aged 2- to 7-years, ranging from 0.01 to 0.09 which, when pooled, gave an overall value of 0.05. This compares favourably with 0.07 obtained by Kennedy on Peppin Merinos aged 2- to 5-years. Roberts (1957) (as quoted by Young, et al., 1963) reported an estimate of repeatability for the number of lambs born to be about 0.1 in five strains of Australian Merinos. The data available for this work were, however, limited.

Ch'ang (1955) using a technique for measuring the amount of association in discrete data obtained values of 0.12 to 0.25 for repeatability in the N.Z. Romney.

Purser (1965) obtained repeatabilities of 0.07 and 0.10 with the Scottish Blackface (2- to 6-years) and Welsh Mountain (2- to 4-years) breeds respectively. These closely agree with Sharafeldin's

(1960) results of 0.10 and 0.07 (quoted by Yalcin and Bichard, 1964b) for two strains of Texel. Inskeep, et al., (1967) found a wider range (0 to 0.21) for various breeding groups although the average of 0.11 is of similar order to the estimates of the other workers; the age of the ewes in this case varied from 2- to 11-years. Desai and Winters (1951b) estimated a repeatability of 0.05 for various breeds.

(c) Number weaned per ewe joined

Results for the Australian Merino are given by Kennedy (1967) and Young, et al., (1963). Kennedy's result was 0.04 for Peppin Merinos aged 2- to 5-years. Young, et al., obtained a slightly higher estimate (0.08) when they pooled the results of three flocks (these ranged from 0.02 to 0.10). While Scottish Blackface and Welsh Mountain results of 0.01 and 0.07 obtained by Purser (1965) were lower than the corresponding repeatabilities of the number born per ewe joined Inskeep, et al., (1967) get a slightly higher value. Inskeep, et al., got values ranging from 0.03 to 0.22 with an average of 0.13 for various breeding groups.

(d) Number born per ewe lambing

Johansson and Hansson (1943) (quoted by Reeve and Robertson, 1953) obtained various estimates for various breeds. When they measured repeatability for litter size at 2- and 3-years of age as a correlation they got estimates of 0.15, 0.17 and 0.19 for Shropshire, Cheviot and Swedish Landrace breeds respectively. The correlation between the average litter sizes at 2- to 3-years and 4- to 5-years of age for the same three breeds were 0.25,0.26 and 0.28 respectively.

Shelton (1969) estimated the repeatability to be 0.13 in 2 flocks of fine wool sheep.

Yalcin and Bichard (1964b) estimated repeatabilities on three flocks of Border Leicester x Cheviot ewes. Ewes lambed at ages of 1- to 7-years. In the flock where ewes first lambed as 1-year-olds the repeatability was 0.035 while in the flock which first lambed as 2-year-olds the repeatability was 0.121. The value obtained in a third flock was 0.033. Purser (1965) got values of 0.19 and 0.24 for the Scottish Blackface and Welsh Mountain breeds respectively. Using four flocks of Polish Merino Knothe (1964) calculated a repeatability of 0.13.

Karam (1957), working with the Rahmani breed calculated the correlation between any two lambing records of a ewe between 2- and 7-years of age as 0.06. The correlation between the first and second lambing was 0.05. When the average of the first and second lambings was correlated with the average of the third and fourth lambings the repeatability was increased to 0.225.

Rendel (1956) estimated the repeatability of multiple births amongst births for ewes having at least five births. The repeatability he obtained for the Swedish Landrace, Cheviot, Oxforddown and Shropshire were 0.06, 0.15, 0.09 and 0.09 respectively.

Mason and Dassat (1954) estimated a repeatability of 0.03 for the Langhe breed were some ewes lived to 12-years of age.

(e) Number weaned per ewe lambing

Yalcin and Bichard (1964b) working with three flocks of Border Leicester x Cheviot ewes found repeatabilities of 0.08, 0.10 and 0. The first flock first lambed as 1-year-olds and the second as 2-year-olds. The third flock was a separate one. Ewes lambed at ages varying from 1- to 7-years. Purser (1965) calculated repeatabilities of 0.07 and 0.10 for Scottish Blackface and Welsh Mountain breeds respectively. The animals in these two breeds were 2- to 6- and 2- to 4-year-olds respectively.

Estimates of repeatability obtained are usually low. The estimates based on ewes lambing rather than ewes mated are generally higher.

Another method sometimes used to estimate repeatabilities is the regression of subsequent on early performances. Turner (1963) reviews this. This method is not used in this study.

(ii) Heritability

Review of estimates of heritability for reproductive rate have been given by Reeve and Robertson (1953), Rae (1956), Clarke (1963) and Turner (1969); the latter being the most extensive. On discussing the estimation of the heritibility of reproductive rate Turner (1969) makes the following comments:

> "Estimation of the heritability of lambs born or weaned by dam-daughter regression on a single record is complicated by the fact the ewes with a zero record have no daughters. The problem is partly overcome by using half-sib analysis (though this estimate is still biased because the sires could not come from barren ewes), by including more than one record (ewes continually barren are, of course, still excluded), or by confining the analysis either to litter size or type of birth (single or multiple)."

This review of heritability looks at the estimates of the different measures of reproductive ability in the same order as the repeatability estimates were reviewed.

(a) Barrenness (ewes failing to lamb)

Purser (1965) found the heritability of barren ewes per ewe joined, using the intra-sire half-sib method, was low for both the Scottish Blackface (0.0) and Welsh Mountain (0.03) breeds respectively. The Scottish Blackface were aged from 2- to 6-years and the Welsh Mountain from 2- to 4-years of age. Shelton (1969), working with two fine wooled flocks, obtained a heritability estimate of 0.17.

(b) Number born per ewe joined

Both Kennedy (1967) and Young, et al., (1963) have given results for the Australian Merino. Kennedy analysed 2-year-old Peppin Merino ewes and arrived at a heritability of 0.20. Young, et al., obtained values of 0.03, 0.35 and 0.19 for 2-year-olds, 3-year-olds and the sum of the two ages. This shows a higher heritability estimate with an increase in age of ewe. Results from another fine wooled breed, the Rambouillet, have been given by Shelton and Menzies (1968). They calculated lifetime values of 0.21 and 0.23 using the paternal half-sib and intra-sire regression methods respectively.

Desai and Winters (1951b) determined heritability by the intra-sire regression of the lambing records of the daughters on those of their dams. Using two different methods of grouping the records of the dams and their daughters they arrived at average heritabilities of 0.03 and 0.07 for various breeds. Sharafeldin's (1960) estimates for the heritability of the Texel breed ranged from 0.03 and 0.17 and averaged 0.08. He used the intra-sire regression of daughter on dam. Karam and Ragab (1958), also using the Texel breed, obtained three estimates of heritability 0.266, 0.538 and 0.298 by daughter dam regression, intra-sire regression of daughter on dam and by half-sib correlation methods respectively. It was felt by the authors that the first method estimate was the most reliable.

Purser (1965) using the intra-sire half-sib method, found the heritability for Scottish Blackface (2- to 6-year-olds) and Welsh Mountain (2- to 4-year-olds) breeds were 0 and 0.07 respectively.

Ch'ang and Rae (1970), working with N.Z. Romneys, calculated heritabilities for the following measures of fertility: the number of lambs born per ewe at the first lambing (Fert 1) and the total number of lambs born per ewe over the first two (Fert 2) and three (Fert 3) lambings. Using the paternal half-sib correlation method the respective values were 0.05, 0.12 and 0.03 and calculating by the regression of daughter on dam the values were 0.05, 0.11 and 0.21. Kangasniemi and Timon on calculating heritability of Finnish Landrace sheep by different methods found the heritability of lifetime performances to be 0.30 to 0.50 which is high in comparison to other results. (Kangasniemi and Timon, 1966).

(c) Number weaned per ewe joined.

Once again Kennedy (1967) and Young, *et al.*, (1963) have calculated results for the Australian Merino. Kennedy's result of 0.06 was calculated for 2-year-old Peppin Merino ewes. Young, *et al.*, obtained results for 2-year-olds, 3-year-olds and the sum of 2- and 3-year-olds of 0.03, 0.15 and 0.09 respectively. Once again a higher heritability at an older age can be noted. Shelton and Menzies (1968) working with the Rambouillet calculated lifetime heritabilities of 0.22 and 0.27 using the paternal half-sib and intra-sire regression methods respectively.

Purser (1965), using the intra-sire half-sib method, found the heritability for Scottish Blackface (2- to 6-year-olds) and Welsh Mountain (2- to 4-year-olds) breeds were 0 and 0.03 respectively.

(d) Number born per ewe lambing

Johansson and Hansson (1943) made weaning weight calculations on their litter size work. In the Cheviot breed they obtained a regression of daughters on dam of 0.022 at 2-years of age. This gives a heritability of 0.044. Again, using the regression of daughters on dams to look at 3 lambings at 2- to 6-years of age, they obtained heritabilities of 0.17, 0.26, 0.13 and 0.23 for the Oxforddown, Shropshire, Cheviot and Swedish Landrace respectively. They also calculated the correlation between ewes from the same sire for the average litter size at 2- and 3-years. For Shropshires and Cheviots the intra-group correlation was 0.049 which gave a heritability of 0.196.

Purser (1965), using the intra-sire half-sib correlation of daughters lambing performance calculated heritabilities for the Scottish Blackface (aged 2- to 6-years) and Welsh Mountain (aged 2- to 4-years) breeds to be 0.14 and 0.16 respectively. A further analysis was made for each age of ewe separately i.e. using one record per daughter at a time. It was found that the heritabilities of litter-size showed a tendency to increase with age of ewes in both flocks, although this was significant (at the 1% level) only in the case of the Welsh Mountain flock. The highest heritability estimates were at the third lambins for the Welsh Mountain ewes (0.32) and at the fourth lambing for the Scottish Blackface ewes (0.31).

Valik, *et al.*, (1963) used the paternal half-sib correlation to obtain a heritability of 0.21 from two flocks of sheep (Rambouillet, Hampshire, Suffolk, Columbia and Corriedale; and Columbia and Corredale) which contained individuals age up to 8-years. Gjedrem (1966) using the paternal half-sib method estimated the heritability to be 0.03 for the Dala and Steigar breeds.

(e) Single or multiple births

Rendel (1956) estimated heritabilities of 0.22, 0.04, 0.09 and 0.03 for the Cheviot, Shropshire, Swedish Landrace and Oxford-down breeds respectively. These results were calculated on ewes that had lambed at least five times.

Sidwell (1956) estimated heritabilities for the Navajo and Navajo cross bred to be 0.12 and 0.22 for mature animals and when based only on 2-year-olds recorded estimates to be 0.40 and 0.03.

Ragab and Asker (1954) estimated the heritability for twinning in the Ossimi bred by the intra-sire regression of lambing averages of daughters on those of the dams based on the first two lambings. The value obtained was 0.036. Karam (1957), working with the Rahmani breed, estimated the type of birth of the offspring on that of the dam to be 0.04. This gives a heritability of twinning of 0.03.

Shelton (1969), using two fine wool breeds and the paternal half-sib analysis, obtained a heritability esimate of 0.121.

(f) Number weaned per ewe lambing

Gjedrem (1966) using the paternal half-sib method estimated the heritability to be 0.03 for the Dala and Steigar breeds. Purser (1965) obtained heritabilities of 0.05 for both the Scottish Blackface (2- to 6-years of age) and Welsh Mountain (2- to 4-years of age) breeds using the intra-sire half-sib correlation of daughters lambing performances.

5. Summary

It is obvious from looking at the effect of environmental factors that the age of ewe at lambing must be taken into account when considering reproductive rate. Estimates of repeatability were generally low and as repeatability sets the upper limit for heritability it is not suprising to find the heritability of reproductive rate was also low. The repeatability of number born is usually estimated as lying within the range of 0.05 to 0.30. Heritabilities are usually less than 0.20 although a few estimates are higher than this. Gains through selection in the current flock depend on repeatability; those in future generations depend on heritability. If the aim were to increase the reproductive rate within a breed then the low heritabilities and repeatabilities suggest that progress will be slow.

But it was seen by Young et al., (1963) and Purser (1965) that the age of the ewe affected the value of heritability. In both cases it was low at the first lambing but for later lambings sufficiently higher to predict that there would be a response to selection. Young et al., found the heritability estimate of number born for Australian Merinos rose form 0.03 at 2-years of age to 0.35 at 3-years of age. Purser found, when he analysed each age group of the Scottish Blackface and Welsh Mountain breeds that the heritability rose with age and the highest estimate were reached at the fourth lambing for the Scottish Blackface (0.31) and the third lambing for the Welsh Mountain (0.32). Ch'ang and Rae (1970) found the estimates of heritability rose when they considered the first, the first two, and the first three lambings (0.045, 0.111 and 0.205 respectively) if they calculated the heritability by the regression of daughter on dam. This was not the case if the heritability was calculated by paternal half-sib correlation (0.053. 0.121 and 0.032 respectively). Therefore for the N.Z. Romney greater gain per generation can be expected if selection is based on the sum of the first two lambings rather than the first lambing alone. Young, et al., also found that the heritability of the sum of the first two lambings was higher than the first lambing alone (0.19 versus 0.03) but was not as high as for the second lambing alone (0.35). It seems, then, that while the heritability of the initial lambing or lifetime lambing may be low lambings at certain ages may have higher heritabilities and worthwhile gains from selection may be attainable.

Where corresponding values of heritabilities exist for both numbers born and numbers weaned (whether it is based on ewes mated or ewes lambed) the values appear to be higher for numbers born. (Purser, 1965; Kennedy, 1967; Young, et al., 1963 but Shelton and Menzies, 1968 found no difference). This can be explained by the additional environmental effects on lambs between birth and weaning. As this is the case then more progress can be expected from selecting for number born rather than number weaned although with the latter progress can still be expected.

