CHAPTER 3

PHENOTYPIC AND GENETIC VARIATION IN MALE MORPHOLOGICAL REPRODUCTIVE TRAITS

3.1 INTRODUCTION

The increasing use of objective selection criteria by Australian sheep studs, and the formation of several large open-nucleus group breeding schemes committed to objective measurement and performance recording, has seen increasing use of sire selection indices which incorporate measures of male reproductive traits. Peart (1982), for example, has reported that the largest of the group breeding co-operatives, the Australian Merino Society, has adopted testicular size as one of the nucleus flock ram selection criteria.

However, there are few estimates of genetic parameters for male reproductive traits in sheep. The reports of Goerke et al. (1970), Fogarty et al. (1980) and Thorsteinsson et al. (1982), present heritability (h^2) estimates for gonadal traits but the experimental design associated with the former study gives cause for concern over the reliability of the estimates. Furthermore, there is a lack of agreement between studies with the respective estimates of h^2 of 0.14 $\pm$ 0.08 and 0.13 $\pm$ 0.08 (130 degrees of freedom for sires) for adjusted 140-day scrotal circumference and mean testicular diameter published by Fogarty et al. (1980), differing substantially from the estimate of 0.47 $\pm$ 0.15 for testicular weight at 129 days of age by Thorsteinsson et al. (1982).

There have been no genetic studies of male reproductive traits reported for either Australian-developed breeds of sheep or for sheep managed under the nutritional conditions typical of those areas of Australia where the sheep breeding enterprises are centred.

The aim of the study reported in this chapter was to identify and quantify the environmental and genetic influences on morphological reproductive traits in rams from a composite Merino flock maintained at Trangie N.S.W. and to estimate genetic parameters for these traits.

3.2 MATERIALS AND METHODS

A general description of (a) the environment at Trangie, both generally and specifically during the years of this study, (b) the pastures and management of animal on Trangie Agricultural Research Centre and (c) the genetic composition of the Trangie D flock have been presented in Chapter 2.

3.2.1 Animals and Management

Ram lambs from the Trangie random breeding "D" flock were utilised in this part of the study. At lamb marking time (approximately 3 weeks of age), seven male progeny (where numbers permitted) of each sire were randomly chosen and left entire. Where male full-sib progeny were available only one sib was left entire.

The numbers of entire ram lambs and their mean birth dates for each of the four year-of-birth groups included in the study are presented in Table 3.1.

Table 3.1. Progeny numbers and mean and range of birth date of ram lambs involved in study.

Year of birth	Number of progeny	Day of birth* Mean	Day of birth* Range
1979	201	222	207 - 248
1980	215	221	206 - 247
1981	190	217	205 - 242
1982	164	217	206 - 239

* January 1 taken as Day 1.

Ram lambs grazed with their dams and female sibs until weaning, after which they were maintained as single monosexual year groups until the end of the study. No direct contact with female sheep or older rams was permitted during this period.

3.2.2 Experimental

3.2.2.1 Testicular diameter

With some variation between years, testicular diameter measurements were taken monthly from weaning (4 or 5 months of age) until 12 months of age. For the rams born in 1980 and 1981, testicular diameter was also identified at approximately 19 months of age.

Between year variation in this measurement schedule is detailed in Table 3.2.

The maximum diameter of each testis was measured with calipers and at the point of this measurement, the diameter of a double skin and wool thickness was similarly identified.

Net testicular diameter (TDM) was calculated as the mean diameter (cm) over both testes after correction for skin and wool thickness.

3.2.2.2 Liveweight

For the animals born in 1979, off-pasture liveweight (LW) was recorded at the time of the five and 12 month of age testicular measurements. For the remaining three year of birth groups , LW (kg) was recorded routinely with each monthly testicular measurement.

3.2.2.3 Testicular and epididymal weights

In May 1983, the surviving rams born in 1981 were transported from Trangie to Gunnedah and slaughtered according to commercial practice at Gunnedah Regional Abbattoir. Immediately following slaughter, the scrotum and contents were severed from each ram by knife and placed in a plastic bag with the rams' ear tag. Within one to six hours after slaughter, the scrotal contents were cut free of the scrotum, the *tunica vaginalis* removed from each testis, the cord severed at its junction with the testis and the epididymes dissected free of each testis. All testes and epididymes were immediately weighted to the nearest 0.01 gram. Testicular weight (TW) and

Table 3.2. Measurement schedule for ram lambs born in 1979, 1980, 1981, 1982.

Year-of-Birth Group	Age and month at measurement									
	4 Nov	5 Dec	6 Jan	7 Feb	8 Mar	9 Apr	10 May	11 June	12 July	19 Mar
1979	–	4-12-79	–	–	5-3-80	11-4-80	16-5-80	20-6-80	18-7-80	–
1980	12-11-80	16-12-80	20-1-80	11-2-81	20-3-81	–	2-6-81*	29-6-81	19-7-81	20-3-82
1981	11-11-81	9-12-81	12-1-82	19-2-82	17-3-82	27-4-82	25-5-82	21-6-82	20-7-82	30-3-83
1982	–	14-12-82	18-1-83	18-2-83	15-3-83	11-4-83	17-5-83	20-6-83	19-7-83	–

* Regarded for analysis purposes as 10 month measurement.

epididymal weight (EW) was calculated for each animal as the mean weight of both testes and epididymes respectively.

3.2.2.4 Penis development

Penis development was monitored monthly from 5 months of age for those animals born in 1982. Mature penis development (MPD) was defined as being reached when there were no adhesions between the prepuce and both the glans penis and urethral process. This stage of development was characterised for each of the 164 animals on the basis of age (MPDAGE), liveweight (MPDLWT) and testicular diameter (MPDTDM).

3.2.3 Statistical

Only those animals with complete records were included in the analysis of testicular diameter. In most cases missing or incomplete records were due to ill health or death, and in order to eliminate biases in prior or subsequent records due to such conditions, animals with incomplete records were therefore omitted.

The statistical procedures utilized in the analysis of the data were as follows:

3.2.3.1 Mixed-model least squares analysis of variance

For the data describing TDM and LW at different ages, and predicted TDM at particular values of LW, the following model (Model 1) was adopted:

$$Y_{ijklmn} = \mu + Y_i + T_j + L_{jk} + S_{ijkl} + (YxT)_{ij} + (YxL)_{ijk} + B_m + dD_{ijklmn} + e_{ijklmn}$$

where

Y_{ijklmn} = an observation on an individual animal,

μ = the overall mean,

Y_i = the fixed effect of the i^{th} year,

T_j = the fixed effect of the j^{th} strain,

L_{jk} = the random effect of the k^{th} line of the j^{th} strain,

S_{ijkl} = the random effect of the l^{th} sire of the k^{th} line, j^{th} strain and i^{th} year,

$(YxT)_{ij}$ = interaction between year and strain,

$(YxL)_{ijk}$ = interaction between year and line,

B_m = the fixed effect of the m^{th} birth type class,

d = partial regression of dependent variable on day of birth,

D_{ijklmn} = day of birth for the n^{th} animal,

e_{ijklmn} = random environmental effects, assumed $N(0,\sigma e^2)$ giving rise to the "error" term.

For the significance tests arising from the analysis of variance, year and year x strain were tested against year x line; strain was tested against line; line and year x line were tested against sire and the other effects were tested against the residual or error variation. Where the specified error line was not significant, the effect was tested against the next appropriate error line.

For the data describing testicular and epididymal weights and penis development the following mathematical model (Model 2) was appropriate:

$$Y_{ijklm} = \mu + T_i + L_{ij} + S_{ijk} + B_l + dD_{ijklm} + e_{ijklm}$$

where the symbols for the effects are the same as for Model 1. For the analysis of variance of those traits described by Model 2, strain was tested against line, line against sire and other effects against the residual or error line. Again, where the specified error line was not significant, the effect was tested against the next appropriate error line.

Comparisons between individual class means within main effects were made using Duncan's Multiple Range test (Steele and Torrie 1981). These comparisons were only carried out when the ANOVA mean square for that effect was significant.

Preliminary analysis of variance established that age of dam effects were an insignificant source of variation for all traits and this effect was not included in the final models.

For those traits described by Model 1, interaction effects between years and the random effect sires were assumed to be non-existent.

3.2.3.2 Multiple Polynomial Regression

For those animals born in 1980, 1981 and 1982 respectively, eight, nine and eight, monthly measurements characterised testicular diameter (TDM) and liveweight growth (LW) between four and 12 months of age.

For each of the 569 animals, the relationship between TDM and LW was quantified by the quadratic regression of TDM on LW:

$$TDM = \alpha + \varphi LW + \psi LW^2$$

Using the constant (α) and coefficients (φ,ψ) thus derived, predicted testicular diameter (PTDM) at liveweights of 17, 23, 28 and 33 kg were calculated for each animal and analysis of variance was performed using Model 1 as previously described. Predicted TDM at 17 kg for a small number of animals was negative. In these cases PTDM was set to zero prior to analysis of variation.

3.2.4. Genetic Parameter Estimation

The within-sire ($\sigma^2 w$) and between-sire variance ($\sigma^2 s$) components were calculated for each trait from the relevant analysis of variance by equating the "error" and between sire within strain/line/year (Model 1) or between-sire within-strain/line (Model 2), mean squares (MS) to their expectations. Thus

"error" MS, $\sigma e^2 = \sigma w^2$ and

Between sire MS $= \sigma e^2 + k\sigma s^2$

where k is the weighted average number of offspring/sire

The between-sire component of variance was then calculated as

$$\sigma s^2 = (\text{Between-sire MS} - \text{"error" MS})/k$$

Heritability was estimated in the usual way as

$$h^2 = 4\sigma^2 s/(\sigma^2 w + \sigma^2 s)$$

The genetic and phenotypic correlations were calculated from the appropriate covariances and variances. Thus

$$r_g = \text{Cov}(a,b)/ \sigma_a^2 . \sigma_b^2$$

Standard errors of heritability and genetic correlations estimates were calculated according to the methods of Tallis (1959), and Swiger et al. (1964).

3.3 RESULTS

3.3.1 Testicular Diameter at different ages

3.3.1.1 General

Unadjusted means, standard deviations and coefficients of variation for each of the 10 age-based measures of testicular diameter are presented in Table 3.3.

Table 3.3. Unadjusted means, standard deviations and coefficients of variation for testicular diameter at 4 to 19 months of age.

Testicular diameter	n	Mean (cm)	Standard deviation	Coefficient of variation (%)
4 months	405	1.34	0.27	20.1
5 months	770	1.40	0.40	28.6
6 months	569	1.84	0.59	32.1
7 months	569	1.84	0.59	32.1
8 months	770	3.27	1.14	34.9
9 months	555	4.08	1.12	27.5
10 months	770	3.86	0.95	24.6
11 months	770	4.07	0.73	17.9
12 months	770	4.29	0.64	14.9
19 months	405	5.49	0.55	10.0

3.3.1.2 Sources of variation

The relative importance of each of the sources of variation (Model 1, Section 3.2.3) in testicular diameter (TDM) were assessed using Least Squares Analysis of Variance methods. The mean squares and their levels of significance are presented in Tables 3.4 and 3.5 for each of the age-based TDM traits.

Table 3.4. Analysis of variance mean squares for testicular diameter at 5, 8, 10, 11 and 12 months of age.