Results from the literature suggest that the repeatability and heritability of barrenness is low (Purser, 1965; Shelton, 1969; although the heritability of the latter was 0.17). Supporting this is the work of Turner (1966) who classed ewes as lambing or failing to lamb at 2-years of age and compared the lambing performances of daughters subsequently born to them. She found no significant difference; in fact, daughters of the ewes which failed had slightly more lambs born per ewe joined. The repeatability and heritability of litter size (the number of lambs born per ewe lambing) is higher and it would appear that more can be gained by selecting for litter size than against barrenness.

The fact that selection for multiple births is possible is borne out by progress reports from two such experiments (Wallace

1958 and 1964 with the N.Z. Romney and Turner, et al., 1962, Turner 1962, 1966 and 1968, with the Australian Merino). Turner (1968) looking at results for both selection flocks estimated the difference in multiple births between high and low groups in each had increased by 0.023 per year in the Australian Merino and 0.011 in the N.Z. Romney. In both breeds selection for multiple births has had some effect in lowering the number of dry ewes. Turner, et al., (1962) has also mentioned another small flock of Australian Merinos founded on animals from a commercial flock selected for multiple births. Animals from this group have performed even better than the high group already mentioned. One probable reason for the success in the Australian Merino flocks advanced by Turner, et al., (1962) is the fact that the environment is favourable to twinning, since selection for any characteristic is most likely to be successful in an environment which allows it to be fully expressed.

D. WEIGHT OF LAMB WEANED

The measure "Weight of lamb weaned" used in this thesis may be considered as a measure of the dam's fertility although fertility is not the only character encompassed by this measure. As well as including information on the number of lambs reared per ewe it summarises the milking and mothering ability of the ewe. To obtain these measures the weaning weight of all lambs are corrected for the effect of age of the lamb at weaning, sex and birth and rearing rank. The correction factors used in this thesis are those calculated by Clarke (1967) and later used, with one change, by the National Flock Recording Scheme (of New Zealand). These are detailed in Chapter 4A. Clarke's estimates make it necessary to consider each age of dam group within each year separately whereas the National Flock Recording Scheme corrects for age of dam effects so all dams within a year can be compared. The dams' weight of lamb weaned value for the season is the corrected weaning weight of her lamb or the sum of the corrected weaning weights of her lambs if she had more than one lamb.

Very little information from the literature is available on weight of lamb weaned. Blackwell and Henderson (1955), working with a mixed flock of Corriedale, Dorset, Hampshire and Shropshire sheep, estimated the weight of lamb weaned for the total weight of the first lamb or lambs born to a ewe. The heritability of this measure of weaning weight performance of ewes was based on the records of ewes that had weaned lambs which in turn also became dams with weaning weight data available for their offspring. 195 dams were used and this gave 195 dam offspring pairs. The estimated heritability was 0.18 ± 0.338. The repeatability of this trait was estimated to be

0.078. This could not be the true situation since repreatability is the theoretical upper limit of heritability. There were approximately three times as many degrees of freedom for ewes in estimating repeatability as there were for estimating heritability of this trait. Part of this discrepancy might be due to sampling or to the method of analysis. The weaning weights used in estimating both the heritabilities and repeatabilities were first adjusted for years, age of dam, age of lamb, sex, and in the case of the Dorset for season of birth as well. The adjusted weights of twins were added together to make a single observation for the ewe.

Knothe (1964) working with data from pedigree flocks of Polish Merinos calculated the repeatability of weight of lambs per ewe at weaning as 0.16. The analysis was done within flock, year of birth and sire and records were adjusted for sex.

Hullet, et al., (1969) use the measure weight of lamb weaned and cumulative weight of lamb weaned and state that the latter is probably the most important lamb production traits. The year of birth, type of birth and inbreeding of the ewe were included as independent variables in the mathematical model. Records were made within age groups and also accumulated by age groups. Ercanbrack, et al., (1968) discussed the gentic progress obtained using a selection index which included weight of lamb weaned.

III. SOURCE OF DATA

III. SOURCE OF DATA

The data used in this study was obtained from a random flock of New Zealand Romney sheep kept at Massey University. The earliest data used were hogget fleece weights recorded in 1956 on the 1955 crop of lambs. As age of dam of these hoggets is considered, the data thus refer back to dams born as early as 1950, as these were full mouth dams to the 1955 crop of lambs. The latest records considered were lambing records in 1966. This flock has been described by Ch'ang (1955 and 1967), Rae (1958), Clarke (1963) and Tripathy (1966).

A. HISTORY AND MANAGEMENT OF THE FLOCK

This flock was originally established in 1944 to investigate the inheritance of many fleece and carcase characteristics of the New Zealand Romney breed. Information on other characters, including the lambing performance of the ewes, was collected as a part of this investigation. Ewes were purchased in 1944 and 1945 and from then on all ewe replacements were bred in the flock. Up until and including 1948 this flock was run on the Pahiatua Block of the Massey University sheep farm. Early in 1949 the flock was transferred to the Tuapaka Farm where it was mainly run on the flats.

Early in 1956 (before mating) a random selection of ewes was taken from the flock to start a separate selection experiment. In 1966 (before mating) the flock was divided at random into two units, the "intensive" and "control", which were run at a high and low stocking rate respectively. Although both are still randomly bred the "control" unit is essentially a continuation of the original flock. Hence, only the data from it has been used in 1966.

The aim of this flock is to have available for study a flock of randomly bred animals. To keep this flock random certain practices are observed:

(1) No selection for any character is practised. Surplus ewes if any are culled at random. After four lambing seasons the ewes are all culled and sold or go into other experimental flocks, as do the culled 2-tooths. The wether lambs are slaughtered.

(2) Each year the flock was randomly divided among the rams available for mating with the proviso that the four age groups of ewes were evenly distributed among the rams.

(3) From 1950 to 1952 inclusive the same seven rams were used. At this stage it was the policy to use the same ram for three consecutive seasons and then change them. These seven rams all came from different studs in the Manawatu-Wairarapa. This policy allowed the assumption to be made that inbreeding was not an important source of variation in this flock. Again from 1953 to 1955 inclusive seven rams were used, but in 1955 one was replaced and another was added in to make eight. Only four of these were bought in (including one of the extra ones in 1955) and the other five were all from the Massey Romney Stud. In 1956 four of the 1955 rams were again used (three of Massey breeding and one bought in). In 1957 and 1958 four Massey stud rams were used for the two seasons. From 1959 on all the rams used came from the P.T. and Massey stud flocks. The rams were changed each year and the number of rams used gradually increased from five in 1959

to ten in 1967.

(4) Up until and including 1965 mating groups were confined to their respective paddocks for a period of six to eight weeks. Since 1965 the ewes at mating time have been run with two vasectomised rams. Ewes marked by a vasectomised ram were hand mated to an entire ram and then placed in a second mob with another vasectomised ram to note if they returned again. If they did then they were again hand mated with an entire ram. For the rest of the year the mob was run together except during lambing when the ewes were drafted into three mobs; early, mid and late according to lambing date. Except where the mating policy necessitated the dividing into mating groups the management of the flock was typical of the Manawatu district. One further exception is that no effort was made to give preferential treatment to individual animals. It was hoped in this way to avoid any environmentally induced correlations between parents and offspring and between members of half-sib groups.

B. DATA AND DATA COLLECTION.

(1) The annual lambing lists supply information on:

(a) the date the lamb was born

(b) the birth rank of the lamb: single, twin or triplet

(c) sex of the lamb; ram or ewe

(d) any deaths occurring from birth to weaning

(e) the eartag number of the dam.

(2) The annual mating list supplies the number of the sire to which the dam was mated.

(3) The annual weaning lists supply:

(a) the date the lambs were weaned. From 1955 to 1966 this was always in the range 25th November to 12th December excepting 1955 itself when it was on the 17th November

(b) the weight of the lamb when it was weaned to the nearest pound

(c) a record of the lambs actually weaned.

(4) The annual hogget shearing lists provide the weight of the hogget greasy fleece to the nearest tenth of a pound. In the years 1956 to 1966 this shearing took place in early October (1st to 19th) when the hoggets were just over a year old. The animals had previously been shorn as lambs after weaning. Consequently hogget fleece weight refers to ten months growth.

C. THE CASE OF THE INFERTILE RAMS USED IN 1962

In 1962 six rams were used, each mated to approximately 64 ewes. At lambing time it was found that, of the 376 ewes present 207 or 55.3 percent were dry. Considering the lambings from 1955 to 1966, excluding the 1962 lambing, 2926 ewes were present at mating and lambing and only 421 or 14.4 percent of these were dry. The individual ram performances in 1962 were:

Ram 1: 29 dry out of 62 present = 46.8% dry
Ram 2: 61 dry out of 61 present = 100.0% dry
Ram 3: 35 dry out of 66 present = 53.0% dry
Ram 4: 39 dry out of 65 present = 60.0% dry
Ram 5: 11 dry out of 60 present = 18.3% dry
Ram 6: 32 dry out of 60 present = 53.3% dry

Consequently, because of the markedly reduced fertility of the rams in this year, the 1962 lambing data has been excluded from the calculations of fertility estimates.

IV THE MEASUREMENTS USED IN THE STUDY

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A. CORRECTION FACTORS FOR ESTIMATING WEIGHT OF LAMB WEANED

In this thesis the "weight of lamb weaned" (Wt.L.W.) may be considered as a measure of the dam's fertility although fertility is not the only character encompassed by this measure. The Wt.L.W. is a measure workedout for each dam at the weaning of her lambs. It is calculated using the figures of Clarke (1967) who said of it:-

> "This includes the information on the number of lambs reared per ewe plus information on the milking and mothering ability of the ewe. It can be measured only on the ewe; the only indication of the ram's ability to breed daughters with high lamb production comes from the performance of his female relatives. (...)
>
> "Fertility is clearly affected by differences between years and between ages of dams. In this recording scheme adjustment for these effects is achieved by expressing the Wt.L.W. as a deviation from the mean of the year-age group class to which the dam belongs. It is also necessary to correct for the age of the lamb at weaning, sex, birth rank, and rearing rank. The following correction factors are being used:
>
> Single lamb reared as single: No correction
> Singles lamb reared as twin: Add 10 lb
> Twin reared as twin: Add 10 lb

Twin reared as single: Add 7 lb

Triplet reared as triplet: Add 15 lb

Triplet reared as twin: Add 12 lb

Triplet reared as single: Add 10 lb

To correct for sex: Add 4 lb to the weaning weight of the ewe lamb to adjust to ram lamb basis.

To correct for age at weaning: Add or subtract 0.3 lb for every day under or over a standard age of 100 days.

"The latter correction may under estimate the growth rate of lambs under some situations. However, if it is in error, the error is in the right direction since it penalizes the late lamb and praises the early lamb, which is in line with the requirements of most breeders."

The reasons for using Clarke's figures is that they are used by the National Flock Recording Scheme operated by the Sheep and Wool Division of the New Zealand Department of Agriculture. The only difference is they add 5 and 2 lb to a lamb born to a 2-tooth and 4-tooth respectively so as to pool all the ewes together (Manual National Flock Recording Scheme) whereas Clarke recommended to consider each age group separately. The latter is the method followed in this thesis.

B. THE MEASUREMENTS OF REPRODUCTIVE RATE

In this thesis three measures of ewe fertility are used. The first "number of lambs born" corresponds to stage 3, as discussed in the review of literature (Chapter 2C). The second measure "number of lambs alive at day two" corresponds to stage 4 and the third "number of lambs weaned" to stage 5 which is a profitable age for many New Zealand farmers. When considering measures of reproductive rate in the literature, the number of lambs at any stage is usually compared to a base of "ewes mated" or "ewes mated and present at lambing" or "ewes lambing". In this thesis "ewes mated and present at lambing" has been used as the base because this includes all those ewes which have a chance to show their potential. To have used the number of ewes mated as base would have meant, in cases where a ewe had died after mating but before parturition, that some ewes who were unable to display their potential would have been classed as having been "dry". Similarly considering only "ewes lambing" would have ignored all the dry ewes and thus would not give a true summary of the flocks ability.

The "number of lambs born (alive and dead) per ewe mated and present at lambing" (No. Born) is the first expression of the ewes fertility that is measurable by the farmer. Each ewe at each lambing is given a score of 0 (for drys), 1,2,3 or 4 (in one case only). Where a ewe aborted or has an obviously premature lamb this was taken as none born, as the No. born is a measure of the ewes capability to carry zygotes to the full term.

The "number of lambs alive at day two per ewe mated and present at lambing" (A.D.2) is a measure of the number born less those that are born dead or die at birth and shortly afterwards. In other words it includes all those that have survived their first day after parturition.

The "number of lambs weaned per ewe mated and present at lambing" (No. weaned) includes all those lambs which are still present on their mothers at weaning time. Where a lamb had to be fostered on to another ewe this was treated as if it had died and was deleted from the credit of the ewe in both the A.D.2. and No. Weaned cases. Weaning is important as it is not only an age at which sale of surplus stock commonly takes place but also marks the end of one biological ere in the life of the offspring and its dam.

Three further fertility characters, all of them special cases of No. Born, are analysed in this thesis. They are "Barrenness", "Multiple Births" and "Triplet Births". The "ewes not lambing but mated and present at lambing" (Barrenness) is measured by giving dry ewes a score of 0 and those with one or more lambs born (alive or dead) a score of 1. Multiple births is a measure of the ewes who are mated and present at lambing who have two or more lambs born (alive or dead). Those ewes with none or one lamb born are given a score of 0 and those with two or more lambs born are given a score of 1. Triplet Births is a measure of the ewes who are mated and present at lambing who have three or more lambs born (alive or dead). Those ewes with none one or two lambs born are given a score of 0 and those with three or more lambs born are given a score of 1.

V METHOD OF ANALYSIS AND RESULTS

V METHOD OF ANALYSIS AND RESULTS

A. ESTIMATION OF ENVIRONMENTAL EFFECTS

When numerical data is being analysed in order to make a genetic assessment of a quantitative character, it is essential to know to what extent various environmental factors influence the character. Once the effects of these factors are estimated then the records for each sheep can be adjusted so that the variation caused by these known environmental fact rs is removed and a more accurate picture of the sheep's genetic worth is obtained. Reviewing the available literature on each character gives a good idea of likely sources of environmental effects. By analysing a model incorporating these factors, the magnitude of the effect of the various environmental factors can be estimated.

1. Least squares model

Yates (1934) put forward the method of least squares for the analysis of multiple classification tables with disproportionate subclass numbers. Hazel (1946) extended Yates' method to include independent variables. The method used in this study is similar to that of Hazel (1946) and Kempthorne (1952) aided by the examples presented by Harvey (1960).

The characters studied, and for which environmental factors are evaluated, are weaning weight, fleece weight, No. Born, AD2, No. weaned, Barrenness, Multiple Births, Triplet Births, and Weight of Lamb Weaned (Wt.L.W.). Of these the model for weaning weight is the most complex and so it will be considered in detail first, and some calculations involving it set out in an appendix, as an example.

From the review of literature the environmental factors appearing most likely to be of importance in affecting weaning weight are year of birth, age of dam, type of birth and rearing, sex of lamb and the age of the lamb at weaning. Percentage inbreeding was not considered as this flock was randomly bred and of sufficient size that inbreeding levels were likely to be low. The data used in studying the environmental effects on weaning weight were based on animals born over the period of ten years from 1956 to 1965 inclusive.

The model used to represent a record of the weaning weight of a lamb was:

$$y_{ijklm} = \alpha + t_i + a_j + b_k + c_l + dx_{ijklm} + e_{ijklm}$$

$i = 1,2,\ldots,p$

$j = 1,2,\ldots,q$

$k = 1,2,\ldots,r$

$l = 1,2,\ldots,s$

$m = 1,2,\ldots,n_{ijkl}$

The y_{ijklm} is the record of the m^{th} individual born in the i^{th} year, reared by the j^{th} age group of dam and belonging to the k^{th} type of birth and rearing class and the l^{th} sex.

α is the overall mean when $x_{ijklm} = 0$.

The t_i is an effect common to all records of a character measured on individuals born in the i^{th} year. The effect is a measure of the variation of the data casued by the environmental conditions Peculiar to each year. This measure is similar to the meaning one conveys when speaking of a good or bad season where all environmental effects are combined and summarised. As well as including the obvious factors of rainfall, temperature, etc., stocking rate, management, parasites, etc., also are involved.

The a_j is the effect due to the age of dam. The four ages present in the flock were a_1 = 2-year-olds (2-tooths), a_2 = 3-year-olds (4-tooths), a_3 = 4-year-olds (6-tooths), and a_4 = 5-year-olds (full mouths).

The b_k is the effect due to type of birth and rearing which has three classes: b_1 = single lamb reared as a single, b_2 = twin reared as a single and b_3 = twin reared as a twin. In the data were 26 triplet births and one quadruplet birth. Because of their very small number, they were included as twins.

The c_l is the effect due to sex of the lamb where c_1 = wether (castrated at 2-3 weeks) and c_2 = ewe lambs.

The x_{ijklm} is the date of birth (in days) of the m^{th} individual born in the i^{th} year, reared by the j^{th} age group of dam and belonging to the k^{th} type of birth and rearing class and the l^{th} sex. The d is a linear partial regression coefficient measuring the average change in value of y_{ijklm} for the difference of one day of age.

To obtain $\hat{\mu}$, the overall mean when equal subclass numbers exist, the equation $\hat{\mu} = \hat{\alpha} + \hat{d}\bar{x}$ is used, where $\bar{x}$ is the arithmetic mean of the x_{ijklm}.

The e_{ijklm} is the error peculiar to each datum. It is the difference between the expected value calculated from the environmental effects of the model and the actual value obtained. It is due to other effects not taken into account by the model including the effect due to sire. The e_{ijklm} are assumed to have zero mean, constant variance and a normal distribution.

In practice, the matrix of coefficients of the least squares equations is obtained by counting the number of times each parameter occurs in the subclass totals for each subclass in the data. The number of lambs in each of the classifications for weaning weight can be seen in Matrix 1 (table 13).

Matrix 2 (table 14) was used to determine the environmental factors for hogget greasy fleece weight. The data in this model came from eight years, 1955-1962 inclusive. The year in each case refers to the year the hoggets were born not the following year in which the fleece weight measurement was taken. Once again the year effect is a measure of the variation in the data caused by environmental conditions, up until the hogget is shorn, peculiar to each year. The model used for the evaluation of the effect of environmental factors on the hogget greasy weight was:

$$y_{ijkl} = \alpha + t_i + a_j + b_k + dx_{ijkl} + e_{ijkl}.$$

The parameters of the model are similar to those for weaning weight with the exception that the c_1 term (for sex effect) is not included as the data were only taken from ewe hoggets.

Matrix 3 (table 15) contains the data for determining the environmental factors effecting No. Born, AD2, No. Weaned, Barrenness, Multiple Births, Triplet Births and Wt.L.W. The model used to estimate these characters is:

$$y_{ijkl} = \mu + t_i + a_j + e_{ijk}.$$

The y_{ijk} is the record of the kth observation in the ith year occurring in a ewe of jth age.

The μ is the mean of all records of a character when equal frequencies exist in each subclass.

The t_i is an effect common to all records measured on the ewe as a dam in the ith year. Records were taken in eleven years from

Table 13: Matrix 1: Least-squares equations for weaning weight

	$\hat{\alpha}$	$\hat{t}_1$	$\hat{t}_2$	$\hat{t}_3$	$\hat{t}_4$	$\hat{t}_5$	$\hat{t}_6$	$\hat{t}_7$	$\hat{t}_8$	$\hat{t}_9$	$\hat{t}_{10}$	$\hat{b}_1$	$\hat{b}_2$	$\hat{b}_3$	$\hat{c}_1$	$\hat{c}_2$	$\hat{a}_1$	$\hat{a}_2$	$\hat{a}_3$	$\hat{a}_4$	$\hat{d}$	R.H.M.
α:	2904	164	167	263	207	259	334	206	422	449	433	1348	221	1335	1401	1503	640	768	783	713	77028	160,320
t_1:	164	164										84	18	62	79	85	35	44	46	39	3759	10,773
t_2:	167		167									109	22	36	76	91	31	42	38	56	3544	11,296
t_3:	263			263								93	20	150	129	134	58	61	90	54	6998	14,358
t_4:	207				207							89	20	98	103	104	41	62	55	49	5776	11,213
t_5:	259					259						162	17	80	133	126	57	61	64	77	5338	13,895
t_6:	334						334					112	28	194	172	162	73	92	86	83	10078	15,064
t_7:	206							206				86	7	113	85	121	37	44	68	57	8551	10,337
t_8:	422								422			180	34	208	213	209	94	115	112	101	12222	23,139
t_9:	449									449		200	31	218	217	232	111	124	118	96	12385	25,848
t_{10}:	433										433	233	24	176	194	239	103	123	106	101	8377	24,397
b_1:	1348	84	109	93	89	162	112	86	180	200	233	1348			668	680	203	284	405	456	34276	81,086
b_2:	221	18	22	20	20	17	28	7	34	31	24		221		99	122	65	47	64	45	5763	12,621
b_3:	1335	62	36	150	98	80	194	113	208	218	176			1335	634	701	372	437	314	212	36989	66,613
c_1:	1401	79	76	129	103	133	172	85	213	217	194	668	99	634	1401		315	339	384	363	37594	79,598
c_2:	1503	85	91	134	104	126	162	121	209	232	239	680	122	701		1503	325	429	399	350	39434	80,722
a_1:	640	35	31	58	41	57	73	37	94	111	103	203	65	372	315	325	640				16332	35,900
a_2:	768	44	42	61	62	61	92	44	115	124	123	284	47	437	339	429		768			19805	42,734
a_3:	783	46	38	90	55	64	86	68	112	118	106	405	64	314	384	399			783		20150	43,990
a_4:	713	39	56	54	49	77	83	57	101	96	101	456	45	212	363	350				713	20741	37,696
d:	77028	3759	3544	6998	5776	5338	10078	8551	12222	12385	8377	34276	5763	36989	37594	39434	16332	19805	20150	20741	2472822	4,072,599

Table 14: Matrix 2: Least-squires equations for fleece weight

	$\hat{\alpha}$	$\hat{t}_1$	$\hat{t}_2$	$\hat{t}_3$	$\hat{t}_4$	$\hat{t}_5$	$\hat{t}_6$	$\hat{t}_7$	$\hat{t}_8$	$\hat{b}_1$	$\hat{b}_2$	$\hat{b}_3$	$\hat{a}_1$	$\hat{a}_2$	$\hat{a}_3$	$\hat{a}_4$	$\hat{d}$	R.H.M.
α:	892	160	64	82	110	100	122	137	117	401	79	412	234	267	229	162	24,194	180,119.3
t_1:	160	160								69	10	81	52	59	37	12	4462	1053.8
t_2:	64		64							32	8	24	12	18	19	15	1324	478.2
t_3:	82			82						52	15	15	31	19	16	16	1721	617.9
t_4:	110				110					35	9	66	17	39	33	21	2771	873.2
t_5:	100					100				44	11	45	24	22	36	18	2761	620.5
t_6:	122						122			79	8	35	34	34	31	23	2321	326.6
t_7:	137							137		45	12	80	33	34	35	35	4070	1098.4
t_8:	117								117	45	6	66	31	42	22	22	4764	1042.4
b_1:	401	69	32	52	35	44	79	45	45	401			143	120	80	58	10657	3009.8
b_2:	79	10	8	15	9	11	8	12	6		79		21	20	19	19	1970	562.9
b_3:	412	81	24	15	66	45	35	80	66			412	70	127	130	85	11567	3038.3
a_1:	234	52	12	31	17	24	34	33	31	143	21	70	234				6894	1646.0
a_2:	267	59	18	19	39	22	34	34	42	120	20	127		267			7241	1994.3
a_3:	229	37	19	16	33	36	31	35	22	80	19	130			229		6029	1701.9
a_4:	162	12	15	16	21	18	23	35	22	58	19	85				162	4030	1268.8
d:	24194	4462	1324	1721	2771	2761	2321	4070	4764	10657	1970	11567	6894	7241	6029	4030	808,699	180,032.3

Table 15: Matrix 3: Least-squares equations for measures of reproductive rate

	$\hat{\alpha}$	$\hat{t}_1$	$\hat{t}_2$	$\hat{t}_3$	$\hat{t}_4$	$\hat{t}_6$	$\hat{t}_5$	$\hat{t}_7$	$\hat{t}_8$	$\hat{t}_9$	$\hat{t}_{10}$	$\hat{t}_{11}$	$\hat{a}_1$	$\hat{a}_2$	$\hat{a}_3$	$\hat{a}_4$	No born	AD2	No wean	Wt.L.W.	Barren	Multi	Trip
α:	2926	398	172	227	238	247	302	320	420	321	219	62	813	764	736	613	3518	3108	2828	179,032.6	2505	988	28
t_1:	398	398											181	115	83	19	477	414	365	22,977.0	352	125	1
t_2:	172		172										52	45	42	33	199	181	164	11,404.3	145	53	1
t_3:	227			227									84	54	46	43	217	186	167	11,545.1	173	45	0
t_4:	238				238								64	82	51	41	324	288	264	16,758.3	215	108	1
t_5:	247					247							87	61	54	45	256	225	206	12,936.7	182	74	1
t_6:	302						302						109	84	57	52	317	285	258	15,126.4	249	66	6
t_7:	320							320					102	85	80	53	421	362	333	19,128.1	274	136	7
t_8:	420								420				134	112	96	78	521	456	420	26,490.8	360	152	8
t_9:	321									321				126	107	88	425	379	351	23,530.8	292	130	3
t_{10}:	219										219				120	99	272	254	225	14,024.9	202	71	0
t_{11}:	62											62				62	89	78	75	5,110.2	61	28	0
a_1:	813	181	52	84	64	87	109	102	134				813				773	647	596	34,836.5	626	145	6
a_2:	764	115	45	54	82	61	84	85	112	126				764			904	786	716	45,613.5	664	231	12
a_3:	736	83	42	46	51	54	57	80	96	107	120				736		988	903	814	52,587.7	661	318	3
a_4:	613	19	33	43	41	45	52	53	78	88	99	62				613	853	772	702	45,977.1	554	291	7

1955 (on ewes born in 1950 to 1953) to 1966 (the ewes born in 1961 were the last to have records collected from them - as 2-year-olds in 1963, 3-year-olds in 1964, 4-year-olds in 1965 and 5-year-olds in 1966) inclusive with the exception that 1962 data were excluded for reasons already given (Chpt. IIIC).

The a_j is the effect due to the age of the ewe at which the record was taken, where a_1 is a 2-year-old, a_2 a 3-year-olds, a_3 a 4-year-old and a_4 a 5-year-old.

Each matrix has a right hand margin (RHM) for each character being assessed by the matrix. In the RHM there is a value for each subclass equation. This value is the sum of the measurements of the character over all the data belonging to the subclass.