		Trait Testicular diameter (cm)				
Source	df	5 month	8 month	10 month	11 month	12 month
Year	3	4.833421***	69.795091***	59.529124***	19.052439***	10.880973***
Strain	3	1.149924***	6.014660***	2.585059***	2.914090	1.656191*
Line within strain	10	0.118975	1.567740	0.865214	1.003833*	0.673556
Year x strain	9	0.07468	1.234229	0.737608	0.660634	0.577068
Year x line	30	0.1325977	0.708942	0.432908	0.508068	0.324084
Sires within line x year	106	0.139315*	0.953209***	0.500433***	0.427253***	0.465150***
Birth type	1	2.939385***	6.345298***	0.432731	0.765347	0.792121
Regression on birth date	1	4.382735***	23.364870***	4.744969***	2.999112***	4.087115***
Remainder	606	0.104418	0.473015	0.310149	0.265209	0.243649

Table 3.5. Analysis of variance mean squares for testicular diameter at 4, 6, 7, 9 and 19 months of age

Source	Testicular diameter (cm) of lambs born 1980, 1981			Testicular diameter (cm) of lambs born 1980, 1981, 1982			Testicular diameter (cm) of lambs born 1979, 1981, 1982	
	df	4 month	19 month	df	6 month	7 month	df	9 month
Year	1	0.333273	3.281960	2	5.999934***	41.935553***	2	87.463059***
Strain	3	0.269609*	1.685975	3	0.721697	3.337735**	3	4.211892***
Line within strain	10	0.046150	0.470876*	10	0.437868	1.394035	10	0.925076
Year x strain	3	0.039113	0.457881	6	0.643537	1.781142	6	1.611281
Year x line	10	0.027782	0.696400**	20	0.312730	0.626053	20	0.963379
Sires within line x year	54	0.090928**	0.309281	81	0.434223***	0.824640***	79	0.757482***
Birth type	1	0.819016***	0.156436	1	2.831183***	5.222408***	1	1.944633*
Regression on birth date	1	0.966707***	0.942716	1	4.736696***	11.883290***	1	5.367242***
Remainder	321	0.057568	0.245001	444	0.258416	0.480965	432	0.4213698

3.3.1.2.1 Year effects

Year of birth and year of measurement effects on TDM were evaluated jointly. TDM growth from four to 19 months of age, for each of the four year-of-birth groups, is illustrated in Figure 3.1. It is apparent from an examination of these curves that the general pattern of TDM growth for the ram lambs born in each of the four years is curvilinear. It is also apparent that there were quite substantial between-year differences in the relative ages at which growth was most rapid, and that in the growth curves after 9 months of age there are substantial departures from the sigmoid pattern.

Table 3.6. Least Squares means (± SE) of testicular diameter at 4 to 19 months of age in rams born in 1979, 1980, 1981, 1982 (cm).

Age	ANOVA significance	Year of birth* 1979 (n=201)	1980 (n=215)	1981 (n=190)	1982 (n=164)
4 months	NS	-	1.41±0.03^{b}	1.33±0.02^{a}	-
5 months	***	1.41±0.03^{b}	1.51±0.03^{c}	1.56±0.03^{c}	1.01±0.04^{a}
6 months	***	-	1.74±0.05^{a}	2.11±0.05^{b}	1.61±0.06^{a}
7 months	***	-	2.02±0.07^{a}	3.31±0.07^{c}	2.46±0.08^{b}
8 months	***	2.23±0.08^{a}	3.05±0.07^{b}	4.32±0.08^{c}	3.27±0.09^{b}
9 months	***	3.13±0.07^{a}	-	5.03±0.07^{c}	3.73±0.08^{b}
10 months	***	3.72±0.06^{b}	3.11±0.06^{a}	4.83±0.06^{d}	4.06±0.07^{c}
11 months	***	3.89±0.06b	3.42±0.05a	4.29±0.05d	4.46±0.06^{c}
12 months	***	4.49±0.05^{c}	4.19±0.05^{b}	3.75±0.05^{a}	4.47±0.06^{c}
19 months	N.S.	-	5.63±0.05^{a}	5.37±0.05^{a}	-

*For each age different superscripts between columns denote significant differences ($P < 0.05$).

Table 3.6 details least squares mean (± SE) for each year-group for these age-based TDM's. Also indicated are the levels of significance of the between-year source of variation as established by the above analyses.

In general between year differences appear to be greatest during the autumn and early winter months of the first year of life, whilst TDM's at the

Figure 3.1 Testicular diameter growth in D flock rams born in 1979 - 1982

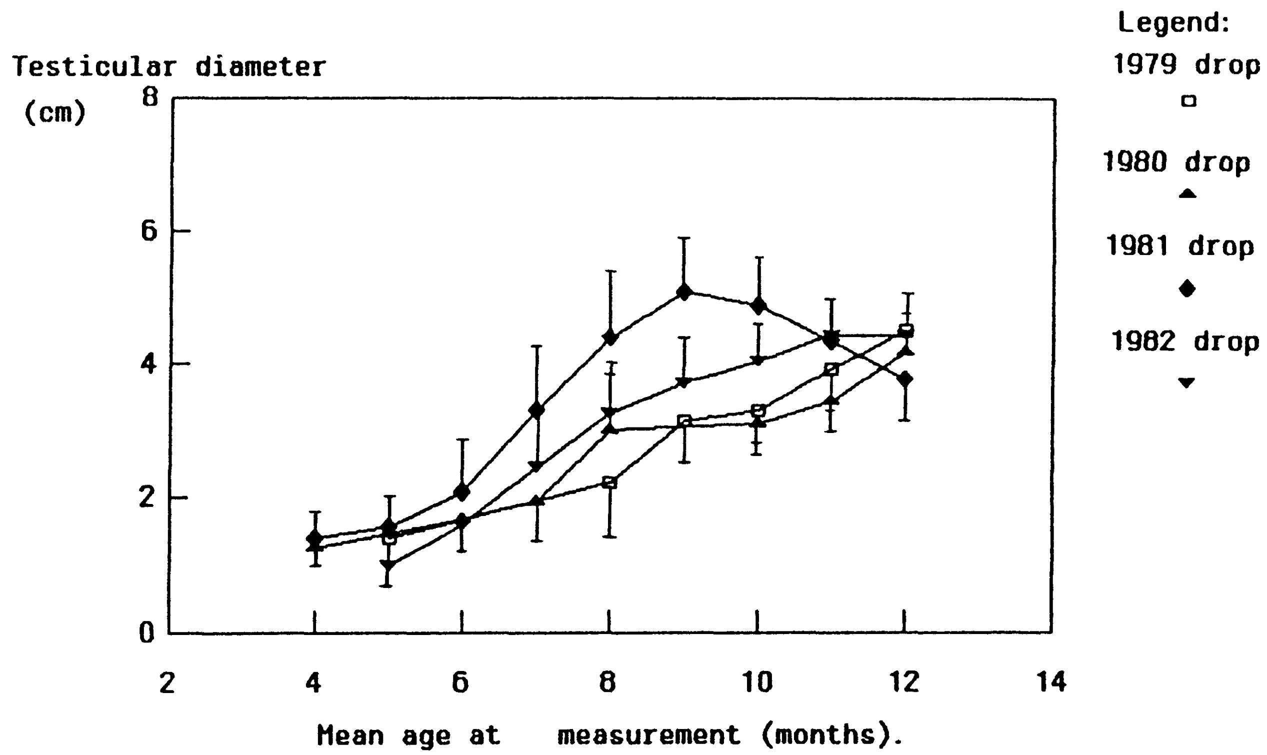
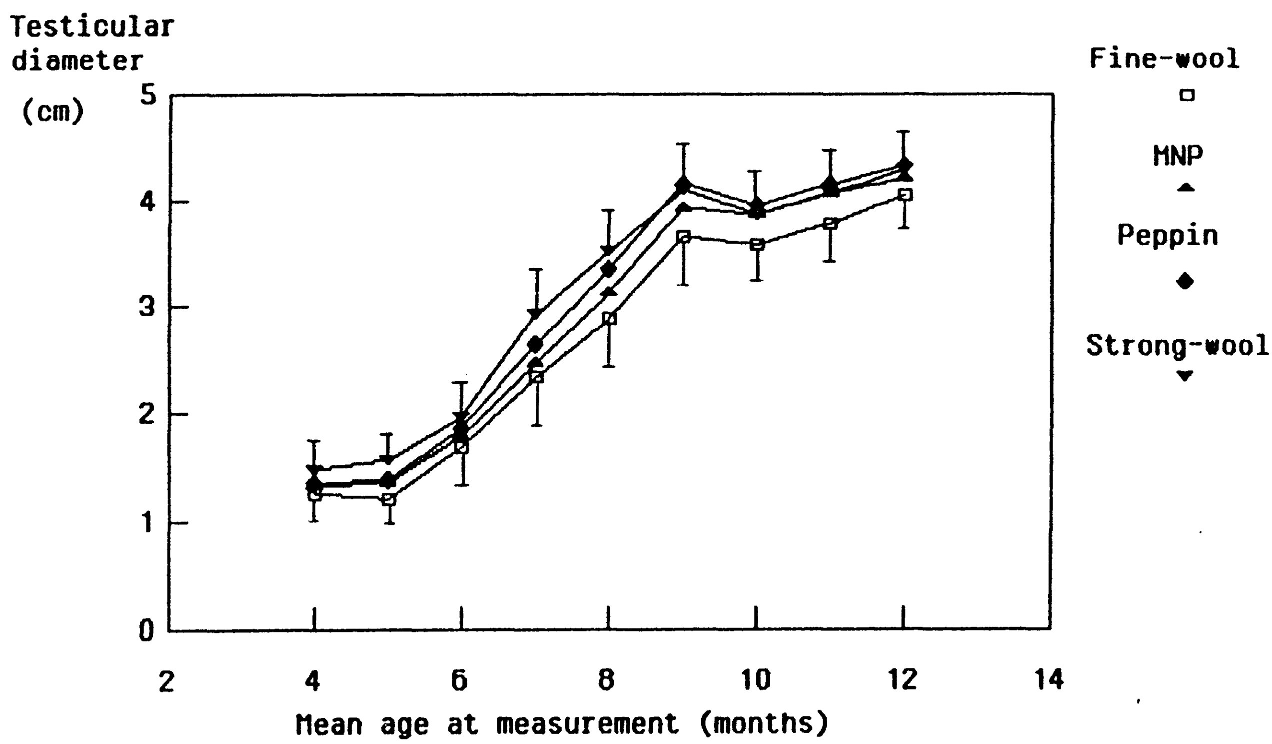


Figure 3.2 Testicular diameter growth of rams of Fine-wool, MNP, Peppin and Strong-wool strains.



extremes of the period of study (4 months and 19 months of age) do not differ significantly between years. There were, however, only two year-of-birth groups represented at these ages. Examination of Figure 3.1 in conjunction with Table 3.6 also reveals relatively frequent changes in the ranking of the TDM of the year-of-birth groups over the growth period under study.

3.3.1.2.2 Birth-type effects

Of the 770 ram lambs included in this part of the study 434 (56.4%) were identified as being single-born whilst the remainder were classified as being from twin or triplet litters. Differences in TDM between animals born as singles or multiples were highly significant ($P < 0.001$) from 4 to 8 months of age, with singles having larger testes than those born as multiples (Table 3.7). After 8 months of age, however, the differences diminished, so that by 10 months of age the two birth-type categories did not differ significantly in TDM.

3.3.1.2.3 Day of birth effects

At all ages up to 19 months a significant component of variation in TDM between animals was accounted for by the inclusion in the model of day of birth as a continuous independent variable (Table 3.8) The regression of TDM on day of birth was consistently negative and ranged from a low of -0.007 at 4 and 19 months of age to a high of -0.027 at 8 months of age.

3.3.1.2.4. Strain effects

TDM growth with age of the four strains is illustrated in Figure 3.2 and the Least Squares means ($\pm$ SE) of each strain at the 10 ages are presented in Table 3.9.

Differences in TDM between the four strains did not show a consistent pattern relative to age. At 6, 11 and 19 months of age, strain differences were a non-significant source of variation in the overall model, whilst at other ages they were significant.