2. Solution of equations

Because the subclasses have disproportionate numbers, the method of fitting constants by the least squares procedure was used to calculate the effects specified by the model. Kempthorne (1952) described the principle of least-squares analysis and Harvey (1960) set out the steps to take, gave numerous examples, and discussed all alternative steps.

As Matrix 1 now stands the sum of the coefficients for the $\hat{t}_i$ equals the coefficient for $\hat{\alpha}$ in the α equation and the sum of the RHM's for the t_i equations equals the RHM for the α equation. Similarly for the sum of the coefficients for the $\hat{a}_j$, $\hat{b}_k$ and $\hat{c}_l$ and the a_j, b_k and c_l equations. Since this is true one cannot solve the equations until some restriction has been imposed on the constants as there are more equations than independent constants. The restriction used in this study, although not the only one available, was to let $\sum_i \hat{t}_i = \sum_j \hat{a}_j = \sum_k \hat{b}_k = \sum_l \hat{c}_l = 0$. When this restriction is imposed, the coefficients of one equation in the t_i, say t_p (and similarly one equation from a_j, b_k and c_l) must be subtracted from other coefficients by columns and rows. The subtraction of the $\hat{t}_p$ coefficients is done only within the $\hat{t}_i$ columns of coefficients. After completion of this subtraction by columns, the coefficients and RHM in the resulting t_p equation are subtracted from the corresponding coefficients and the RHM's in the other t_i equations. Similarly for the a_q, b_r and c_s equations.

Matrix 4 (Table 16) was produced from Matrix 1 by imposing the restriction $\sum_i \hat{t}_i = \sum_j \hat{a}_j = \sum_k \hat{b}_k = \sum_l \hat{c}_l = 0$. Once the simultaneous equations in the reduced Matrix are solved, the values for the subtracted factors areobtained by equating, each set of factors to zero. The value of $\hat{\mu}$ is obtained by using the formula $\hat{\mu} = \hat{\alpha} + \hat{d}\bar{x}$ already given. The values thus obtained are the values for the flock mean and the estimates of the effect of environmental factors.

The method used to solve the simultaneous equations was to use a computer program that found the inverse of the matrix, multiplied it by the RHM, and so produced the constant estimates. These could be checked by substituting these values back into the equations and comparing the answer with the corresponding RHM.

The reduction in S.S. due to fitting α, t, a, b, c and d or $R(\alpha,t,a,b,c,d)$ which is used later may be computed from all constant estimates and the original RHM's:

$$R(\alpha,t,a,b,c,d) = \hat{\alpha}Y_{....} + \hat{t}_1Y_{1...} + \dots + \hat{t}_pY_p + \dots + \hat{d}\sum_{ijklm} D_{ijklm}Y_{ijklm}$$

where the Y's are the summed weaning weight values for each equation: they are the values in the RHM of the matrix. When the restriction has been imposed then $R(\alpha,t,a,b,c,d)$ may be computed more easily from

Table 16: Matrix 4: Reduced least-squares equations for weaning weight

	$\hat{\alpha}$	$\hat{t}_1$	$\hat{t}_2$	$\hat{t}_3$	$\hat{t}_4$	$\hat{t}_5$	$\hat{t}_6$	$\hat{t}_7$	$\hat{t}_8$	$\hat{t}_9$	$\hat{b}_1$	$\hat{b}_2$	$\hat{c}_1$	$\hat{a}_1$	$\hat{a}_2$	$\hat{a}_3$	$\hat{d}$	RHM
α:	2904	-269	-266	-170	-226	-174	-99	-227	-11	16	13	-1114	-102	-73	55	70	77,028	160,320
t_1:	-269	597	433	433	433	433	433	433	433	433	-35	108	39	-6	-17	2	-4618	-13,624
t_2:	-266	433	600	433	433	433	433	433	433	433	16	138	30	-27	-36	-23	-4833	-13,101
t_3:	-170	433	433	696	433	433	433	433	433	433	-114	22	40	2	-15	31	-1379	-10,039
t_4:	-226	433	433	433	640	433	433	433	433	433	-66	74	44	-10	-9	1	-2601	-13,184
t_5:	-174	433	433	433	433	692	433	433	433	433	25	89	52	-22	-38	-18	-3039	-10,502
t_6:	-99	433	433	433	433	433	767	433	433	433	-139	-14	55	-12	-13	-2	1701	-9333
t_7:	-227	433	433	433	433	433	433	639	433	433	-84	46	9	-22	-35	6	174	-14,060
t_8:	-11	433	433	433	433	433	433	433	855	433	-85	-22	49	-9	-8	6	3845	-1258
t_9:	16	433	433	433	433	433	433	433	433	882	-75	-35	30	13	6	17	4008	1451
b_1:	13	-35	16	-114	-66	25	-139	-84	-85	-75	2683	1335	55	-413	-397	-153	-2713	14,473
b_2:	-1114	108	138	22	74	89	-14	46	-22	-35	1335	1556	44	-140	-223	-83	-31,226	-53,992
c_1:	-102	39	30	40	44	52	55	9	49	30	55	44	2904	-23	-103	-28	-1840	-1124
a_1:	-73	-6	-27	2	-10	-22	-12	-22	-9	13	-413	-140	-23	1353	713	713	-4409	-1796
a_2:	55	-17	-36	-15	-9	-38	-13	-35	-8	6	-397	-223	-103	713	1481	713	-936	5038
a_3:	70	2	-23	31	1	-18	-2	6	6	17	-153	-83	-28	713	713	1496	-591	6294
d:	77,028	-4618	-4833	-1379	-2601	-3039	1701	174	3845	4008	-2713	-31,226	-1840	-4409	-936	-591	2,472,822	4,072,599

the constant estimates and the reduced RHM's

$$R(\alpha,t,a,b,c,d) = \hat{\alpha}Y_{\cdots\cdot} + \hat{t}_1(Y_{1\cdots} - Y_{p\cdots}) + \ldots + \hat{d}\sum_{ijklm} D_{ijklm}Y_{ijklm}.$$

Matrices 2 and 3 are solved in the same manner as has been describe for Matrix 1.

3. Testing for an Interaction between Age of Dam and Birth and Rearing Effect for Weaning Weight and Hogget Fleece Weight

To test for an interaction between age of dam and birth and rearing effect on weaning weight the following model is used:

$$y_{ijklm} = \alpha + t_i + a_j + b_k + (ab)_{jk} + c_l + dx_{ijklm} + e_{ijklm}$$

where the $(ab)_{jk}$ is the interaction associated with the j^{th} age of dam and k^{th} type of birth and rearing. This type of interaction will exist if a type of birth and rearing effect has different effects for different ages of dams. For example and interaction would occur if the difference between twins reared as twins and twins reared as singles was greater for the 2-year-old age group than for the other age groups. If this were the case then the main effects a_j and b_k would not be additive. For this reason it is important to first test for such an interaction as the main purpose the main environmental effects were calculated was to use them as additive correction factors to reduce the amount of environmental variance in the data prior to genetic analysis. The numbers involved in each subclass are arranged in a matrix and to solve this matrix the restrictions $\sum_i \hat{t}_i = \sum_j \hat{a}_j = \sum_k \hat{b}_k = \sum_l \hat{c}_l = \sum_j \widehat{(ab)}_{jk} = \sum_k \widehat{(ab)}_{jk} = 0$ were first imposed. The Sum of Squares due to the interaction between age of dam and birth and rearing effect (A.B. Interaction S.S.) is found from the difference between the reduction in Sum of Squares due to fitting all the constants,

$R(\alpha,t,a,b,ab,c,d)$, and that due to fitting all the constants except the interaction effect, $R(\alpha,t,a,b,c,d)$ (this is the reduction from the original model above). The Error S.S. was calculated as the difference between the Raw S.S. (the 2904 individual weaning weights all squared and summed) and the reduction in S.S. due to fitting all constants. The interaction d.f. are equal to $(q - 1)(r - 1)$ and the error d.f.:- $n_{....} + r + q - rq - p$ s. An F test was used for a test of significance.

A similar procedure was used to test for the interaction between age of dam and type of birth and rearing effect for hogget greasy fleece weight. The model used, incorporating the interaction effect, was:

$$y_{ijklm} = \alpha + t_i + a_j + b_k + (ab)_{jk} + dx_{ijklm} + e_{ijklm} .$$

The results obtained, on testing for the interaction, are summarised in Table 17.

Table 17: Testing for the interaction between age of dam and birth and rearing effect for weaning weight and hogget fleece weight

Source of Variation	d.f.	M.S.	F.
Weaning weight			
Interaction	6	33.823	1.073 n.s.
Error	2887	31.520	
Hogget Fleece Weight			
Interaction	6	0.08116	0.055 n.s.
Error	878	1.45915	

As the interaction tested for in both cases was not significant the original model proposed is taken as suitable for calculating the effects of the environmental factors. The interaction between the age of dam and birth and rearing effect was the only interaction tested for as results of other workers discussed in the review of literature indicated it was likely to be the most important.

4. Analysis of variance of environmental effects and partitioning the variance components.

The reduction in S,S. due to fitting all the constants, $R(\alpha,t,a,b,c,d)$ (for weaning weight), was obtained from the estimates of the effects (detailed above). The various S.S. for the tests of significance of the effects were obtained in the following way:

Error S.S. $= \sum_{ijklm} Y_{ijklm} - R(\alpha,t,a,b,c,d)$

Year S.S. $= R(\alpha,t,a,b,c,d) - R(\alpha,a,b,c,d)$

Age of dam S.S. $= R(\alpha,t,a,b,c,d) - R(\alpha,t,b,c,d)$

Birth and rearing S.S. $= R(\alpha,t,a,b,c,d) - R(\alpha,t,a,c,d)$

Sex S.S. $= R(\alpha,t,a,b,c,d) - R(\alpha,t,a,b,d)$

Regression S.S. $= R(\alpha,t,a,b,c,d) - R(\alpha,t,a,b,c)$

These additional reductions are derived from the model used when all constants are fitted except that the rows and columns corresponding to the factor being tested are dropped out. For each reduction the linear model is set up, the restrictions are imposed and then the simultaneous equations are solved by matrix methods. Instead of each time setting up the linear model and imposing the restrictions the restricted matrix can be obtained directly from the restricted matrix where all constants are fitted (Table 16: Matrix 4) by simply omitting the terms being tested as required. The restricted matrix required for the reduction - $R(\alpha,a,b,c,d)$ - necessary for calculating the Year Effect is shown in Matrix 5 (Table 18) as an example. All the equations for t_i have been deleted by row and column.

Table 18: Matrix 5: Reduced least-squares equations necessary for the analysis of variance of the weaning weight year effect.

	$\hat{\alpha}$	$\hat{b}_1$	$\hat{b}_2$	$\hat{c}_1$	$\hat{a}_1$	$\hat{a}_2$	$\hat{a}_3$	$\hat{d}$	RHM
α:	2904	13	-1114	-102	-73	55	70	77,028	160,320
b_1:	13	2683	1335	55	-413	-397	-153	-2713	14,473
b_2:	-1114	1335	1556	44	-140	-223	-83	-31,226	-53,992
c_1:	-102	55	44	2904	-23	-103	-28	-1840	-1124
a_1:	-73	-413	-140	-23	1353	713	713	-4409	-1796
a_2:	55	-397	-223	-103	713	1481	713	-936	5038
a_3:	70	-153	-83	-28	713	713	1496	-591	6294
d:	77028	-2713	-31226	-1840	-4409	-936	-591	2,472,822	4,072,599

After estimatin environmental effects an analysis of the variance components is carried out to estimate the relative importance of each effect on the various traits. These variance component estimates are obtained by equating the least-squared S.S. or M.S. to their corresponding expectations and solving the resulting equations. For weaning weight the Expected M.S. (E.M.S.) are as follows:-

Source of Variation	d.f.	E.M.S.
Years	(1-p)	$\sigma_e^2 + k_4\sigma_t^2$
Age of dam	(1-q)	$\sigma_e^2 + k_3\sigma_a^2$
Birth and rearing	(1-r)	$\sigma_e^2 + k_2\sigma_b^2$
Sex	(1-l)	$\sigma_e^2 + k_1\sigma_c^2$
Regression	1	$\sigma_e^2 + k_0\sigma_d^2$
Error	difference	σ_e^2
	N.... - 1	

To find the k values, the methods of Henderson (1953) as set out by Harvey (1960) were used. The direct method of Harvey was used to find k_1, k_2 and k_3 while the indirect method is used to find k_4. These methods and the computation of the k values are set out in Appendix 2.

5. Results and discussion

The magnitude of the environmental effects, for the various characters, as calculated by least-squares analysis, are presented in Tables 19a and 19b and their tests of significance have been summarised in Tables 20a and 20b.

Table 19a: Magnitude of environmental effects as deviations from the mean.

Character	No Born	AD2	No Weaned	Barren.	Multi Birth	Trip Birth	Wt.L.W.
Mean	1.22	1.07	0.98	0.36	0.35	0.008	62.80
Year effect							
1955	.09	.08	.03	.05	.05	.005	2.24
1956	.06	.06	-.02	-.04	.04	.002	12.96
1957	-.19	-.19	-.19	-.09	-.10	-.004	-9.06
1958	.16	.16	.05	.04	.12	-.006	11.48
1959	-.18	-.13	-.09	-.07	-.03	-.013	-9.36
1960	-.26	-.19	-.17	-.04	-.19	.010	-10.39
1961	.16	.11	.11	.00	.12	.015	-.02
1963	.11	.09	.09	.03	.06	.012	4.70
1964	.06	.05	.06	.02	.30	.001	5.90
1965	-.09	-.06	-.07	.03	-.11	-.005	-8.80
1966	.08	.04	.10	.07	.01	.02	.34
Age of dam effect							
2-th	-.26	-.28	-.24	-.08	-.17	-.003	-18.53
4-th	-.05	-.06	-.05	.01	-.06	.006	-3.63
6-th	.13	.15	.13	.04	.09	-.005	9.60
F.M.	.18	.19	.16	.04	.14	.002	12.56

Table 19b: Magnitude of environmental effects as deviations from the mean.

Character	Weaning Weight	Fleece Weight
Mean α	66.10	7.82
μ	56.32	7.37
Year effect		
1955		-.75
1956	7.71	-.12
1957	8.02	-.01
1958	-.38	.51
1959	-1.17	-1.21
1960	-5.90	-.86
1961	-8.43	.68
1962	.92	1.76
1963	-.01	
1964	2.05	
1965	-2.83	
Age of dam effect		
2-th	-3.16	-.38
4-th	.02	.03
6-th	1.33	.12
F.M.	1.81	.28
Type of birth and rearing effect		
Single	4.44	.33
Twin reared singly	.83	-.20
Twin	-5.27	-.14
Sex effect		
Ram	1.74	
Ewe	-1.74	
Regression on date of birth	-.37	-.017

Table 20a: Analysis of variance of weaning weight and fleece weight

Character	Weaning weight		Fleece weight	
Source of variation	d.f.	M.S.	d.f.	M.S.
Years	9	6,343[a]	7	96.351[a]
Age of dam	3	3,242[a]	3	15.079[a]
Sex of lamb	1	8,755[a]		
Birth and rearing	2	28,563[a]	2	23.038[a]
Reg on age at measurment	1	44,556[a]	1	31.582[a]
Error	2887	31.59	878	1.460

a = significance at 1% level

Table 20b: Analysis of variance of characters measuring reproductive rate

Character		No born	AD2	No weaned	Barrenness
Source of variation	d.f.	M.S.	M.S.	M.S.	M.S.
Years	10	6.0213[a]	4.2333[a]	3.9812[a]	.9824[a]
Age of dam	3	24.7819[a]	29.0435[a]	21.3906[a]	2.1656[a]
Error	2912	.4231	.4753	.4547	.1174

Character		Multi Birth	Trip Birth	Wt.L.W.
Source of variation	d.f.	M.S.	M.S.	M.S.
Years	10	2.2315[a]	.0201[b]	24,124[a]
Age of dam	3	12.4387[a]	.0174[c]	129,218[a]
Error	2912	.2034	.0094	1839

a = significance at 1% level
b = significance at 5% level
c = not significant

The tests of significance agree with most other workers results. All the effects studied for each trait are highly significant except for the effect of years and age of dam on the number of triplets born per ewe mated. As they have significant effects these sources of environmental variation must be eliminated if an accurate assessment of a sheep's genetic worth is to be obtained. Tables 21a and 21b, which are calculated from Tables 19a and 19b, show the size of the difference within classes of environmental effects for the various characters.

Table 21a: The magnitude of effects between subclasses of environmental factors

Character	Weaning weight	Fleece weight
Age of dam effect		
F.M. - 2th	4.97	.66
- 4th	1.80	.30
- 6th	.48	.15
Birth and rearing effect		
Single - twin	9.72	.47
- twin reared singly	3.61	.53
Sex of lamb effect		
Ram - ewe	3.49	
Reg on date of birth	.368	.016

Table 21b: The magnitude of the effect of different ages of dam on various measures of reproductive rate

Character	No Born	AD2	No Weaned	Barrenness	Multi Birth	Wt.L.W.
F.M. - 2th	.43	.46	.40	.120	.31	31.09
- 4th	.22	.25	.21	.028	.20	16.19
- 6th	.05	.04	.03	.002	.05	2.96

Results for weaning weight and hogget greasy fleece weight mostly agree with other published results. As would be expected lambs born and reared as singles shear the heaviest fleeces and this agrees with other published results. Within the twins those reared as singles produce lighter fleeces than those reared as twins. Tripathy (1966), working with the same flock of N.Z. Romneys as this author, found, as other authors have done, that those twins reared as singles produced heaveir fleeces than those reared as twins. No good explanation for this result can be suggested.

The effect of increasing weights with age of dam on weaning weight and hogget greasy fleece weight is in line with other estimates (Tables 1 and 4). The ewes in this study have not been kept long enough to see when the age of dam effect on weaning weight reaches a peak.

With one exception the figures obtained here compare favourably with those used by the National Flock Recording Scheme. The exception is in considering correction factors for birth and rearing effects. Using a single lamb reared as a single as their basis the National Flock Recording Scheme adds 10 lb to a lamb born and raised a twin and 7 lb to a twin lamb reared as a single. The 9.7 lb value obtained in this study for the difference between a single and a twin agrees well but the 3.6 lb difference noted between a single and a twin reared singly does not. The Recording Scheme figures were used in this study to calculate weight of lamb weaned. This was done to calculate the repeatabilities and heritabilities that would apply to a farmer using this scheme. For this flock if the values obtained for the weaning weight environmental factors had been used in calculating weight of lamb weaned then different values of heritability and repeatability may have been obtained.

The effect of age of dam is not significant for the character "triplet births". For all other measures of reproductive

Table 22: The variance components as a percentage of total variance

Source of Variation	W.W.	F.W.	No Born	AD2	No Weaned	Barren	Multi	Trip	Wt.L.W.
Years	24.55		7.60	2.08	2.67	2.06	2.61	.33	1.60
Age of dam	4.96		3.41	8.02	6.36	2.47	7.98	.12	9.17
B & R Type	12.54								
Sex	21.44								
Reg on age	2.35								
Error	34.16		88.99	89.90	90.97	95.47	89.41	99.55	89.22

ability a marked trend of increasing reproductive rate with increasing age of the ewe can be noted for the four years lambing the flock is studied. Numbers of lambs at all ages, numbers of multiple births and weight of lamb weaned all increase. The number of ewes lambing also increases; barrenness decreases. These results are all in accordance with results in the literature (Tables 8,9 and 10).

The variance components are presented in Table 22 as a percentage of the total variance. The most striking feature of these results is the large size of the error variance for the measures of reproductive ability. Therefore the recognised environmental effects only control a small amount of variation (these agree with other published results: Tables 11 and 12). Both Dunlop (1963) and De Haas and Dunlop (1969) considered that this was partly due to the broard units the characters were measured in. While weight of lamb wenaed does consider weight of lamb this is imposed on top of a discrete scale for number weaned so it is not suprising that its error variance is so large.

B. ESTIMATION OF REPEATABILITY.

1. Introduction and method of analysis

A characteristic, such as fleece weight, will vary from one period to another if measured at different times in an animals life. Many factors such as age of ewe, season, pregnancy and lactation can effect measurements of a trait, so changes in those traits from period to period are likely to be due to changes in environment.

With some characters it is found that if an animal is near the top of the scale at one period then at a subsequent period it will again rank in a similar, although not necessarily exact, position: with other characters, later observations do not agree so closely with the first.

In selecting animals, the intention is to choose them for superiority early in life, and so to gain increased production because they retain that superiority throughout life. Repeatability is a measure of the extent to which this is likely to happen. A highly repeatable character does not mean that the animal will have exactly the same measurement every year but it will rank consistently no matter how much the average value of the measurement may change.

If several measurements on each individual of a group are considered more light is shed on the nature of repeatability. The value of the character measured can be analysed into a component within individuals, measuring the difference between the performances of the same individual, and a component between individuals, measuring the permanent differences between individuals. The within-individual component is entirely environmental in origin, caused by temporary differences of environment between successive performances. The between-individual component is partly environmental and partly genetic, the environmental part being caused by circumstances that affect the individual permanently.

The repeatability (t) of the character, expressed in terms of variance, is the ratio of the between-individual variance component to the total phenotypic variance.

$$t = \frac{\sigma_s^2}{\sigma_p^2}$$

In this study repeatabilities are calculated for the characters No. Born, AD2, No. Weaned and Wt.L.W. The first three of these characters are discrete with only a few classes of observations (0,1,2, or 3 lambs). These characters have an underlying continuity with a "threshold" which imposes a discontinuity on the visible expression of the character. Wt.L.W. is a character with continuous observations. Analysis of variance can be used to estimate repeatability in both the continuous and discrete characters.

Here it is assumed that the record of the ith animal taken in the jth year is:

$$y_{ij} = \mu + s_i + b_j + e_{ij}$$

where μ = population mean

s_i = effect due to the ith animal

b_j = effect due to the jth year

e_{ij} = error

The analysis of variance for this model is of the form:

The analysis of variance of n animals with k records per animal

Source of variation	d.f.	M.S.	E(MS)
Between Years	k-1	MS_y	$\sigma_e^2 + n\sigma_y^2$
Between Animals	n-1	MS_s	$\sigma_e^2 + k\sigma_s^2$
Within Animals	(k-1)(n-1)	MS_e	σ_e^2

The repeatability is calculated as:

$$t = \frac{(MS_s - MS_e)/k}{MS_e + (MS_s - MS_e)/k}$$

$$= \frac{\sigma_e^2}{\sigma_p^2}$$

In this study as the ewes upon which the measurements were taken were born over a number of years it is necessary to combine estimates from several groups. Sums of squares and degrees of freedom are simply pooled in an analysis, and the resultant M.S. are equated to their expected values.

When the number of animals is large, the appropriate standard error is: $\sigma_t^2 = \dfrac{(1-t)(1-(k-1)t)}{\sqrt{\frac{1}{2}k(k-1)(n-1)}}$

where k = no. of records per animal.

Records of a ewe were only used where she was present for four lambings. Eight groups of ewes were available. They were ewes born in 1953 to 1956 and 1961 to 1964. The intermediate years data were left out as they all included the 1962 lambing which was not used for reasons explained in Chapter IIIC. The records of 375 ewes were included giving 1500 lambing observations. The same ewes were used in estimating the repeatabilities for all four characters.

2. Results and discussion

Table 23: Repeatability estimates				
Character	No. born	AD2	No. Weaned	Wt.L.W.
Repeatability	.191	.178	.169	.187
σ_t^2	.027	.027	.026	.027

Table 23 shows the estimated repeatability results. These values seem to be slightly higher than similar measures (No. Born and No. Weaned per ewe joined) from the literature. Purser (1965) measured the repeatability of No. Born per ewe mated, barren ewes per ewe mated and litter size per ewe mated on Scottish Blackface and Welsh Mountain breeds and noted that repeatabilities measured at weaning were about half those measured at birth. As the lambs become older they are subject to additional environmental effects and this may tend to lower the repeatability. Inskeep, et al.,(1967), Yalcin and Bichard (1964b), Young, et al., (1963) all measured repeatabilities at both lambing and weaning and none of them found a decrease in value with the increase in age of the lamb. The values obtained in this paper for No. Born, AD2 and No. Weaned show only a very slight decline with advancing age of the lamb.

C. ESTIMATION OF HERITABILITY

1. Introduction and methods of analysis

Heritability of a trait measures the proportion of the difference between individuals which are additively genetic in origin. Heritability measures the extent to which the superiority of a parent for a character is passed on to its offspring.

Heritability is defined as the ratio of additive genetic variance to phenotypic variance:

$$h^2 = \frac{\sigma_a^2}{\sigma_p^2} .$$

The symbol h^2 stands for the heritability itself and not for its square. The phenotypic variance, σ_p^2 , is the total variance. Variation from additive genetic effects, σ_a^2 , arises from the summed effects of individual genes, and so contributes directly to the resemblance between parents and offspring. So heritability is the additive genetic variance as a fraction of the total. To estimate h^2 estimates of σ_p^2 and σ_a^2 are required; σ_p^2 can be obtained directly from a population, while σ_a^2 can only be estimated from the correlation between relatives. The sets of relatives most commonly used for estimating heritability in animal breeding and those used in this study are:

(a) Parent-offspring. As one male is usually mated to a number of females, the parent is usually the dam. Regression and correlation techniques are used.

(b) Half-sib. The analysis of variance is used in estimating it.

2. Dam-offspring relationship method

There are several methods of estimating heritability based on dam-offspring covariance. $2\ \mathrm{Cov}(\text{parent} \times \text{offspring}) = \sigma_a$ (approx). One disadvantage with this value is that maternal effects may be included in the estimate. In this study weaning weight of the lamb was the only character directly effected by maternal environment. The remaining characters were all expressed by the individual after weaning and therefore could be influenced by the maternal environment only if carryover maternal effects exist. For this reason no attempt was made to estimate the heritability of weaning weight from the dam-offspring relationship. In fact the only character whose heritabilities were estimated by this method was Wt.L.W.

For weight of lamb weaned each weaning record was adjusted for sex, birth and rearing rank and date of birth using the figures of the National Flock Recording Scheme except that age of dam was not corrected for. In deciding to use these figures, the end use of the estimate calculated was considered. If the heritability was to be used to predict the accuracy of selection in this present flock then it would have been best to adjust for the effect of environmental factors by using correction factors estimated for weaning weight for this flock. But because the main interest was in a heritability estimate that will predict the accuracy of selection under commercial conditions, the correction factors of the National Flock Recording Scheme were used. This will give a more realistic estimate of the progress expected by a member of this scheme.