Table 3.7. Least squares means (± SE) of testicular diameter at 4 to 19 months of age for rams born as singles or multiples (cm)

Age	ANOVA Significance	Birth type	
		Single	Multiple
4 months	***	1.39 ± 0.02	1.29 ± 0.02
5 months	***	1.44 ± 0.02	1.31 ± 0.02
6 months	***	1.91 ± 0.04	1.73 ± 0.04
7 months	***	2.72 ± 0.05	2.46 ± 0.06
8 months	***	3.30 ± 0.05	3.13 ± 0.05
9 months	*	4.03 ± 0.05	3.89 ± 0.05
10 months	N.S.	3.85 ± 0.04	3.79 ± 0.04
11 months	N.S.	4.06 ± 0.03	3.98 ± 0.04
12 months	N.S.	4.26 ± 0.03	4.19 ± 0.04
19 months	N.S.	5.46 ± 0.04	5.54 ± 0.05

Table 3.8. Least Squares mean (± SE) regression coefficients of testicular diameter at 4 to 19 months of age on date of birth (cm)

Age	ANOVA Significance	Day of birth	
		Coefficient	SE
4 months	***	-0.007	0.002
5 months	***	-0.012	0.002
6 months	***	-0.014	0.003
7 months	***	-0.022	0.005
8 months	***	-0.027	0.004
9 months	***	-0.012	0.003
10 months	***	-0.016	0.005
11 months	***	-0.010	0.003
12 months	***	-0.011	0.003
9 months	*	-0.007	0.004

Comparison of strain means at the ages where differences were significant, revealed that rams of the fine-wool strain had smaller testes than those of the strong wool strain in all instances. However, they were not significantly different from MNP rams at 4 and 7 months and from the Peppin strain at 4 months of age. The two medium-wool strains differed in TDM only at 8 and 9 months of age and they were both significantly different from the strong-wool strain at 4, 5 and 7 months of age whilst the MNP strain was also different at 8 months of age.

Table 3.9. Least squares means (± SE) testicular diameter at 4 to 19 months of age for fine, MNP, Peppin and Strong wool strains (cm)

Age	ANOVA significance	Strain*			
		Fine	MNP	Peppin	Strong
4 months	*	1.25±0.04[a]	1.32±0.03[a]	1.34±0.02[a]	1.47±0.05[b]
5 months	***	1.21±0.04[a]	1.35±0.03[b]	1.38±0.02[b]	1.55±0.05[c]
6 months	N.S.	1.68±0.07	1.77±0.06	1.85±0.03	1.96±0.09
7 months	**	2.33±0.10[a]	2.47±0.08[ab]	2.64±0.04[b]	2.93±0.12[c]
8 months	***	2.88±0.09[a]	3.12±0.07[b]	3.34±0.04[c]	3.52±0.10[c]
9 months	***	3.66±0.1-[a]	3.92±0.07[b]	4.16±0.04[c]	4.10±0.11[bc]
10 months	***	3.58±0.07[a]	3.86±0.05[b]	3.95±0.03[b]	3.87±0.08[b]
11 months	N.S.	3.78±0.07	4.06±0.05	4.16±0.03	4.08±0.07
12 months	*	4.05±0.06[a]	4.22±0.05[b]	4.33±0.03[b]	4.30±0.07[b]
18 months	N.S.	5.21 ± 0.08	5.59±0.07	5.49±0.03	5.72±0.09

*For each trait different superscripts between columns denote significant differences ($P < 0.05$).

3.3.1.2.5 Line within strain effects

Only at 11 and 19 months of age was the line within strain a signifiant source of variation ($P < 0.05$) (Table 3.5 and 3.4 respectively). As this effect was regarded as a random variable, investigation of specific contrasts between lines was not undertaken.

3.3.1.2.6 Interaction effects

Year x strain and year x line interaction effects were part of the overall model. The only significant interaction effects on the 10 age-based TDM traits was the year x line source for TDM at 19 months of age ($P < 0.01$).

3.3.1.2.7 Sire within strain-line-year

Differences between sires constituted a significant source of variation ($P < 0.01$ or $P < 0.05$) for all the age based TDM traits, except at 19 months of age ($P > 0.05$).

3.3.1.3 Genetic parameters

3.3.1.3.1 Heritability estimates

Table 3.10 details the paternal half-sib heritability estimates for each of the 10 TDM traits. All estimates except that for TDM at 19 months of age are significantly different from zero ($P < 0.05$), whilst the 95% confidence limits are such that none of the 10 estimates are significantly different from each other.

3.3.1.3.2 Phenotypic and genetic correlations

The phenotypic (r_p) and genetic (r_g) correlations between the 10 TDM traits are presented in Table 3.11. All estimates of genetic correlations are positive and relatively high except for those of 4 months TDM with 9, 10, 11 and 12 month TDM, and of TDM at 6 months with that at 9 months of age. The genetic correlation estimates for TDM at 19 months of age with the other 9 TDM traits are all high but are characterised by very high standard errors.

The phenotypic correlations between the TDM traits are all positive and show a consistent pattern of declining relationship with increasing length of time between measurements.

3.3.2 Testicular diameter and liveweight relationships

3.3.2.1 General

Liveweight growth relative to age is illustrated in Figure 3.3 for each

Table 3.10. Half-sib heritability estimates, standard errors, and 95% confidence limits for testicular diameter at 4 to 19 months of age.

Age	Sire df	h^2	SE(h^2)	95% confidence limits	
				Lower	Upper
4 months	54	0.45	0.19	0.07	0.83
5 months	106	0.28	0.13	0.03	0.53
6 months	81	0.54	0.16	0.22	0.86
7 months	81	0.57	0.16	0.25	0.91
8 months	106	0.75	0.15	0.46	1.04
9 months	79	0.62	0.17	0.28	0.96
10 months	106	0.49	0.14	0.22	0.76
11 months	106	0.49	0.14	0.22	0.76
12 months	106	0.69	0.14	0.42	0.96
19 months	54	0.22	0.17	-0.12	0.56

of the three year-of-birth groups where liveweight was recorded at each TDM measurement. Figure 3.4 depicts, for the same groups, TDM growth relative to liveweight at each successive measurement.

Figure 3.3 illustrates the variable nature of liveweight growth in the three groups of ram lambs. The 1982-drop animals were substantially retarded in liveweight at early ages in comparison to the other two groups, but by 12 months of age this group was clearly the heaviest. The other noticeable feature of the liveweight growth patterns was that animals born in 1980 and 1982 achieved relatively rapid gains in LW between 10 and 12 months of age, while in those animals born in 1981, there was a slight decline of 1.1kg. This slight decline in LW of the 1981-born group was accompanied by a substantial contraction in TDM.

3.3.2.2 Genetic parameters

TDM measurements were available for all four year-of-birth groups at

Table 3.11 Genetic (above diagonal) and phenotypic (below diagonal) correlations (± SE) for testicular diameter at 4 to 19 months of age (sire df below genetic correlations).

Age	4 months	5 months	6 months	7 months	8 months	9 months	10 months	11 months	12 months	19 months
4 months	–	1.04±0.12 (54)	0.94±0.11 (54)	0.91±0.15 (54)	0.62±0.19 (27)	0.57±0.26 (54)	0.48±0.26 (54)	0.55±0.30 (54)	0.38±0.28 (54)	1.06±0.51 (54)
5 months	0.76	–	0.82±0.13 (81)	0.77±0.15 (81)	0.75±0.16 (106)	0.76±0.22 (79)	0.83±0.22 (106)	0.87±0.24 (106)	0.78±0.22 (106)	1.28±0.60 (54)
6 months	0.70	0.71	–	0.87±0.08 (81)	0.78±0.10 (81)	0.52±0.23 (54)	0.75±0.15 (81)	0.72±0.9 (81)	0.71±0.16 (81)	1.07±0.44 (54)
7 months	0.61	0.63	0.80	–	0.89±0.06 (81)	0.82±0.14 (54)	0.88±0.12 (81)	1.03±0.14 (81)	0.90±0.14 (81)	1.54±0.56 (54)
8 months	0.51	0.61	0.73	0.83	–	0.84±0.09 (79)	0.83±0.10 (106)	0.80±0.12 (106)	0.76±0.11 (106)	1.40±0.48 (54)
9 months	0.42	0.44	0.49	0.65	0.74	–	0.92±0.08 (106)	0.90±0.11 (79)	0.73±0.13 (79)	1.15±0.25 (27)
10 months	0.42	0.45	0.52	0.59	0.65	0.79	–	1.04±0.07 (106)	0.96±0.07 (106)	1.59±0.47 (54)
11 months	0.40	0.36	0.46	0.50	0.56	0.65	0.76	–	1.05±0.05 (106)	1.79±0.67 (54)
12 months	0.40	0.37	0.48	0.54	0.57	0.64	0.74	0.79	–	1.33±0.42 (54)
19 months	0.21	0.25	0.27	0.34	0.40	0.57	0.47	0.43	0.48	–

Figure 3.3 Liveweight growth in D flock rams born in 1980-1982

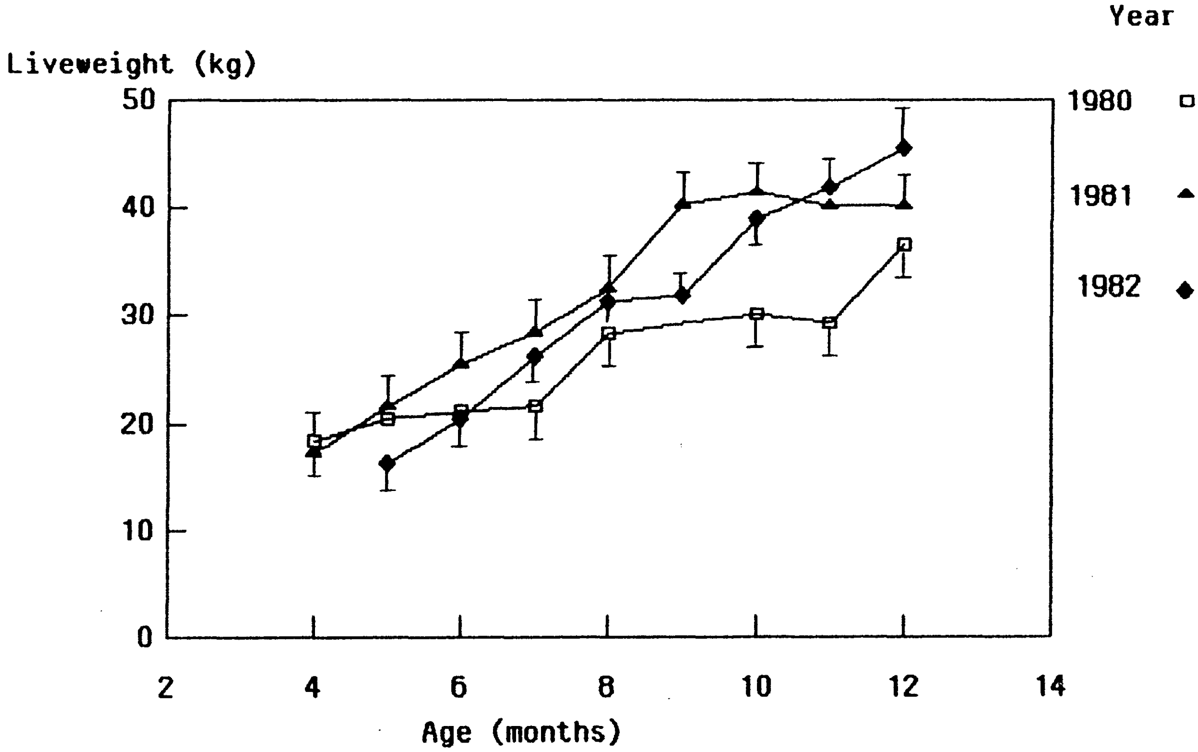


Figure 3.4 Testicular diameter changes relative to liveweight at each successive measurement for D flock rams born in 1980-1982.

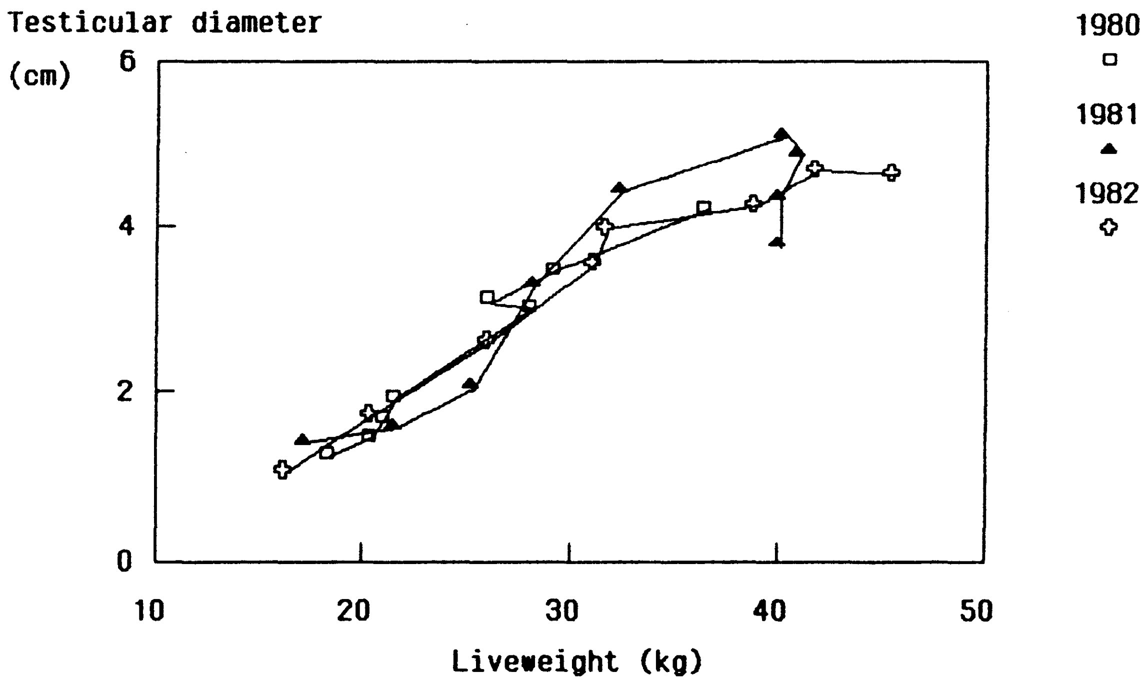


Table 3.12. Genetic (r_g) and phenotypic (r_p) correlations ($\pm$ SE) between liveweight at weaning and 12 months of age and testicular diameter at 5, 8, 10, 11 and 12 months of age (cm)

Liveweight		Testicular diameter at various ages					Liveweight at weaning
		5 month	8 month	10 month	11 month	12 month	
Weaning	r_g	0.84±0.18	0.15±0.26	0.11±0.31	0.26±0.29	0.22±0.26	–
	r_p	0.65	0.49	0.38	0.32	0.34	–
12 months of age	r_g	0.51±0.29	0.70±0.15	0.65±0.18	0.74±0.17	0.80±0.15	0.34±0.31
	r_p	0.44	0.59	0.59	0.56	0.58	0.57

only 5 ages (5,8,10,11 and 12 months). The phenotypic and genetic correlations between liveweight at weaning and at 12 months of age with these 5 age-based measures of TDM, are presented in Table 3.12.

Liveweight at weaning was highly correlated, genetically, with TDM at 5 months of age, but the genetic correlation coefficients with TDM at later ages were all relatively low and had relatively large standard errors. In contrast the genetic correlations with liveweight at 12 months of age were moderate to high with coefficients ranging from 0.51 with TDM at 5 months of age to 0.80 when TDM was measured at the same age (12 months).

3.3.3 Predicted testicular diameter at specific liveweights

3.3.3.1 General

For each of the ram lambs born in 1980, 1981, and 1982, paired measurements of TDM and LW were taken at each monthly measurement. The relationship between TDM and LW for each of the 569 animals born in 1980, 1981 and 1982 was quantified by regression analysis, and predictions of TDM at liveweights of 17, 23, 28 and 33 kg were derived. These particular liveweights were chosen to be representative of the pre-pubertal (17 kg), pubertal (23 and 28 kg) and immediate post-pubertal (33 kg) stages of sexual development, as suggested by the report of Watson _et al_. (1956) and by the results of this study in respect of penis development (Section 4 of this Chapter).

The quadratic regression (see Section 3.2.3.2) of TDM on LW was highly efficient at describing the relationship between these two variables over the period under study. The coefficient of multiple determination, corrected for the degrees of freedom, R^2 (Draper and Smith, 1966) averaged 85.9% (SD = 0.09%) for the 569 regressions, whilst minimum R^2 for an individual animal was 49.0% and the maximum 99.6%.

3.3.3.2 Sources of variation

Least squares analysis of variation for PTDM at the four liveweights (utilising Model 1, Section 3.2.3.1) shows that some different influences were operating on these liveweight-based traits when compared to the analysis of variance of age-based measures of TDM (Table 3.4).

Details of the four analyses of variance of PTDM which are presented in Table 3.13 reveal that variation due to years, birth type and year x strain interaction were all highly significant at all four liveweights. Strain differences were only of significance at 17 kg LW whilst the random line effect was a highly significant ($P < 0.01$) scource of variation on PTDM at 23, 28, and 33 kg. Between-sire variation at 17 KG LW was just significant ($P < 0.05$), but was highly significant at the other three liveweights ($P < 0.001$). Neither the year x line interaction nor the regression on date of birth accounted for significant components of variation at any of the four liveweights.

Table 3.13. Analysis of variance mean squares for predicted testicular diameter (PTDM) at 17, 23, 28 and 33 kg liveweight.

Source	df	Predicted TDM at liveweights of:			
		17kg	23kg	28kg	33kg
Year	2	4.977403***	1.496995**	6.615249***	5.863978***
Strain	3	0.862788**	1.159771	1.585058	1.910503
Line within strain	10	0.305776	0.707747**	1.012763***	1.123289***
Year x strain	6	1.911484***	2.381095***	3.020236***	3.086253***
Year x line	20	0.198855	0.172350	0.221730	0.254561
Sire within line x year	81	0.210513*	0.225411***	0.257258***	0.307179***
Birth type	1	5.904393***	5.050057***	3.342056***	2.147957***
Regression on					
Birthdate	1	0.588618	0.039838	0.000341	0.000688
Remainder	444	0.150454	0.116640	0.132898	0.169000

Least squares mean PTDM at 17, 23, 28 and 33kg for each of the three year-of-birth and the two birth-type categories are presented in Table 3.14.

Animals born in 1980 had larger predicted TDM's ($P < 0.01$) at 17kg liveweight than the other two year groups, but were characterised by smaller testes at the other three liveweights. At 28 and 33kg LW, those rams born in 1981 had significantly larger predicted TDM's than the other two year groups.

Table 3.14. Least squares means (±SE) of predicted TDM at 17,23,28 and 33kg LW for rams born in 1980,1981,1982 and born as singles or multiples.

Year or Birth-type	Predicted TDM at liveweight of: 17kg	23kg	28kg	33kg
1980	1.36±0.04a	2.05±0.04b	2.70±0.04c	3.42±0.04c
1981	0.92±0.04b	2.29±0.04a	3.21±0.04a	3.90±0.04a
1982	1.06±0.05b	2.24±0.04a	3.05±0.05b	3.70±0.04b
Single	1.00±0.03	2.10±0.03	2.93±0.03	3.65±0.03
Multiple	1.24±0.03	2.32±0.03	3.11±0.03	3.79±0.03

*For each year classification, different superscripts between rows denote significant differences (p .05).

Table 3.14 also shows that when rams were compared on an equal liveweight basis, those born in twin or triplet litters had larger testes than those males born as singles. These results are in direct contrast to those obtained with age-based measures of TDM (Table 3.7).

3.3.3.3 Genetic parameters

Half-sib heritability estimates for PTDM at 17, 23, 28 and 33 kg are presented in Table 3.15 along with phenotypic and genetic correlations among these traits and three of the age-based TDM traits.

Heritability estimates tended to be lower at 17 kg (0.34 ± 0.15) than at the higher weights (23, 28 and 33 kg; 0.71 ± 0.17, 0.71 ± 0.17 and 0.58 ± 0.16 respectively), although none of the estimates were significantly different from each other ($P > 0.05$).

The genetic correlations between adjacent measures of PTDM are high

Table 3.15. Heritability (± SE) of predicted TDM at 17,23,28 and 33kg LW and genetic (±SE) and phenotypic correlations between these traits and TDM at 5,8 and 12 months of age.*

Trait	Predicted TDM at liveweight: 17kg	23kg	28kg	33kg	TDM at age: 5 months	8 months	12 months
PTDM at 17kg	0.34±0.15	0.87±0.12	0.62±0.24	0.36±0.31	-0.39±0.43	0.19±0.30	-0.22±0.33
PTDM at 23kg	0.72	0.71±0.17	0.93±0.04	0.79±0.11	0.22±0.29	0.50±0.19	0.29±0.22
PTDM at 28kg	0.35	0.88	0.71±0.17	0.96±0.02	0.56±0.26	0.71±0.15	0.63±0.18
PTDM at 33kg	0.08	0.66	0.93	0.64±0.17	0.79±0.25	0.83±0.13	0.85±0.13
TDM at 5 months	-0.22	-0.02	0.14	0.20			
TDM at 8 months	-0.15	0.21	0.41	0.46			
TDM at 12 months	-0.22	0.07	0.31	0.47			

* a) Genetic correlations (± SE) above the diagonal;
b) Heritability (± SE) on the diagonal;
c) Phenotypic correlations below the diagonal.

but they tend to decline as the age interval increases. A similar pattern exists for the phenotypic correlations between these traits.

Genetic and phenotypic correlations between PTDM at 17 kg liveweight and the three age-based measures of TDM are, with one exception negative, are generally low and the r_g's have high standard errors. In contrast PTDM at 28 and 33 kg have high, positive genetic correlations with TDM at 5, 8 and 12 months of age and these r_g estimates have much smaller standard errors. The equivalent phenotypic correlations are lower by comparison.

3.3.4 Testicular and epididymal weights

3.3.4.1 General

Of the 190 rams from the 1981 year-of-birth group, which were utilised in the study of testicular diameter described previously , 171 were slaughtered in May 1983 when they were 21 months of age.

At slaughter, the trimmed testicular weights (mean of both testes) of the 171 rams averaged 239.7g (SD = 53.7, coefficient of variation = 22.4%), and epididymal weights (mean of both epididymes) averaged 37.5 g (SD = 7.3 , coefficient of variation = 19.5%).

Analyses of the sources of variation in testicular weight (TW) and epididymal weight (EW) revealed highly significant differences between sires in both traits ($P < 0.005$, 27 df). Differences between strains in EW were also significant ($P < 0.05$), with rams from the fine-wool strain having significantly smaller EW than rams from the other three strains which themselves did not differ. (Table 3.16).

3.3.4.2 Genetic parameters

With only 27 degrees of freedom for sires, both the heritability and genetic correlation coefficients calculated from these data are characterised by high standard errors (Table 3.17). The heritability estimate for TW was 1.19 ± 0.34 and for EW 0.85 ± 0.33 and the genetic correlation between these two traits was estimated at 0.95 ± 0.07. Genetic correlations

Table 3.16. Analysis of variance mean squares for testicular and epididymal weights (g) of 21 month-old rams born in 1981.

Source	df	Trait	
		Testicular weight	Epididymal weight
Strain	3	7437.428129	261.883213*
Line within strain	10	5454.910202	71.894333
Sire within line	27	5468.311309***	83.029236**
Birth type	1	230.427733	0.092153
Regression on birth date	1	3186.620673	97.996301
Remainder	128	2065.592313	40.327484

between TW and EW and TDM at all ages were positive although associated with large standard errors.

3.3.5 Penis development

3.3.5.1 General

Routine examination of penis development at each monthly measurement was conducted only on the 164 ram lambs born in 1982. Achievement of mature penis development (MPD) (see Section 3.2.2.4 for definition), was quantified on the basis of age (MPDAGE), liveweight (MPDLWT), and testicular diameter (MPDTDM).

The 164 ram lambs achieved MPD on average at 8.15 months of age (SD = 1.09, CV% = 13.4); at 31.0kg liveweight (SD = 4.3, CV% = 13.9%) and at a TDM of 3.54 cm (SD = 0.66, CV% = 18.6%). Minimum and maximum values for these parameters were 8 and 11 months, 22 and 41 kg and 1.7 and 5.2 cm respectively.

3.3.5.2 Sources of Variation

Least squares analysis of variance, utilizing Model 2 (Section 3.2.3.1) revealed significant effects due only to lines ($P < 0.05$) on MPDAGE and MPDTDM and of birth type ($P < 0.05$) on MPDLWT and MPDTDM (Table 3.18).