The regression of daughter on dam ignoring sires was used. When, as in this case, matings are at random and when all sire groups are run together, the between sire components in the covariance analysis have zero expectation and the analysis can be simplified by ignoring sires and calculating the regression coefficient directly. Various regression values were worked out on the sheep. Firstly each age in the dam was compared with the corresponding age in the daughter. Then the first, the sum of the first two, the sum of the first three and the total lambing of the dam were each compared with the performance for the four years total for the daughters. For each heritability the ewes were studied in a number of groupings, each grouping consisting of dams and daughters born in a certain pair of years. The regression lines for the different groupings are then tested for equality and if there is no significant difference they are all pooled to give a common regression line.

3. Paternal half-sib method

An analysis of variance is used in estimating the variance components σ_S^2 and σ_E^2 used in calculating the heritability by the paternal half-sib method. Using weaning weight as an example the mathematical model including sire as follows is used:

$$y_{ijklmn} = \alpha + t_i + s_m + a_j + b_k + c_l + dx_{ijklmn} + e_{ijklmn}$$

$$i = 1, \ldots, p$$
$$j = 1, \ldots, q$$
$$k = 1, \ldots, r$$
$$l = 1, \ldots, s$$
$$m = 1, \ldots, t$$
$$n = 1, \ldots, n_{ijklm}$$

were n_{ijklm} is the number of observations in the $ijklm^{th}$ subclass.

The α, t_i, a_j, b_k, c_l, x_{ijklmn} and d are respectively, the mean when $x = 0$, year of birth, age of dam, type of birth and rearing, sex of lamb, date of birth and the partial liner regression coefficient on age. These elements have the same meaning as those described for the model used in studing the environmental effects. The s_m is the effect common to records of all daughters of the m^{th} sire group. From the matrix based on this model the reduction due to fitting all constants $R(\alpha, t_i, s_m, a_j, b_k, s_l, d)$ was obtained. The between sires S.S. was computed as the difference between $R(\alpha, t, s, a, b, c, d)$ and that due to sitting all except the sire effect $R(\alpha, t, a, b, c, d)$. The error S.S. was obtained as a difference between the raw S.S. (each individual weaning weight squared and summed) and that due to fitting all constants.

$E(\sum_{ijklmn} y^2_{ijklmn}) = s + N.... (\sigma_s^2 + \sigma_e^2)$ where N.... equals the total number of observations.

$E\ R(\alpha, t, s, a, b, c, d) = s - N.... \sigma_s^2 + (s.inc.d.f.)\sigma_e^2$ where s.inc.d.f. is the total degrees of freedom of the factors in the model with sires included remembering that as sires are nested within years of d.f. for $\alpha + t_i + s_m$ = the number of sires.

$E\ R(\alpha, t, a, b, c, d) = s + K\sigma_s^2 + (s.exc.d.f.)\sigma_e^2$ where s.exc.d.f. is the total d.f. of the factors in the model with sires excluded where the d.f. for $\alpha + t_i$ equals the number of years and K is the coefficient for the variance component in the reduction in the sum of squares due to fitting all except the set being considered.

Therefore:

$$\text{Error S.S.} = (N.... - s.inc.d.f.)\sigma_e^2$$

$$\text{Between sires S.S.} = (N.... - K)\sigma_s^2 + (s.inc.d.f. - s.exc.d.f.)\sigma_e^2$$

$$\text{Error M.S.} = \frac{\text{Error S.S.}}{N.... - s.inc.d.f.}$$

$$= \sigma_e^2$$

$$\text{Between sires M.S.} = \frac{\text{Between sires S.S.}}{s.inc.d.f. - s.exc.d.f.}$$

$$= \sigma_e^2 + \frac{N.... - K}{s.inc.d.f. - s.exc.d.f.}\sigma_s^2$$

$$= \sigma_e^2 + k\sigma_s^2$$

where $k = \dfrac{N... - K}{s.inc.d.f. - s.exc.d.f.}$

is known as the coefficient for the variance component. The problem lies in finding a value for K. This is accomplished best by using the indirect method of Henderson (1953) which is ably set out with examples by Harvey (1960). Appendix B shows the calculation of this for weaning weight.

Similarly to calculate the heritability of hogget greasy fleece weight the mathematical model:

$$y_{ijklm} = \alpha + t_i + s_l + a_j + b_k + dx_{ijklm} + e_{ijklm}$$

is used where t_i, a_j, b_k, d and x are the same as when they were previously defined for calculating the environmental effect of hogget greasy fleece weight. s_l is the effect common to all individuals with the l^{th} sire.

The characters No. Born, AD2, No. Weaned, Barrenness and Multiple Births are all descrete characters but one can imagine that for each there is a normally distributed background, which is a combination of genetic and environmental effects, equivalent to the distributions of the phenotypes of a continous variable. The discrete observations result from a number of thresholds which divide the distribution into sections, and the phenotypic expression can only be changed when a threshold is passed. Hence discrete variables may be considered as a special type of continous variable with coarse classification. It thus seems reasonable to use analysis of variance for estimating heritability for both types. The model used for these five characters and Wt.L.W. is:

$$y_{ijkl} = \mu + t_i + s_k + a_j + e_{ijkl}$$

where μ, t_i and a_j are the same as when they were previously defined for calculating the environmental effects of the characters and s_k is the effect common to all ewes of the same sire. The two way nested analysis of variance with unequal subclasses was used to find the Between Sires and Within Sires variance and the heritabilities were calculated within age group of dam. Thus for each character four heritabilities instead of one were found.

Although in the 2-tooths and 4-tooths in two pairs of years similar sires were used and in the 6-tooths and full mouths in one pair of years similar sires were used they were treated for the purpose of ease of calculation as if these were different sires in different years.

4. Results and discussion

The heritability estimates are given in Tables 24 and 25.

Table 24: Heritability estimates by paternal half-sib method

Character	(d.f.)	Heritability
Weaning Wt.	(45)	.348
Hogget F.W.	(34)	.225

Age of dam	2-th	4-th	6-th	F.M.
No Born	(41) .0409	(42) .0106	(43) .0164	(43) .0363
AD2	(41) .0528	(42) .022	(43) .0497	(43) .0298
NoWeaned	(41) .0583	(42) .0663	(43) -----	(43) .0262
Wt.L.W.	(41) .0639	(42) .0616	(43) .0121	(43) .0055
Barrenness	(41) .1347	(42) .0171	(43) -----	(43) .0841
Multiple Births	(41) .0314	(42) .0169	(43) .0125	(43) .1200

The heritability of weaning weight is in close agreement with those obtained by Ch'ang and Rae (1961) and Ch'ang (1967) for the N.Z. Romney. They were calculated on the same flock as this but

Table 25: Heritability estimates for Wt.L.W. by dam-offspring regression

Heritabilities between Dam	 Daughter	Pairs	No. of groups	Significance between regs	h^2
2-th	2-th	602	26	n.s.	.079
4-th	4-th	518	26	n.s.	.195
6-th	6-th	431	26	n.s.	.038
F.M.	F.M.	334	24	1%	.158
2-th	Total	181	16	n.s.	.034
2-,4-th	Total	137	12	n.s.	.327
2-,4-,6-th	Total	82	8	n.s.	.549
total	Total	59	7	n.s.	.352

in different years. The heritability obtained for hogget greasy fleece weight lies between the earlier and more recent results of Rae (1948 and 1950, 0.10 to 0.17; and 1958 0.31 to0.32) and others (McMahon, 1943, 0.10 to 0.15 and Tripathy, 1966, 0.43).

Heritabilities for the traits measuring reproductive ability are uniformly low where they are calculated by the paternal half-sib method. This method of estimation is considered the most accurate for calculating heritabilities for reproductive traits. This is because when numbers of lambs are considered using the dam-daughter regression on a single record ewes with a zero record have no daughters. If to overcome this problem more than one record of the ewe is included then the ewes continually barren are still excluded. Using half-sib analysis partly overcomes this problem but the results are still biased as rams cannot come from barren ewes.

The results for weight of lamb weaned which are estimated by daughter-dam regression do show that selection based on the second lambing has a higher heritability than that based on the first lambing (0.195 versus 0.079). If the total of the first, the first two and the first three lambings of the dam are considered then the first is the worst and the latter the best measure to select on if the aim is to increase the lifetime production of the daughter. The heritability between the dams first two lambings and the daughters total lambings is 0.327 and the heritability between the dams first three lambings and the daughters total lambing is 0.547. A year in time could be saved if the selection is based on the first two lambings of the dam and then the next year and subsequently the first three lambings considered. It is better to include the sum of the first two or three lambings than individual lambing results alone.

SUMMARY

SUMMARY

This thesis contains results of studies of certain characters made on a flock of randomly bred N.Z. Romney sheep kept at Massey University, Palmerston North. The characters studied were Weaning weight, Hogget greasy fleece weight, Weight of lamb weaned (Wt.L.W.), and various measures of reproductive ability (No. born; number of lambs alive at their second day of age, AD2; No. weaned; Multiple births; Barrenness and Triplet births. All these measures were based on ewes mated and present at lambing). Wt.L.W. as well as being a measure of the ewes reproductive ability also includes the effect of the ewes mothering and milking ability. It was calculated using the corrections of the National Flock Recording Scheme (of N.Z.) with the exception that each age of dam was treated separately instead of being corrected for and pooled.

It was found, on studying the environmental factors, that the effects of year, age of dam, type of birth and rearing and date of birth all had highly significant effects on Weaning weight and Hogget fleece weight. The sex effect also had a highly significant effect (at the 1% level) on Weaning weight: only ewe hoggets were involved in studying greasy fleece weight. All the remaining characters (with the exception of Triplet births) were found to be highly significantly affected by age of dam and year effect: the only two effects looked at. For Triplet births the effect of year was significant. (at the 5% level) but the effect of age of dam was not significant.

For Weaning weight and Hogget fleece weight all the estimates

of the magnitude of the environmental effects were similar to results obtained by other authors with the exception that fleece weights from twins reared singly were found to be slightly lighter than those of twins reared as twins. This is the reverse of the expected result and no explanation for it is available. For the characters measuring reproductive rate (excluding Triplet births) there was an increase in lamb numbers (and a decrease in barrenness) as the age of the ewe increased from 2- to 5-years. A similar increase was found for Wt.L.W.

Very high values of error variance (all greater than 89%) were found for the characters measuring reproductive rate and Wt.L.W., when the total variance was partitioned into its components. It is considered this is due to the broad units the characters are measured in. Values were also calculated for Weaning weight and Hogget fleece weight.

Repeatability estimates are calculated for No. born, AD2, No. weaned and Wt.L.W. These were calculated by the intra-class correlation method using the result of those ewes with four lambing records available. The results obtained were 0.191, 0.178, 0.169 and 0.187 respectively.

Heritabilities were calculated by both the dam-offspring relationship and paternal half-sib methods. The dam-offspring method was only used for calculating Wt.L.W. heritabilities. Heritabilities of 0.079, 0.195, 0.038 and 0.158 were obtained when dam and daughter pairs were compared at similar ages (2-tooths, 4-tooths, 6-tooths and full mouths respectively). Following this the first and the sum of the first two, first three and all four lambing results of the dam were compared with the results of the four lambings for the daughters to give heritabilities of 0.084, 0.327, 0.549 and 0.352 respectively.

Using the paternal half-sib method, values of 0.35 and 0.23 were obtained for the heritability of Weaning weight and Hogget fleece weight respectively. For the characters No. born, AD2, No. weaned, Multiple births, Barrenness and Wt.L.W. heritabilities were calculated within age of dam. All estimates were within the range 0 to 0.08 with the exception of the barrenness 2-tooth result and the Multiple births full mouth result which were 0.13 and 0.12 respectively.

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APPENDICES

APPENDICES

APPENDIX A: AN ANALYSIS OF THE VARIANCE COMPONENTS FOR WEANING WEIGHT

The variance component estimates are obtained by equating the least-squares sum of squares or mean squares to their corresponding expectations and solving the resulting equations. For weaning weight the analysis of variance is as follows:

Source of Variation	d.f.	S.S.	E(MS)
Years	1-p	$R(\alpha,t,a,b,c,d) - R(\alpha,a,b,c,d)$	$\sigma_e^2 + k_4\sigma_t^2$
Age of Dam	1-q	$R(\alpha,t,a,b,c,d) - R(\alpha,t,b,c,d)$	$\sigma_e^2 + k_3\sigma_a^2$
B & R Type	1-r	$R(\alpha,t,a,b,c,d) - R(\alpha,t,a,c,d)$	$\sigma_e^2 + k_2\sigma_b^2$
Sex	1-s	$R(\alpha,t,a,b,c,d) - R(\alpha,t,a,b,d)$	$\sigma_e^2 + k_1\sigma_c^2$
Regression	1	$R(\alpha,t,a,b,c,d) - R(\alpha,t,a,b,c)$	$\sigma_e^2 + k_o\sigma_d^2$
Error	difference	$\Sigma y^2_{ijklm} - R(\alpha,t,a,b,c,d)$	σ_e^2
	N....-1		

To find the k values the method of Henderson (1953) is used and this has been ably explained and used by Harvey (1960). The "direct method" is used to find k_1, k_2 and k_3 as these have only a small number of degrees of freedom, 1,2 and 3 respectively, while k_4 dealing with 9 degrees of freedom is easier estimated by the "indirect method".

The direct method of computing the coefficient for the major variance component in each category in the E(MS) uses the formula:

$$k = \frac{1}{n}\left({}_{i}Z^{ii} - \frac{1}{d.f._{ij}} Z^{ij} \right)$$

where d.f. is the number of degrees of freedom for that category in the analysis of variance and m is the number of classes. The superscript on Z identify the elements in the matrix-inverse to the square symmetrical segment from the variance-covariance inverse matrix.

To estimate the k values for weaning weight the inverse of the variance-covariance matrix when all effects are included (Table 13: Matrix 1) is needed.

(a) the sex effect.