Table 3.17. Heritability (± SE) of testicular and epididymal weights (g), and genetic (±SE) phenotypic correlations between them and with TDM at 5,8 12 and 19 months of age*.

Trait	Testicular weight	Epididymal weight	TDM at age: 5 mths	8 mths	12 mths	19 mths
Testicular weight	1.19±0.34	0.95±0.07	0.68±0.32	1.06±0.21	0.67±0.27	1.41±0.66
Epididymal weight	0.82	0.85±0.33	1.11±0.34	1.28±0.27	0.94±0.26	1.38±0.64
TDM at 5 months	0.25	0.25				
TDM at 8 months	0.35	0.32				
TDM at 12 months	0.44	0.41				
TDM at 19 months	0.53	0.52				

* a) Heritabilities (± SE) on diagonal;
b) Genetic correlations (± SE) above diagonal;
c) Phenotypic correlations below diagonal.

Table 3.18 Analysis of Variance mean squares for age (MPDAGE), liveweight (MPDLWT) and testicular diameter (MPDTDM) at attainment of mature penis development.

Source	df	Trait		
		MPDAGE	MPDLWT	MPDTDM
Strain	3	1.74872	13.23721	0.81831
Line within strain	10	2.06877	17.71843	0.97083**
Sire within line	27	1.28737	15.52646	0.40980
Birth type	1	0.46359	102.92515*	1.55602*
Regression on birth date	1	0.94003	34.01856	1.09530
Remainder	121	1.08580	19.18577	0.38913

Ram lambs born as multiples achieved MPD at 30.1 ± 0.7 kg liveweight (Least Squares mean ± SE) and at 3.36 ± 0.14 cm TDM compared to 32.1 ± 0.7 kg and 3.60 ± 0.13 cm for those born as singles.

3.3.5.3 Genetic parameters

Variation between sires was a non-significant source of variation for MPDAGE, MPDTDM and MPDLWT, and the estimate of the "sires" component of variance for the latter trait was negative. Estimates of genetic parameters involving this trait were therefore not calculated.

Half-sib heritability estimates for MPDAGE and MPDTDM were 0.18 ± 0.29 and 0.05 ± 0.28 respectively and the genetic correlation between them was estimated as 1.39 ± 3.43.

3.4. DISCUSSION

3.4.1. Testicular diameter at different ages.

The results presented in this Chapter, highlight once again the importance of environmental influences in genetic studies of grazing animals in areas such as Central-Western NSW where both the incidence and reliability of rainfall is low (Dun, 1964; Robards and Pattie, 1967).

Testicular size and rate of growth of the gonads have been shown to be particularly responsive to nutrition, both during the pre-pubertal (Pretorius and Marincowitz, 1968) and post-pubertal (Oldham et al., 1978; Sutama, 1983) stages of sexual development. In this study, between-year variation in the pattern of testicular growth was substantial, both in terms of testicular size at any one age and in the rate of change between ages. This between-year variation, when examined in conjunction with the rainfall records for Trangie during the period 1979 to 1983 (Table 2.1, Chapter 2) would appear to be closely associated with the pattern and magnitude of rainfall. Biddiscombe, Cuthbertson and Hutchings (1954), on the basis of a five year study of the autecology of native pasture species growing in the Trangie district, found that available moisture was the principal factor in the variable success of germination and seedling survival among perennial grasses and was also the prime factor ensuring recurrence of winter annuals.

Although TDM growth in the ram lambs in each of the four year-of-birth groups followed a general sigmoid pattern up to nine months of age, subsequent changes in TDM ranged from relatively rapid continued growth in those animals born in 1980 and 1982, through to a steady decline in TDM in those animals born in 1981. At nine months of age this latter group had substantially larger testes than the other three groups which could suggest that the negative photoperiod effect on gonadal size, associated with the approach of the winter solstice (as reported by Courot and Ortavant, 1981, for example), is only able to exert a substantial influence when ram lambs have achieved a certain minimum level of physiological maturity, and that this status had not been reached by the other three groups. More likely, however, the contraction of TDM in the 1981 drop primarily reflects the very low rainfall during the period April to June 1982 (33.2 mm) as compared to falls during the other three years (157.8, 114.4, and 223.4 mm in 1980, 1981, and 1983 respectively).

The highly significant effect of birth type (single or multiple born) on age-based TDM was maintained up to an age of nine months, with lambs born as twins or triplets having smaller testes than singles. Whilst Fogarty et al. (1980) identify birth type as a significant source of variation in their study of testicular size, they do not identify the direction of the effect. A recent report by Shrestha, Fiser, Langford and Heaney (1983) on testicular dimensions of ram lambs maintained in a constant light environment and fed high quality rations to promote rapid liveweight gain, indicated that under such conditions birth-type effects were not a source of variation on testicular dimensions at 6, 8 and 10 months of age. The results presented here, however, suggest that under the nutritional conditions prevailing in many of the traditional sheep breeding areas of Australia, selection on testicular size at early ages, without account being taken of birth type, will favour rams born as singles.

There are reports of birth date having a significant effect on testicular size at specific ages (Fogarty et al., 1980; Shrestha et al., 1983). Similarly, in the present study, adjustments for date of birth accounted for significant components of variation at all ages up to and including 19 months. The joining and hence the lambing periods of the D flock were of a similar length to that practiced commercially. Thus selection of rams for testicular size without correction for variation in birth date will tend to discriminate against those lambs conceived later in a joining period.

Genotype effects, as represented by differences between strains and lines within strain, were not consistent across ages. Rams of the fine-wool strain tended to have significantly smaller testes up to 12 months of age than those of the other three strains, whilst rams of the line representing the South Australian strong-wool strain had the largest testes up to seven months of age. Thereafter, the strong-wool animals did not differ from the Peppin or the MNP strain. This could, again, reflect the effect of photoperiod manifesting itself only in those animals whose gonads have achieved a certain minimum size and state of activity (Dyrmundsson and Lees, 1972).

Comparisons among the genetic parameters estimated from the sire-components of variance for the 10 age based traits, are complicated by the variation in sire degrees of freedom contributing to each of the estimates. TDM is moderately to highly heritable at all ages from 6 to 12 months, but at 5 months of age, the heritability estimate of 0.28 $\pm$ 0.13 may suggest that environmental influences play a more important role. The heritability estimate of 0.22 $\pm$ 0.17 at 19 months of age also appears to be lower than those at earlier ages, but the small number of sire degrees of freedom (54) precludes firm conclusions.

It could be expected that the size of the testes at 4 and 5 months would reflect a component due to the dams' mothering ability and milk production and hence reduce paternal half-sib heritability estimates, and this has been noted in heritability estimates of liveweight at various ages, where the experimental design has allowed quantification of maternal components of variance (Pattie, 1968). However, weaning in this flock was not accompanied by any check in liveweight or TDM growth rate and so the significance of the maternal influence may not be as great as would be expected under conditions of more rapid pre-weaning growth. The suggestion that the heritability of testicular size may be lower at ages up to weaning is supported by the report of Fogarty <u>et al</u> (1982) who obtained a heritability estimate of 0.13 $\pm$ 0.07 for testicular diameter at 140 days of age.

The genetic correlations between TDM from five to 12 months of age are all high, indicating a high degree of common genetic control influencing testicular size over this period of the animals' development. The r_g's involving TDM at 4 months of age with TDM between ages 5 to 12 months decline to relatively low levels with increasing age difference, but these estimates are based on fewer sire degrees of freedom and may simply reflect sampling variation. It is likewise difficult to draw firm conclusions about the genetic correlations involving TDM measurement at 19 months of age.

Given the high genetic correlations between these age-based measures of testicular size it is appropriate to calculate an "average" value of heritability for TDM. The unweighted average is 0.49, whilst that weighted for the number of sire degrees of freedom upon which the estimates were based is 0.52.

The phenotypic correlations between the monthly measures of TDM show a regular pattern of decline with increasing age difference between measurements, to the extent that r_p's between TDM at early ages (4 and 5 months) and later ages (11 and 12 months) are relatively low (< 0.40). This suggests that early selection or culling of potential sires on the basis of testicular size may not be particularly accurate in terms of mature gonadal size of current flock rams. Further study of this suggestion is needed to establish whether this apparently low repeatability extends to later ages than those studied here.

3.4.2. Testicular diameter and liveweight relationships

Analysis of the relationship between TDM and LW reveals that like the relationship between age and testicular size, there is considerable variation between the three year-of-birth groups, both in the size of the testes at particular liveweights and in the pattern of testicular growth relative to liveweight. For example, Figure 3.4 shows that at approximately 32kg LW, TDM was 3.5, 4.4 and 4.0 cm for the rams born in 1980, 1981 and 1982 respectively and these parameter values had been obtained at 10 months of age by the 1980-drop rams, but by two months earlier in the other two year groups.

Figures 3.3 and 3.4 also illustrate that rams born in 1982 had substantially lower LW and smaller testes at 5 months of age, but due to sustained rapid growth, by 12 months of age were the heaviest group and had the largest testes. Rate of body growth may therefore be as important a component as absolute liveweight in influencing TDM growth during the first year of life.

The genetic relationship between LW at weaning (4 or 5 months of age) and TDM at 5 months of age is particularly close (0.84 $\pm$ 0.18), but declines at later ages (0.11 to 0.26). These estimates suggest that correction for weaning LW would substantially reduce the heritability of and effectiveness of selection for TDM at five months of age. In comparison, selection on TDM at later ages would be relatively less affected by correction for liveweight at weaning.

Liveweight at 12 months of age is more closely correlated, genetically, with TDM at other ages (range 0.51 to 0.74) than was weaning LW, and the genetic correlation between TDM and LW at 12 months of age (0.85 $\pm$ 0.15) was similar to that for the same traits at 5 months of age. Thus selection of rams on testicular size at any age between 5 and 12 months, will result in the choice of genotypes with desirable genes for liveweight at 12 months of age.

3.4.3. Predicted testicular diameter at specific liveweights.

The aim of examining testicular size of the D flock rams at specific liveweights was to identify the sources of variation in TDM over and above that due to body size, and at liveweights which reflected different stages of sexual development. It was thought that these analyses would provide information on the nature of the genetic control of testicular size, and hence potential sperm production, at developmental stages where it is known that the endocrine milieu controlling gonadal activity are quite different (Lee _et al_, 1976a). In addition, the phenotypic and genetic relationships between these liveweight-based measures and TDM, would establish the extent to which measures of TDM at early ages identifies differences in the rate of attainement of mature gonadal function.

Like the age-based measures of TDM, predicted testicular diameter (PTDM) at all four liveweights showed significant variation between years with the ranking of the different year groups not being constant. This feature of the data reinforces the earlier conclusion that the gonad is more sensitive to environmental influences than the body as a whole.

Differences between strains in PTDM were found only at 17kg LW, where the smaller-framed fine-wool strain animals had larger testes than those from the other three strains. This is in contrast to the strain differences in the age-based measures of TDM, where the fine-wool strain consistently had the smallest testes. As 17kg LW was chosen to represent liveweight at the late pre-pubertal stage of sexual development, this finding could be interpreted as indicating that males of the fine-wool strain begin the pubertal stage of development at a lower liveweight (but at a similar percentage of mature weight) than the other three strains. However Butterfield, Griffiths, Thompson and Zamora (1983) have shown that rams from the fine-wool strain deposit fat at an earlier liveweight than males from the strong-wool strain and therefore the larger testes of the fine-wool ram lambs could be due to earlier scrotal fat deposition rather than seminiferous tubule enlargement.

A significant strain x year interaction was found on PTDM at all four liveweights. Examination of this effect revealed that PTDM of the strong-wool strain rams tended to be the smallest of the four strains in the year groups with the smallest testes, but generally ranked higher than the rams from the two medium-wool strains in the year group with the largest testes. This suggests that the strong-wool strain is either more sensitive to poor nutrition or more responsive to good nutrition than the animals from the medium-wool strains.