For k_1 the inverse matrix to the Z segments of the complete matrix is as follows:

$$Z_c^{-1} = \left[.00034749209\right]^{-1}$$

$$= \left[2877.76334\right]$$

$$k_1 = \tfrac{1}{2}(2877.76334)$$

$$= 1438.88167$$

(b) type of birth and rearing effect.

$$Z_b^{-1} = \begin{bmatrix} .00096786618 & -.0011021927 \\ -.0011021937 & .0022017161 \end{bmatrix}^{-1}$$

$$= \begin{bmatrix} 2403.2615 & 1203.0876 \\ 1203.0887 & 1056.4648 \end{bmatrix}$$

$$k_2 = \tfrac{1}{3}(2403.2615 + 1056.4648 - \tfrac{1}{2}(1203.0876 + 1203.0887))$$

$$= 752.21273$$

(c) the regression

$$Z_d^{-1} = \left[.0000030366274\right]^{-1}$$

$$= \left[329,312.3\right]$$

$$k_0 = 1(329,312.3)$$

$$= 329,312.3$$

(d) age of dam effect.

$$Z_a^{-1} = \begin{bmatrix} .0011653583 & -.0003474303 & -.0003745085 \\ -.0003474304 & .0010217131 & -.0003097462 \\ -.0003745078 & -.0003097458 & .0010013952 \end{bmatrix}^{-1}$$

$$\begin{bmatrix} 1260.2360 & 630.5525 & 666.3508 \\ 630.5517 & 1395.5191 & 667.4728 \\ 666.3497 & 667.4719 & 1454.2717 \end{bmatrix}$$

$$\begin{aligned} k_3 &= \tfrac{1}{4}(1260.2360 + 13955191 + 1454.2717 - \tfrac{1}{3}(630.5525 \\ &\qquad + 666.3508 + 630.5517 + 667.4728 + 6663497 + 667.4719)) \\ &= \tfrac{1}{4}(4110.0268 - \tfrac{1}{3}(3928.7494)) \\ &= 700.1109 \end{aligned}$$

(e) year effect.

The indirect method for computing k's is well explained by Harvey (1960). The estimation of k_4, using the indirect method, is as follows: It is first necessary to comput the coefficient for the variance component in the appropiate reduction in the sum of squares. This is done by computing the cross products between corresponding elements of two square matrices. The first matrix requires is the inverse of the variance-covariance matrix for the model $Y_{ijklm} = \alpha + a_j + b_k + c_l + dx_{ijklm} + e_{ijklm}$ which is the model for all the effects except for years which are being computed. The Variance-Covariance Matrix for all weaning weight effects except years after the restriction $\sum_j \hat{a}_j = \sum_k \hat{b}_k = \sum_l \hat{c}_l = 0$ have been imposed is set out in Table 18. The inverse of this matrix is shown in Table 26. In this inverse matrix (R^{-1}) R^{ij} are the elements.

The "associated sums" matrix is the second square matrix required for this indirect method and is computed from the matrix multiplication NN' where N is the segment of the original complete set of least squared equations which contains the coefficients

Table 26: The inverse of the reduced least-squares equations for weaning weight for all effects except the set for years

	$\hat{\alpha}$	$\hat{b}_1$	$\hat{b}_2$	$\hat{c}_1$	$\hat{a}_1$	$\hat{a}_2$	$\hat{a}_3$	$\hat{d}$
α:	2.3506091E-3	-5.1516579E-4	8.3010868E-4	3.5892899E-5	-7.7890380E-5	-6.5525118E-5	-7.2665184E-5	-6.3458278E-5
b_1:	-5.1516538E-4	9.5443915E-4	-1.0972012E-3	-1.4496739E-5	1.5107524E-4	5.5914918E-5	-3.6692101E-5	3.5103170E-6
b_2:	8.3010831E-4	-1.0972013E-3	2.1856270E-3	1.8153292E-5	-8.1896496E-5	5.2452633E-5	-1.5259801E-5	4.2159200E-7
c_1:	3.5892669E-5	-1.4497042E-5	1.8153253E-5	3.4606797E-4	-8.9246959E-6	2.7850828E-5	-4.9527357E-6	-6.5377190E-7
a_1:	-7.7890248E-5	1.5107751E-4	-8.1894790E-5	-8.9222408E-6	1.1633532E-3	-3.4796410E-4	-3.7288779E-4	3.4046489E-6
a_2:	-6.5526079E-5	5.5912624E-5	5.2452940E-5	2.7851753E-5	-3.4796451E-4	1.0192349E-3	-3.0673543E-4	2.4776246E-6
a_3:	-7.2665105E-5	-3.6692634E-5	-1.5255952E-5	-4.9578948E-6	-3.7288780E-4	-3.0673596E-4	9.9165486E-4	1.4829599E-6
d:	-6.3458291E-5	3.5103420E-6	4.2157417E-7	-6.5377383E-7	3.4046509E-6	2.4776287E-6	1.4829568E-6	2.3971625E-6

associating the effects under consideration with all others in the model.

$$N' = \begin{bmatrix} 164 & 34 & 18 & 62 & 79 & 85 & 35 & 44 & 46 & 39 & 3759 \\ 167 & 109 & 22 & 36 & 76 & 91 & 31 & 42 & 38 & 56 & 3544 \\ 263 & 93 & 20 & 150 & 129 & 134 & 58 & 61 & 90 & 54 & 6998 \\ 207 & 89 & 20 & 98 & 103 & 104 & 41 & 62 & 55 & 49 & 5776 \\ 259 & 162 & 17 & 80 & 133 & 126 & 57 & 61 & 64 & 77 & 5338 \\ 334 & 112 & 28 & 194 & 172 & 162 & 73 & 92 & 86 & 83 & 10078 \\ 206 & 86 & 7 & 113 & 85 & 121 & 37 & 44 & 68 & 57 & 8551 \\ 422 & 180 & 34 & 208 & 213 & 209 & 94 & 115 & 112 & 101 & 12222 \\ 449 & 200 & 31 & 218 & 217 & 232 & 111 & 124 & 118 & 96 & 12385 \\ 433 & 233 & 24 & 176 & 194 & 239 & 103 & 123 & 106 & 101 & 8377 \end{bmatrix}$$

$$
NN' = \begin{bmatrix}
955{,}050 & 438{,}592 & 69{,}882 & 446{,}576 & 461{,}622 & 493{,}428 & 215{,}531 & 256{,}163 & 254{,}397 & 228{,}959 & 25{,}100{,}320 \\
 & 208{,}380 & 31{,}954 & 198{,}258 & 211{,}146 & 227{,}446 & 99{,}073 & 117{,}594 & 115{,}577 & 106{,}348 & 11{,}224{,}609 \\
 & & 5{,}423 & 32{,}505 & 34{,}031 & 35{,}851 & 15{,}673 & 18{,}803 & 18{,}546 & 16{,}860 & 1{,}834{,}428 \\
 & & & 215{,}813 & 216{,}445 & 230{,}131 & 100{,}785 & 119{,}766 & 120{,}274 & 105{,}751 & 12{,}041{,}283 \\
 & & & & 223{,}859 & 237{,}763 & 104{,}199 & 123{,}865 & 122{,}907 & 110{,}651 & 12{,}150{,}149 \\
 & & & & & 255{,}665 & 111{,}332 & 132{,}298 & 131{,}490 & 118{,}308 & 12{,}950{,}171 \\
 & & & & & & 48{,}944 & 57{,}986 & 57{,}249 & 51{,}352 & 5{,}526{,}901 \\
 & & & & & & & 69{,}116 & 67{,}878 & 61{,}183 & 6{,}699{,}913 \\
 & & & & & & & & 68{,}505 & 60{,}765 & 6{,}763{,}150 \\
 & & & & & & & & & 55{,}659 & 6{,}010{,}347 \\
 & & & & & & & & & & 635{,}143{,}764
\end{bmatrix}
$$

The off-diagonals on the left are omitted

This 11 x 11 matrix was reduced to an 8 x 8 matrix by subtracting b_3, c_2 and a_4 by rows and columns. (Instead of reducing the NN' matrix one could have built up the R^{-1} matrix from an 8 x 8 to a 11 x 11 matrix by setting $\sum_j \hat{a}_j = \sum_k \hat{b}_k = \sum_l \hat{c}_l = 0$; this being the restriction that was originally imposed.)

$$\begin{bmatrix}
955{,}050 & -7984 & -376{,}694 & -31{,}806 & -13{,}428 & 27{,}204 & 25{,}438 & 25{,}100{,}320 \\
 & 27{,}577 & 17{,}004 & -2614 & -2309 & -2769 & -5294 & -816{,}674 \\
 & & 156{,}226 & 11{,}866 & 3779 & -12{,}072 & -12{,}837 & -10{,}206{,}855 \\
\multicolumn{3}{l}{\text{The off-diagonals on}} & 3998 & 524 & -776 & -926 & -800{,}022 \\
\multicolumn{3}{l}{\text{the left are omitted}} & & 1899 & 1110 & 791 & -383{,}437 \\
 & & & & & 2409 & 1589 & 689{,}566 \\
 & & & & & & 2634 & 752{,}803 \\
 & & & & & & & 685{,}143{,}764
\end{bmatrix}$$

The coefficient for the variance component in the reduction in sum of squares due to fitting all effects except years is given by $\sum_{ij} R^{ij}N_{ij}$ i.e. computing the sum of the cross products between corresponding elements of the two square matrices.

$$= (.002350691)(955{,}050) + (-.00051516579)(-7984) + \dots +$$

$$= 401.96044$$

The coefficient for the variance component in the E(MS) of the analysis of variance is given by:

$$k = (N_{....} - \sum_{ij} R^{ij}N_{ij})/\text{d.f.for years}$$

$$= (2904 - 401.96044)/9$$

$$= 278.004$$

Table 27: The analysis of variance with the MS expectations

Source of Variation	d.f.	M.S.	E(MS)
Years	9	6,343.311	$\sigma_e^2 + 278.004\sigma_t^2$
Age of dam	3	3,242.886	$\sigma_e^2 + 700.111\sigma_a^2$
Birth & rearing	2	28,568.171	$\sigma_e^2 + 752.213\sigma_b^2$
Sex	1	8,755.180	$\sigma_e^2 + 1438.881\sigma_c^2$
Regression	1	44,556.958	$\sigma_e^2 + 329{,}312.3\sigma_d^2$
Error	2887	31.592	σ_e^2
	2904	92.479	

$$\sigma_b^2 = (28{,}568.171 - 31.592)/752.213 = 37.937$$

$$\sigma_c^2 = (8755.180 - 31.592)/1438.882 = 6.063$$

$$\sigma_a^2 = (3242.886 - 31.592)/700.111 = 4.587$$

$$\sigma_t^2 = (6343.311 - 31.592)/278.004 = 22.704$$

$$\sigma_d^2 = (44{,}556.958 - 31.592)/329{,}312.3 = 0.136$$

$$\sigma_e^2 = 31.592$$

Table 28: Variance components as a percentage of total variance

Source of variation	%
Years	22.04
Age of dam	4.45
Birth and rearing	36.83
Sex	5.88
Regression	0.13
Error	30.67
	100.00

APPENDIX B: ESTIMATION OF WEANING WEIGHT HERITABILITY BY THE PATERNAL HALF-SIB METHOD

1. Estimation of the k value

In this case the k value is obtained from a value K which is in turn obtained in a similar manner to that used to find the k_4 value for year effect in Appendix A. This was the indirect method. To compute the coefficient for the variance component in the appropriate reduction in sums of squares, K, two square matrices whose corresponding elements are multiplied together and summed are needed. The first matrix is the inverse of the variance-covariance matrix for the model of all effects except the sire effect. The "associated sums" matrix is the second square matrix required and is computed from the matrix multiplication NN', where N is the segment of the original complete set (including sire effects) of least squares equations which contains the coefficients associating the effects under consideration with all others in the model. The first 17 x 17 (plus one RHM) matrix was then built up to a 21 x 21 (plus one RHM) matrix by letting $\sum_i \hat{t}_i = \sum_k \hat{b}_k = \sum_l \hat{c}_l = \sum_j \hat{a}_j = 0$. This is the restriction that was originally applied to obtain the first matrix required.

The coefficient for the variance component in the reduction in sums of squares due to fitting all effects except sires is given by multiplying the corresponding elements of the two square matrices together and summing. All this is similar to obtaining the k_4 value for year effect in Appendix A. It is found that

$$K = 544.93447$$

The coefficient for the variance component in the E(MS) of the analysis of variance is given by

$$k = \frac{N.... - K}{s.\ inc.\ d.f. - s.\ exc.\ d.f.}$$

where s.inc d.f. is the d.f. of the mathematical model with sires included remembering that as sires are nested within years the d.f. for $\alpha + t_i + s_m$ equals the number of sires. The d.f. for s. inc d.f. are therefore $\alpha + t_i + s_m = 55$, c = 1, b = 2, a = 3 and d = 1 which is a total of 62. S. exc. d.f. is the d.f. of the mathematical model with sires excluded remembering that the d.f. for $\alpha + t_i$ equals the number of years. Therefore s. exc. d.f. = 10 + 1 + 2 + 3 + 1 totaling to 17. N...., the number of individual weaning weight observations, is equal to 2904.

$$k = (2904 - 544.93447)/(62 - 17)$$

$$= 2359.06553/45$$

$$= 52.4236$$

2. Estimation of "Sires Included" reduction

To estimate the heritability of weaning weight by the paternal half-sib method four figures must be estimated from the data on weaning weight and all these are detailed in their calculation. These figures are the coefficient for the variance component, k; the sum of all the squared observations, $\sum_{ijklm} y^2_{ijklm}$; the reduction due to fitting all except the sire effects, $R(\alpha,t,b,c,a,d)$; and the reduction due to fitting all, including the sire effects, $R(\alpha,t,s,b,c,a,d)$. The only one that has yet to be estimated is the reduction due to fitting all effects and to calculated this is a complicated proceedure which will now be detailed.

The matrix from which this reduction is estimated is a square matrix of 76 equations (1 for 2, 10 for year effects, 55 for sire effects, 3 for birth and rearing effect, 2 for sex effects, 4 for age of dam effects and 1 for the regression of age at weaning) with one RHM. As it is this matrix after the restrictions have been imposed is still far too large to be easily and correctly inverted and solved by the computer programs available.

By applying an absorption procedure this large matrix can be greatly reduced in size. As sires are nested within years we can in this instance write $\tilde{s}_{im} = \alpha + t_i + s_{im}$. This in fact deletes the first 11 columns and rows of the matrix. (It can be shown for a one way classification that the equations for $\alpha + t_i$ are identical with the equations for t_i. When α is combined with the t_i it is unnecessary to impose a restriction on the t_i since there are p d.f. associated with the $\alpha + t_i$ but only p-1 d.f. associated with t_i alone. By carrying this a step further we can, as sires are nested within years, combine each year equation with the sire equations for that year and instead of having t (for sires) - p (for years) d.f. associated with s_m alone have t d.f. associated with $\alpha + t_i + s_{im}$.) Now we can absorb the $\tilde{s}_{im}$ equations into the equations for b_k, c_l, a_j and d. To do this we set up 3 tables which are then used in setting up a fourth table which is the required matrix with α, t_i and s_{im} absorbed. The first table (Table 29) is the segment from the full matrix which includes the $\hat{b}_k$, $\hat{c}_l$, $\hat{a}_j$, $\hat{d}$ and RHM portions of the $\tilde{s}_{im}$ equations. The second table is the first table with each row divided by the corresponding $\tilde{s}_{im}$ diagonal element. (Divisions were carried out to 6 decimal places to stop errors accumulating.) The third table (Table 30) is that segment

Table 29: $\tilde{s}_{in}$ diagonal element and $\hat{b}_k$, $\hat{c}_l$, $\hat{a}_j$, $\hat{d}$ and RHM segment of the $\tilde{s}_{im}$ equations of the full (sires included) weaning weight

Equation	Diag elem	$\hat{b}_1$	$\hat{b}_2$	$\hat{b}_3$	$\hat{c}_1$	$\hat{c}_2$	$\hat{a}_1$	$\hat{a}_2$	$\hat{a}_3$	$\hat{a}_4$	$\hat{d}$	RHM
$\tilde{s}_{11}$	36	25	3	8	17	19	8	9	11	8	755	2435
s_{12}	41	19	4	18	19	22	6	11	13	11	911	2649
s_{13}	43	20	3	20	22	21	9	14	11	9	1134	2947
s_{14}	44	20	8	16	21	23	12	10	11	11	959	2742
s_{21}	38	20	8	10	10	28	6	8	9	15	749	2448
s_{22}	43	28	9	6	17	26	7	12	12	12	912	2893
s_{23}	47	29	2	16	29	18	11	12	9	15	1055	3180
s_{24}	39	32	3	4	20	19	7	10	8	14	828	2775
s_{31}	69	22	7	40	28	41	12	15	25	17	1789	3640
s_{32}	60	26	4	30	33	27	15	13	19	13	1493	3184
s_{33}	64	28	6	30	34	30	15	14	24	11	1355	3617
s_{34}	70	17	3	50	34	36	16	19	22	13	1361	3917
s_{41}	32	17	3	12	19	13	6	10	10	6	871	1744
s_{42}	47	18	3	26	26	21	9	18	13	7	1290	2521
s_{43}	59	18	3	38	27	32	11	16	13	19	1548	3200
s_{44}	36	18	6	12	22	14	10	6	10	10	947	1967
s_{45}	33	18	5	10	9	24	5	12	9	7	1120	1781
s_{51}	37	19	2	16	21	16	4	12	8	13	750	1874
s_{52}	49	36	1	12	28	21	11	11	13	14	1113	2601
s_{53}	40	19	3	18	21	19	10	13	8	9	911	2150
s_{54}	56	38	4	14	27	29	15	10	15	16	1068	3158
s_{55}	34	22	4	8	18	16	9	6	8	11	649	1915
s_{56}	43	28	3	12	18	25	8	9	12	14	847	2197
s_{61}	58	17	3	38	32	26	12	17	18	11	1645	2644
s_{62}	56	19	7	30	35	21	11	11	19	15	1552	2515
s_{63}	56	18	4	34	26	30	10	17	12	17	1727	2392
s_{64}	60	24	4	32	26	34	13	18	14	15	1759	2743
s_{65}	53	18	3	32	26	27	16	16	11	10	1777	2384
s_{66}	51	16	7	28	27	24	11	13	12	15	1618	2386
s_{71}	37	16	1	20	19	18	4	10	12	11	2080	1785
s_{72}	44	13	3	28	21	23	7	9	13	15	1600	2145
s_{73}	27	13	–	14	8	19	6	4	11	6	947	1480
s_{74}	66	23	2	41	28	38	16	15	19	16	2854	3164
s_{75}	32	21	1	10	9	23	4	6	13	9	1070	1763
s_{81}	69	29	6	34	33	36	15	20	15	19	1747	3998
s_{82}	58	25	5	28	33	25	12	15	18	13	1390	3377
s_{83}	61	19	4	38	32	29	15	16	17	13	2876	2729
s_{84}	66	19	9	38	35	31	17	21	12	16	1853	3536
s_{85}	47	32	1	14	16	31	8	14	13	12	1414	2523
s_{86}	66	29	5	32	35	31	17	17	18	14	1536	3786
s_{87}	55	27	4	24	29	26	10	12	19	14	1406	3161
s_{91}	60	30	2	28	23	37	17	15	14	14	1359	3487
s_{92}	65	30	5	30	33	32	12	16	21	16	1658	3833
s_{93}	68	23	3	42	30	38	20	20	15	13	1516	4016
s_{94}	60	30	8	22	29	31	15	17	14	14	1513	3572
s_{95}	74	21	3	50	42	32	23	21	17	13	3231	3636
s_{96}	63	30	7	26	30	33	12	17	20	14	1433	3720
s_{97}	59	36	3	20	30	29	12	18	17	12	1675	3584
s_{101}	58	34	2	22	24	34	15	17	12	14	1221	3309
s_{102}	55	29	6	20	20	35	11	13	16	15	1127	3160
s_{103}	68	34	2	32	31	37	17	20	18	13	1198	3870
s_{104}	55	26	7	22	26	29	12	17	14	12	1042	3071
s_{105}	61	38	1	22	28	33	13	19	14	15	1329	3343
s_{106}	68	44	4	20	32	36	14	19	14	21	1294	3945
s_{107}	68	28	2	38	33	35	21	18	18	11	1166	3699

Table 30: The $\hat{b}$, $\hat{c}$, $\hat{a}$, $\hat{d}$ and RHM segment of the b , c , a , and d equations of the full (sires included) weaning weight model

Equation	$\hat{b}_1$	$\hat{b}_2$	$\hat{b}_3$	$\hat{c}_1$	$\hat{c}_2$	$\hat{a}_1$	$\hat{a}_2$	$\hat{a}_3$	$\hat{a}_4$	$\hat{d}$	RHM
b_1	1348	–	–	668	630	203	284	405	456	34,276	81,036
b_2	–	221	–	99	122	65	47	64	45	5763	12,621
b_3	–	–	1335	634	701	372	437	314	212	36,989	66,613
c_1	668	99	634	1401	–	315	339	384	363	37,594	79,598
c_2	680	122	701	–	1503	325	429	399	350	39,434	80,722
a_1	203	65	372	315	325	640	–	–	–	16,332	35,900
a_2	284	47	437	339	429	–	768	–	–	19,805	42,734
a_3	405	64	314	384	399	–	–	783	–	20,150	43,990
a_4	456	45	212	363	350	–	–	–	713	20,741	37,696
d	34,276	5763	36,989	37,594	39,434	16,332	19,805	20,150	20,741	2,472,822	4,072,599

Table 31: Full (sires included) weaning weight matrix with α, t_i and s_n equations absorbed

Equation	$\hat{b}_1$	$\hat{b}_2$	$\hat{b}_3$	$\hat{c}_1$	$\hat{c}_2$	$\hat{a}_1$	$\hat{a}_2$	$\hat{a}_3$	$\hat{a}_4$	$\hat{d}$	RHM
b_1	671.232700	-102.281052	-563.949338	23.474716	-23.473460	-90.553011	-70.117371	42.884560	117.738225	-154.435776	5361.008235
b_2		198.586445	-96.304629	-7.331042	7.331042	17.234374	-10.761402	4.413676	-10.886243	81.079676	239.073794
b_3			665.255736	-16.142696	16.143933	73.319896	30.830218	-47.297208	-106900736	73.407390	-5600.080565
c_1				703.917951	-703.916659	3.970116	-31.887443	6.992499	20.927424	312.939235	2434.226575
c_2					708.918174	-3.968857	31.888888	-6.991131	-20.926183	-312.938095	-2434.225061
a_1						492.834027	-169.079442	-170.129358	-153.624041	-570.933771	612.938823
a_2							559.124119	-203.833130	-136.210096	-575.477175	345.003733
a_3								564.391272	-190.427362	-822.795459	309.964464
a_4									530.262740	1969.207595	-1767.955555
d										268,687.991775	106,039.031337

from the full matrix which includes the $\hat{b}_k$, $\hat{c}_l$, $\hat{a}_j$, $\hat{d}$ and RHM portion of the b_k, c_l, a_j and d equations. The fourth table (Table 31: Matrix 6) is the same size as the third and for each postion is built up by taking the element in that postion in the third table and subtracting from it the sum of the cross products of the two columns (one from the first and the other from the second table) which by name signifies that position.

For example the element in the $b_1 b_1$ position equals $1348 - 25(25/36) - 19(19/41)$ and so on down the pair of columns. Likewise the element in the $b_1 b_2$ position equals $0 - 25(3/36) - 19(4/41) - \ldots$. All elements including the RHM are computed in this way.

This matrix is symmetrical and so it is only necessary to compute the elements on one side of the diagonal. To test the accuracy of the computed elements check the $0 = b_1b_1 + b_1b_2 + b_1b_3 = b_1c_1 + b_1c_2 =$ etc.

To solve the matrix the restrictions that $\sum_k \hat{b}_k = \sum_l \hat{c}_l = \sum_j \hat{a}_j = 0$ are applied and the constants estimated in a similar way as in obtaining the weaning weight environmental constants.

Estimates of the $\alpha + t_i + s_{im}$ are obtained by simply solving the equations in the original matrix using the constants $\hat{a}_j$, $\hat{b}_k$, $\hat{c}_l$ and $\hat{d}$ computed.

e.g. $\tilde{s}_{11} = \alpha + t_1 + s_{11} = (2435 + 275.787601 - 433.533001)/36$

$$= 63.2570472$$

etc.

The required reduction was obtained by multiplying all these estimates by their corresponding RHM's to give

$R(\alpha,t,s,b,c,a,d) = 9,067,630.165959$

3. Estimation of the weaning weight heritability by the paternal half-sib method

Now available are the four main figures that are necessary to estimate the heritability of weaning weight.

$k = 52.4236784$ (Calculated from $K = 544.93447$)

$\sum_{ijklm} y_{ijklm}^2 = 9,150,922$

$R(\alpha,t,b,c,a,d) = 9,059,716.697461$

$R(\alpha,t,s,b,c,a,d) = 9,067,730.165959$

$\text{Error S.S.} = 9,150,922 - 9,067,630.165959$

$= 83,291.834041$

$\text{Between Sires S.S.} = 9,067,630.195959 - 9,059,716.697461$

$= 7,913.468498$

But $E(\sum_{ijklm} y_{ijklm}^2) = S + N....(\sigma_s^2 + \sigma_e^2)$

($N....$ total number of observations $= 2904$)

$E\,R(\alpha,t,s,b,c,a,d) = S + N....\sigma_s^2 + (\text{s.inc.d.f.})\sigma_e^2$

(s.inc.d.f. = 62 - see Appendix B(1))

$E\,R(\alpha,t,b,c,a,d) = S + K\sigma_s^2 + (\text{s.exc.d.f.})\sigma_e^2$

(s.exc.d.f. = 17 - see Appendix B(1))

$\text{Error S.S.} = (N.... - \text{s.inc.d.f.})\sigma_e^2$

$= (2904 - 62)\sigma_e^2$

$\text{Error M.S.} = \text{Error S.S.}/(2904 - 62)$

$= 83,291.8340409/2842$

$= \sigma_e^2$

$\text{Between Sires M.S.} = \text{Between Sires S.S.}/(\text{s.inc.d.f.} - \text{s.exc.d.f.})$

$= 7,913.4684984/45$

$= 175.8548555$

but $\text{Between Sires S.S.} = (N.... - K)\sigma_s^2 + (62 - 17)\sigma_e^2$

$\text{Between Sires M.S.} = ((N.... - K)\sigma_s^2 + 45\sigma_e^2)/45$

$$= \sigma_e^2 + k\sigma_s^2$$

$$= 29.30747151 + 52.4236784\sigma_s^2$$

$$\text{but this} = 175.8548555$$

$$\sigma_s^2 = (175.8548555 - 29.30747151)/52.4236784$$

$$= 2.7954426$$

$$h^2 = \frac{4 \times 2.7954426}{29.30747151 + 2.795446}$$

$$= .348$$