The finding that twin and triplet-born rams had greater PTDM than those born as singles at all liveweights also contrasts with the effect of birth-type on the age-based measures of testicular size, where a significant penalty in being born as a twin or triplet, on TDM up to 9 months of age, was found. It is likely that this effect reflects the same mechanisms that result in slower growing lambs attaining puberty at lighter liveweights but older ages than faster growing cohorts (Dyrmundsson and Lees, 1972) Thus although multiple-born males have larger testes than singles when examined at the same weight, it would be expected that they would be older animals. There may also be a genetic component in this difference and this possibility is pursued further in Chapter 6.

The heritibility estimate of PTDM at 17kg liveweight (0.34 ± 0.15) was lower than that at 23, 28 (0.71 ± 0.17) and 33kg (0.64 ± 0.17). These estimates reinforce the conclusion that maternal effects, if unaccounted for, can substantially reduce the heritability of male reproductive traits up to the stage of development at which animals are normally weaned.

Relatively high estimates of genetic correlations were found between PTDM at all four liveweights (Table 3.17), except for that between PTDM at 17 and 33kg LW (0.36 ± 0.31). The large standard error of this estimate and also those associated with the negative r_g estimates between PTDM at 17kg and TDM at 5 to 12 months of age may reflect a decreased accuracy of predicted TDM at the lower end of the liveweight scale. In contrast to the above mentioned negative estimates of r_g, those between PTDM at 33 kg LW and all three age-based measures of TDM were high (> 0.79), whilst those at 28kg were lower and those at 23kg lower still. This pattern probably reflects the fairly large between-animal range in liveweights at early ages, a situation which has substantially diminished by 12 months of age, as evidenced by the comparative coefficients of variation of liveweight (at age 5 months, 20.7%, and at 12 months, 14.9%).

3.4.4. Testicular and epididymal weights.

The mean testicular (TW) and epididymal (EW) weights of 239.7g and 37.5g respectively for the rams slaughtered at 21 months of age are comparable with those of 257g and 50g reported by Knight (1977) for 67 Merino rams aged between one and four years. The substantial variation in age in this study, may largely account for the higher coefficients of variation (43.3% and 32.7% for TW and EW, respectively) than were found in the 171 rams of the present study (22.4% and 19.5%, respectively).

The only significant source of variation in TW in these rams was that between sires ($p < 0.001$), whilst between-sire ($p < 0.01$) and strain ($p < 0.05$) variation was of significance for epididymal weight. Rams from the fine-wool strain had smaller epididymes than those of the other three strains and this was associated with smaller liveweight at 19 months of age. Several authors have reported a close relationship between EW and LW within the one genotype and over a range of sexual developmental stages (Watson et al., 1956; Colyer, 1971 and Hawker, 1976).

The estimates of genetic parameters for TW and EW were based on too few sires to be regarded with confidence. However, they do suggest that TW and EW have a large additive genetic variance component and thus are likely to be highly heritable. The lower but more reliable estimates of Thorsteinsson et al, (1982), who reported the heritability of TW and EW to be 0.47 ± 0.15 and 0.38 ± 0.13, were from lambs slaughtered at 129 days of age. However, on the basis of the results reported earlier in this Chapter, on age-based measures of TDM, it could be expected that the heritability would increase as the masking effect of maternal influences declined.

The genetic correlation between TW and EW was 0.85 ± 0.33 and this value agrees closely with the estimate of 0.85 ± 0.11 reported by Thorsteinsson et al, (1982). Selection for testicular size would therefore be expected to result in closely correlated changes in epididymal size. The genetic correlations between these two organ weights and testicular diameter at ages between 5 and 19 months are suggestive of a close and positive relationship. The phenotypic correlations however, are much lower, suggesting that choice of sires on TDM at early ages will not efficiently identify those animals which have high sperm producing capacities in their second year of life.

3.5 Conclusions

These data, from progeny of the Trangie random breeding D flock, which characterise gonadal growth up to 12 months of age, confirm that the gonad is a volatile organ in terms of its response to environmental influences during this period of growth. They also demonstrate that gonadal growth has a high additive genetic component strongly displayed in the phenotype once the masking effects of the maternal influences diminish. Thus, selection for testicular size in Merino males, maintained under similar environmental conditions to those prevailing at Trangie, NSW, would result in relatively rapid response if selection was based on measurements taken at any time from one to two months post-weaning up to 12 months of age. The apparently lower heritability at 19 months of age suggests that selection during the second year of life may not yield as rapid a response.

The importance of correction factors is also emphasised by the results presented in this Chapter. Both date of birth and birth type continued to have an important influence on gonadal size through to 12 months of age and indicate that selection without correction for these environmental sources of variation, would mitigate against selection of animals born in multiple litters and against animals born later in a lambing period.

Genetic correlations between testicular size at the ages monitored in this study are such that the same basic genetic control would appear to be operating on gonadal size over a wide range of ages.

The genetic relationships between liveweight at weaning and testicular size at different ages indicate that liveweight at weaning, whilst having a high degree of common genetic control with testicular size at this age, is not closely related to testicular size at later ages. Thus, correction for weaning liveweight differences, when selecting on testicular size at ages greater than 7 months, would not be expected to greatly influence expected selection responses, while correction for 12 month liveweight would be expected to result in substantial reductions in selection progress.

CHAPTER 4

PHENOTYPIC AND GENETIC VARIATION IN THE LIBIDO AND SERVING CAPACITY OF MERINO RAMS.

4.1 INTRODUCTION

Successful fertilization of the female germ cell requires optimal functioning of a complex physiological and behavioural system which involves both male and female. Whilst it is difficult and sometimes misleading to examine independently, specific components of this system, one such component that has received considerable research attention is that of male sexual behaviour. General principles and features relating specifically to the ram have been reviewed in Chapter 1.

The conclusions arising from that review are summarised below:

i) Ram libido and serving capacity can be assessed by single- or multiple-ram pen-tests using spayed oestrous or restrained non-oestrous ewes. The total number of services (ejaculations) achieved in two single ram pen-tests of one hours' duration gives the most accurate prediction of paddock mating performance.

ii) Rams that are sexually inactive or of low serving capacity in pen-tests may perform better than predicted in paddock mating.

iii) Flock fertility has been shown to be related to serving capacity when mating is for periods of less than three weeks or where mating loads are maintained at high levels for longer periods. However, under normal commercial conditions where mating is for five weeks or more, it is likely that rams of high serving capacity will not be able to express their maximum capacity after the third week.

iv) Of the environmental factors which affect ram serving capacity, nutrition and health can have pronounced effects, whilst the effects of physiological age and prior heterosexual experience need more study.

The review of literature also established that whilst breed differences in ram behavioural traits have been found, there have been no reports of research which aimed to identify and partition environmental and genetic sources of variation in such traits.

The aim of the work reported in this chapter was to identify the sources of variation in various measures of male sexual performance in young Merino rams, and to estimate genetic parameters from the appropriate variance components.

4.2 MATERIALS AND METHODS

4.2.1 Animals

Merino rams from the Trangie D flock which were born in 1979 (n = 201), 1980 (n = 215) and 1981 (n = 190) and utilised in the investigation of testicular size described in Chapter 3, together with an additional 231 rams from the same flock and born in 1978, formed the basis of this study.

Approximately 280 mature-aged ovariectomised Merino ewes of unknown genetic background were used in the serving capacity tests.

4.2.2 Experimental

Each year-of-birth cohort of rams was run as a single monosexual group from weaning until tested for serving capacity at approximately 20 months of age in March/April of 1980-1983. The 1978-born animals were managed as previously described for the other three year-of-birth groups with the exception that no testicular measurements were taken at any stage from these animals.

All four birth-groups were shorn in October at approximately 14 months of age.

4.2.2.1 Serving capacity tests

Serving capacity tests were conducted in a 10-pen test area.

Each pen was approximately 6 metres x 6 metres and the fences were approximately one metre in height. The pens were situated in an open paddock area and rams were maintained, during the period of testing, in holding paddocks of between 0.5 and 5 hectares. Supplementary feed in the form of high quality lucerne hay was provided to rams and ewes during this period.

Oestrus was induced in the ovariectomised (OVX) ewes by two intra-muscular injections of 25mg of progesterone in peanut oil on days one and three and one intra-muscular injection of 200μg of oestradiol benzoate in peanut oil on day 5. Pen-tests were conducted on day 6 and for each ewe, involved approximately 4 hours of testing. The OVX ewes were divided into three groups of 80 and following the first round of testing, were re-cycled using the above oestrus preparation schedule.

Each ram received two 20-minute introductory tests and two one-hour tests. For each year-of-birth group, the time required to complete the two 20-minute tests was 4 to 5 days, whilst the one-hour tests extended over a further two weeks. Visual contact between rams was permitted during the 20-minute tests but was eliminated for the one-hour tests by placing hessian around each pen.

Tests consisted of observations on the number of mounts and services performed by a ram in the presence of four oestrous OVX ewes. Observations on pen activity were made from an elevated platform adjacent to the test pens. Normally three observers were in attendance. Mounts were defined as occurring when a ram raised both forelegs onto the rump of a ewe, whilst services were defined as being achieved when a mount was accompanied by a distinctive pelvic thrust, elevation of the head, immediate dismounting and a subsequent period of inactivity (Banks, 1964).

An index of serving capacity was calculated for each ram based on the number of mounts and services for each of the one-hour tests. Index values were allocated on the following basis:

0 - No mounts or services,

1 - One to five mounts but no services,

2 - Greater than five mounts but no services,

3 - One service,

4 - Two or three services

5 - Four to six services

6 - Greater than six services.

4.2.2.2 Other measurements

One week prior to the commencement of the serving capacity tests, rams born in 1980 and 1981 were measured for testicular diameter (as described in Chapter 3, Section 2.3) and had their liveweights recorded.

4.3 STATISTICAL

4.3.1 General

Data on the sum of the number of services (SERVES) and index values (INDEX) were examined by Least Squares Analysis of Variance. The model used to partition the variation was that designated as Model 1 in Section 3.2.3.1 of Chapter 3.

Preliminary analyses revealed that 37.9% of the 837 rams tested failed to serve in either of the two one-hour pen-tests. Two additional sets of analyses were therefore performed. In the first, rams were allocated to one of two categories on the basis of number of services performed in the two one-hour tests; category 0 for those rams failing to serve and category 1 for those achieving at least one service. This categorical trait was designated as ALLNON. For the second set of analyses, the data was transformed by allocating rams to one of four classes on the basis of the number of serves achieved in the two 1-hour tests. Allocation was on the following basis:

1 - zero serves,

2 - one or two serves,

3 - three to five serves,

4 - six or more serves.

This parameter is referred to as TRANSF.

4.3.2 Genetic parameters

The same procedures as utilized in Chapter 3 and detailed in section 3.4, were adopted for estimation of genetic parameters. Genetic correlation coefficients were not calculated when negative sire components of variance were found for any trait.

4.4 RESULTS

4.4.1 General

Table 4.1 details mean values and statistics of dispersion for the eight measures of serving capacity derived from the two one-hour pen-tests. All measures are characterised by large coefficients of variation with the three variables associated with the number of serves performed having coefficients

Table 4.1. Mean values, standard deviations, coefficients of variation and range of values for measures of serving capacity derived from the two one-hour pen tests (n = 837)

Measure of serving capacity	Mean	Standard deviation	Coefficients of variation %	Range
No. of serves in first test	1.20	1.60	133	0-7
No. of serves in second test	1.49	1.80	121	0-8
No. of serves in both tests	2.69	2.99	111	0-14
Index value in first test	2.24	1.83	82	0-6
Index value in second test	2.58	1.81	70	0-6
Index value in both tests	4.82	3.33	69	0-12
TRANSF	2.25	1.15	51	1-4
ALLNON	0.62	0.49	79	0-1

greater than 100%. When the total number of serves performed in the two tests was transformed as previously described to the new variable TRANSF, the coefficient of variation was reduced from 111% to 51%.

The frequency distributions of the number of serves and index values for each test and the combined total for the two tests are illustrated in Figures 4.1 and 4.2. Of the 837 rams tested, 447 (53.4%) did not serve in the first test, 399 (47.7%) of the total failed to serve in the second test and 317 (37.9%) failed to serve in both tests.. Index scores of one or more were achieved by 567 (67.7%) rams in the first test, whilst 633 (75.6%) rams were similarly classified in the second test. Thus 177 (21.1%) and 195 (23.3%) showed mounting activity but did not achieve service in the first and second tests respectively.

4.4.2 Sources of variation

Least Squares ANOVA mean squares for the effects in the model describing variation in the eight measures of serving capacity are presented in Tables 4.2 and 4.3.

These analyses show the highly significant effect ($P < 0.001$) of variation between years (year of birth and year of measurement accounted for co-jointly) in all eight parameters. Examination of the Least Squares year means, which are detailed in Table 4.4, reveals that for all parameters, rams born in 1981 and tested in 1983 had significantly higher measures of serving capacity ($P < 0.01$) than the other three year-groups whilst the latter did not differ from each other. The superiority of the 1981-born rams manifested itself not only in the number of serves per ram which served ($P < 0.01$), but also in the lower percentage of rams which did not serve.

The only other consistently significant source of variation was due to the differences between lines within strains which were significant ($P < 0.05$) for all parameters except for the number of serves in the second pen-test. Differences between the nine lines within the Peppin strain were the principal source of this variation, with rams from one line being of

Figure 4.1 Frequency distribution of number of serves in 1st, 2nd and combined 1-hour tests.

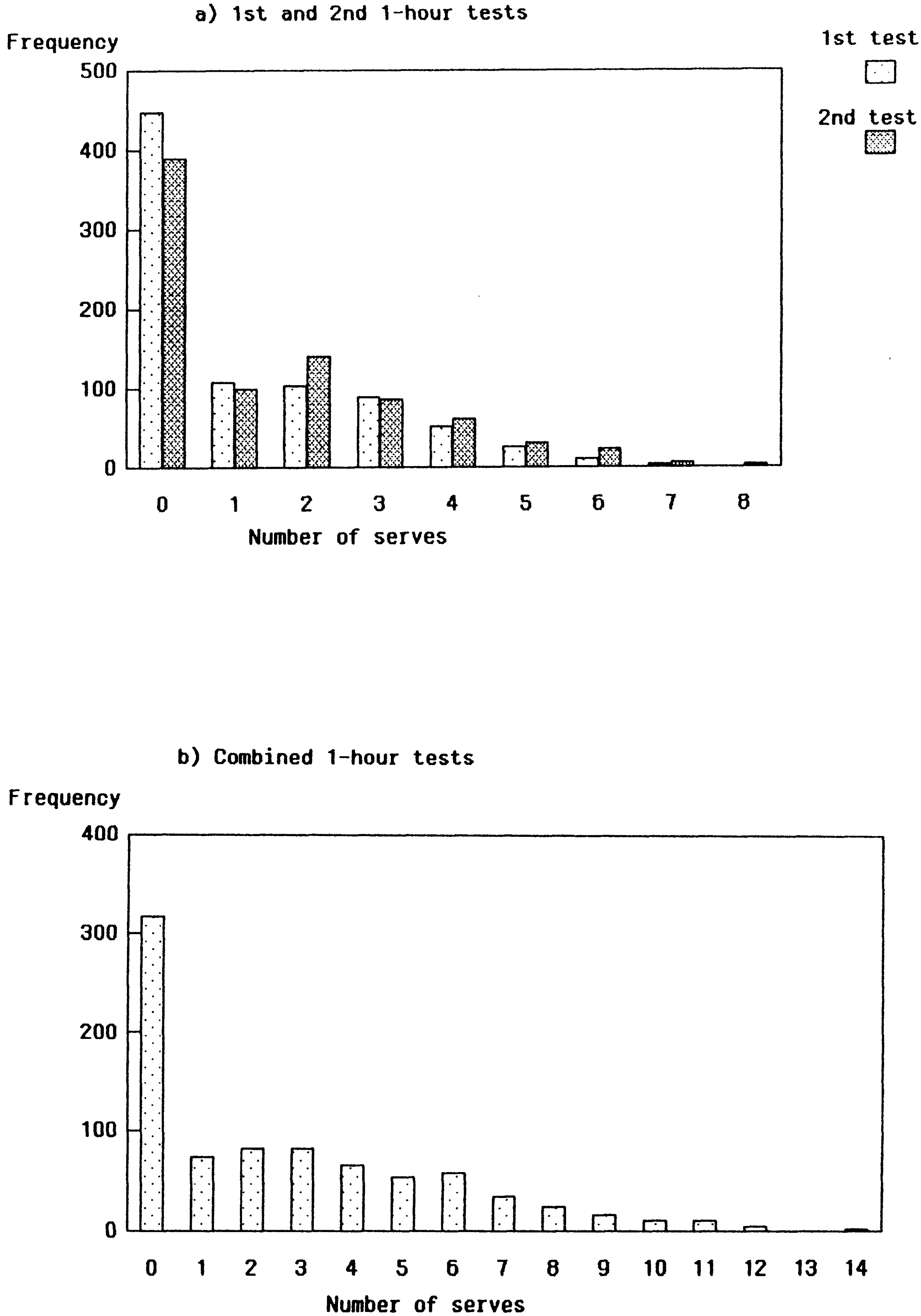
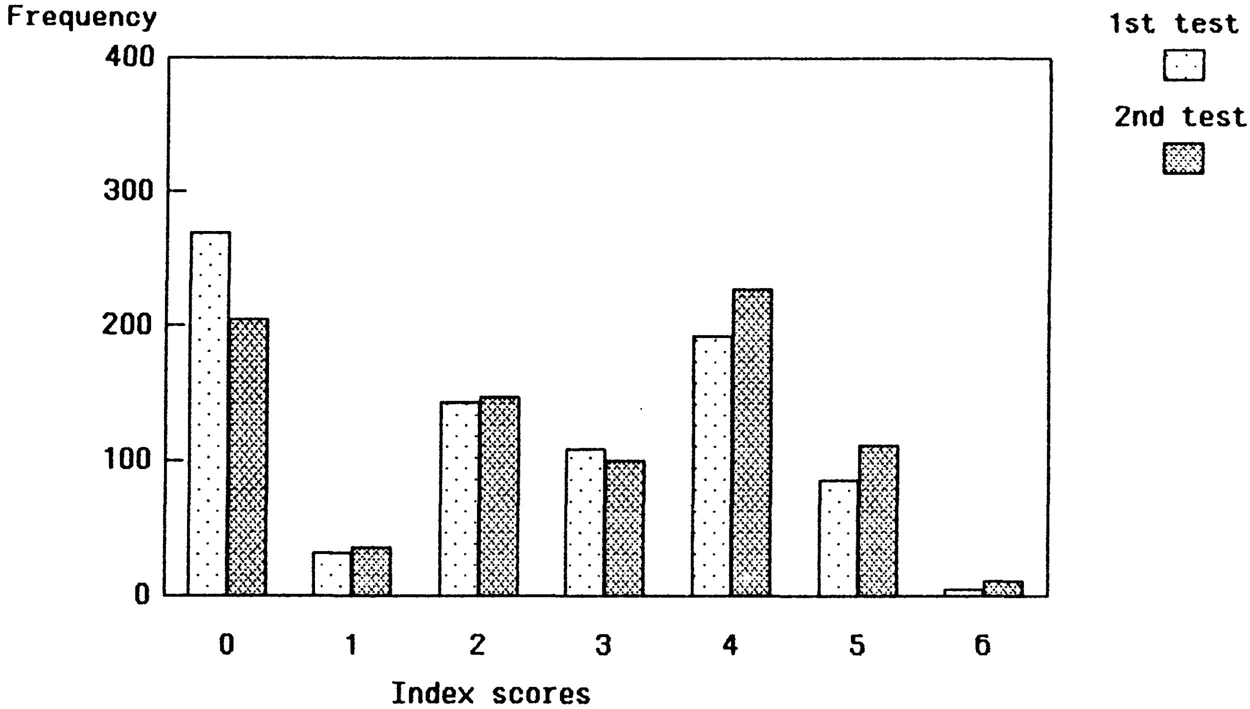


Figure 4.2 Frequency distribution of index scores in 1st, 2nd and combined 1-hour tests.

a) 1st and 2nd tests



b) Combined 1-hour tests

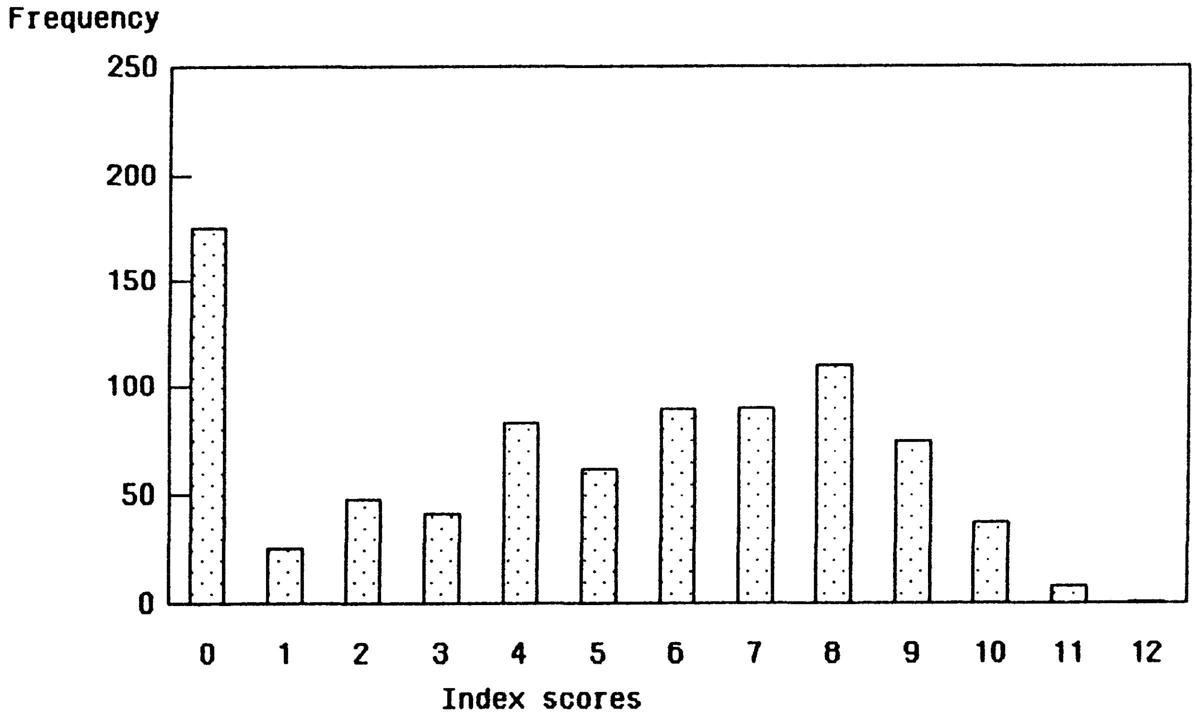


Table 4.2. Analysis of Variance mean squares for index of serving capacity measures

Source	df	Index of serving capacity in: 1st 1-hour test	2nd 1-hour test	Combined tests
Year	3	58.923710***	55.606748***	191.553831***
Strain	3	0.480294	3.623280	9.559929
Line within strain	10	7.840403**	6.296209*	15.424496*
Year x strain	9	3.685989	1.7128971	12.981025
Year x line	30	3.941435	3.434638	9.759342
Sire within year x line	107	2.640345	2.847910	6.744851
Birth type	1	14.668717*	6.786011	20.184929
Regression on birth date	1	4.770264	0.816824	2.063033
Remainder	672	2.897012	2.840149	7.528708

consistently poorer performance than the representatives of the other eight lines.

Birth type was a significant source of variation ($P < 0.05$) for the index values assigned to the rams for the first one-hour test and the two tests combined. Single-born animals had index values of 2.34 ± 0.09 and 5.02 ± 0.16 for these two parameters, respectively, whilst those rams born as multiples had values of 2.04 ± 0.10 and 4.51 ± 0.18. Variation attributable to birth type approached significance for the number of serves in the first test ($P < 0.08$), the total number of serves over both tests and TRANSF ($P < 0.10$) with the direction of the effect being the same as for the two index parameters.

The between-sire source of variation was not of significance for any of the eight serving capacity measures and the calculated sire components of

Table 4.3. Analysis of Variance mean squares for serving capacity parameters involving numbers of serves

Source	df	Serving capacity measures				
		Number of serves in first test	Number of serves in second test	Combined test number of serves	TRANSF	ALLNON
Year	3	31.271644***	71.136411***	191.553831***	26.765206***	3.107128***
Strain	3	1.110191	5.308544	9.559929	0.759815	0.202514
Line within strait	10	5.031185*	4.045268	15.424496*	2.546181*	0.443134
Year x strain	9	3.885392	3.821342	12.981025	0.897585	0.061089
Year x line	30	3.161360	3,246030	9.759342	1,477603	0.284703
Sire within year x line	107	2.071997	2.657315	6.744851	1.027387	0.203307
Birth type	1	7.164515	3.298230	20.184929	3.677653	0.414290
Regression on birth date	1	1.788431	0.009802	2.063033	0.057663	0.089181
Remainder	672	2.329633	2.770009	7.528708	1.150596	0.209248

Table 4.4. Least squares means (± SE) of measures of serving capacity in the two one-hour pen-tests*

		Number of serves			Index score				
Year	n	1st test	2nd test	Combined tests	1st test	2nd test	Combined tests	TRANSF	ALLNON
1978	231	0.97 ± 0.13^{a}	1.25 ± 0.25^{a}	2.22 ± 0.24^{a}	1.88 ± 0.15^{a}	2.20 ± 0.15^{a}	4.08 ± 0.27^{a}	2.05 ± 0.09^{a}	0.52±0.04a
1979	201	0.82 ± 0.16^{a}	1.11 ± 0.17^{a}	1.94 ± 0.28^{a}	1.60 ± 0.18^{a}	2.22 ± 0.17^{a}	3.82 ± 0.32^{a}	1.95 ± 0.11^{a}	0.52 ± 0.05^{a}
1980	215	1.00 ± 1.15^{a}	0.77 ± 0.16^{a}	1.77 ± 0.27^{a}	1.97 ± 0.17	1.92 ± 0.17^{a}	3.89 ± 0.30^{a}	1.94 ± 0.10^{a}	0.51 ± 0.04^{a}
1981	190	2.06 ± 0.15^{b}	2.71 ± 0.17^{b}	4.76 ± 0.28^{b}	3.35 ± 0.17	3.60 ± 0.17^{b}	6.94 ± 0.31^{b}	3.03 ± 0.11	0.87 ± 0.05^{b}

* Means within columns differing in subscripts, significantly different ($p < 0.01$)

variance were negative in all cases except for the second test index value.

4.4.3 Repeatability of serving capacity

Over the two tests, repeatability of the number of services achieved by the 837 rams was 0.54 ± 0.02. This value, however, includes the records of the 317 rams which did not serve in either test and were therefore perfectly repeatable. For the 520 rams which served in at least one of the two tests, the repeatibility of performance was 0.26 ± 0.04, whilst for the 318 rams which achieved at least one serve in both tests, the repeatability was 0.30 ± 0.05.

4.4.3.1 Identification of rams of high serving capacity

The efficiency with which the pen-test procedure identifies rams of high serving capacity (HSC) can in part be tested by examination of the repeatability of serving performance in the two pen-tests for those rams classified as being of HSC on the basis of their first test performance.

A criterion frequently used to distinguish groups at the extremes of distributions is that they should lie more than two standard deviations above the mean value. Whilst the frequency distribution of the number of serves achieved in the first test does not fit closely the shape of any conventional distribution, it does approximate that of the Poisson distribution.

Utilizing the property of the Poisson distribution, that the sampling variance is equal to the mean value, the cutoff value of two standard deviations above the mean number of serves in the first test (1.20 serves) was (approximately) four serves.

The performance statistics of the 91 (10.9%) rams thus classified as being of HSC by the above criterion are presented in Table 4.5.

Table 4.5. Distribution (%) of the number of serves in the two tests for the 91 rams classified as being of high serving capacity in the first test.

Test	n	0	1	2	3	4	5	6	7	8	Mean
		Number of serves									
First test	91	-	-	-	-	56	27	12	5	-	4.65
Second test	91	8	5	25	14	18	11	12	4	3	3.46

These data reveal that on the basis of their second pen-test serving performance, only 47% of the 91 rams would have been similarly classified as being of HSC. In more formal terms the repeatability of serving performance of this group of rams was 0.18 $\pm$ 0.10 which is not significantly different to zero.

4.4.3.2 Identification of sexually inactive rams and rams of low serving capacity

Of the 447 (53.4% of the total) rams which did not achieve service in the first one-hour pen-test, 317 (70.9%) of these, did not serve in the second test. Of the 130 rams which therefore began to serve only in the second test, 22 did so at a level of four or more serves, a performance which would have had them classified as being of high serving capacity if the criterion developed in the previous section had been used (Table 4.6).

Table 4.6. Distribution (%) of the number of serves in the second test for rams with zero, one or two serves in the first test.

Number of serves in first test	n	0	1	2	3	4	5	6	7
0	447	71	10	10	4	3	1	0.5	0.5
1 or 2	210	24	18	26	15	8	5	3	1

Of the 317 rams which did not serve in either test, 98 (30.9%) exhibited mounting behaviour in the second test, and thus could not be regarded as being sexually inactive.

Table 4.6 also details the serving performance of the 210 rams which achieved one or two services in the first pen-test. Examination of the second test performance of this group of rams reveals a similar wide variation in serving capacity as for the other groups previously considered, with values ranging from zero to seven serves.

4.4.4 Genetic parameters

The sire component of variance, derived from the Least Squares Analysis of Variance (Section 4.3.2), was a negative value for all eight measures of serving capacity, except for the index score in the second one-hour pen-test. Heritability has, however, been estimated for all eight measures of serving capacity and these estimates are presented in Table 4.7.

Table 4.7. Heritability estimates (half-sib) for measures of serving capacity (sire df = 107; weighted number of offspring/sire = 4.76).

Trait	h^2	SE (h^2)
No. of serves in first test	-0.095	0.13
No. of serves in second test	-0.034	0.12
No. of serves in both tests	-0.089	0.13
Index value in first test	-0.076	0.13
Index value in second test	0.002	0.10
Index value of both tests	-0.069	0.13
TRANSF	-0.092	0.13
ALLNON	-0.024	0.12

These heritability estimates are not significantly different from zero and all have standard errors of greater magnitude than the estimate itself.

4.4.5 Relationships between measures of serving capacity and testicular size and liveweight

For the 405 animals born in 1980 and 1981, testicular diameter and liveweight were measured immediately prior to these rams being pen-tested for serving capacity in 1982 and 1983.

Uniformly negative estimates of the sire components of variation in measures of serving capacity precludes any estimation of genetic relationships with other traits. However, phenotypic correlations between the combined number of serves and index values from the two one-hour pen-tests and testicular diameter at five, eight, 12 and 19 months of age and liveweight at 19 months of age for the 405 rams are presented in Table 4.8. None of the estimated phenotypic correlations was significantly different from zero.

Table 4.8. Phenotypic correlations between the total number of serves or index score and TDM at 5, 8, 12 and 19 months of age and LW at 19 months of age for rams born in 1980 and 1981 (n = 405)

Trait	Total serves r_p	Index score r_p
TDM at 5 months	-0.02	-0.08
TDM at 8 months	0.02	0.00
TDM at 12 months	-0.02	0.01
LW at 19 months	-0.06	-0.07

4.5 DISCUSSION

4.5.1 General

There are no reports in the literature of investigations which have aimed to estimate genetic parameters for ram libido and serving capacity. This is not surprising, given the extremely time-consuming and labour-intensive nature of the test systems which have been developed to quantify ram sexual performance and the necessity to test large numbers of animals for precise estimation of genetic parameters.

The aim of testing rams for serving capacity is to predict the mating performance of individual rams in a paddock mating situation. In normal commercial flock joinings, rams are mated in groups or syndicates, a situation where interactions between rams occurs. There is conflict in the literature, however, as to whether dominance order in a ram group has an effect on the serving performance of individual rams (Lindsay and Robinson, 1961; Hulet, 1962; Lindsay, 1966 and Fowler and Jenkins, 1976). These studies have differed in respect of one or more of the following; ram percentage, paddock size and topography, age of rams and ewes and level of nutrition, and differences in these factors could easily account for the disparity in the conclusions reached.

Allowing for the fact that social interactions between rams in syndicate matings may influence individual ram performance, there have been no studies of the relationship between performance in serving capacity tests and subsequent quantified performance in syndicate group matings. Kilgour,(1980) and Kilgour and Whale, (1980) have established, however, that paddock mating performance when rams are joined singly, can be accurately predicted by the performance in the pen-test system which was utilized in the work reported in this Chapter.

The mean serving performance of the 837 young rams from the D flock appears to be low in comparison to other reports. Although in most of these other studies, mature and sexually experienced rams were used, Fletcher (1976) also tested one and a half year old Merino rams and found for those rams showing sexual activity the mean number of ejaculations in one hour of pen-testing (three 20-minute tests) was 11.3. This figure is extremely high compared to the levels of performance found in the D flock rams.

The rams studies by Fletcher (1976) also displayed a very low level of sexual inhibition with only 5% being so classified. In the rams studies here, 37.9% failed to serve in either test, whilst at the conclusion of the second test, 24% had not shown any sexual activity. These levels of inactivity are similar to those reported by Hulet et al. (1964) and Mattner et al. (1973). The latter reported on the serving performance of 75 eighteen-month-old Merino rams and found 22.7% showed no sexual activity after three 20-minute pen-tests and 48 hours of association with oestrous ewes in a paddock. A subsequent five week joining of the inactive rams found that the majority began to mount and serve at some stage over the five week period. On the basis of the above finding, and the fact that there was a significant decrease in the level of sexual inhibition in the D flock rams in the second pen-test, additional testing or flock mating experience would result in a further decline in the level of sexual inactivity in the rams studied here.

4.5.2 Sources of variation

Analysis of the sources of variation in the eight measures of serving capacity revealed a highly significant difference between the year-of-birth groups. The substantially higher serving performance and lower levels of sexual inactivity of the 1981 drop rams cannot be readily explained by the physiological parameters measured in this study. Although this group of rams also differed markedly in the rate and pattern of liveweight and gonadal growth from those born in 1979, 1980 and 1982, there was no consistent association between these differences and the superior serving performance of the 1981-born animals. For example, in comparison to the rams born in 1980, the 1981-drop were heavier at 5 and 12 months of age (21.1 kg versus 20.8 kg and 39.8 kg versus 36.7 kg respectively) but at 19 months of age the situation was reversed with the 1980-drop rams weighing 53.0 kg compared to 50.5 kg for those born in 1981. This may therefore suggest that if rate of growth or absolute liveweight influenced the development of patterns of sexual behaviour, that these effects were carried over from the first sexual season. Howles et al. (1980) have shown that short-daylength photoperiod promotes the development of sexual behaviour in pubertal males when compared to long-daylength photoperiod. Given the more rapid attainment of the pubertal stage of development by the 1981 drop rams (Figure 3.3), it can be hypothesised that their initial development of sexual behaviour, albeit in a homosexual environment, may have occurred during their first sexual season. They may therefore have been behaviourally, far more mature at the time of pen-testing in the second season than the other three year groups.

The tendency for single born rams to have better serving performance than those rams born as twins (a finding which was of statistical significance for the first test and combined test index scores) also suggests that the slower growth and later attainment of physiological maturity of the latter group may have resulted in delayed establishment of the full pattern of sexual behaviour. Although twin-born rams were lighter than singles ($P < 0.01$) in the two years that liveweight was recorded at 19 months of age (52.3 versus 51.2 kg), the fact that there was no phenotypic association between liveweight and serving capacity measures at this age suggests again that the effect is mediated through mechanisms other than those associated with liveweight at the time of pen-testing.

Variations between lines within the three Merino strains represented by more than one line, was a significant source of variation in all measures of serving capacity. Whilst formal investigation of the specific source of this variation was not attempted, the data suggested that variation between the nine Peppin lines was the major reason for the significance of this source. Previous studies of variation in serving capacity in sheep have been restricted largely to examination of between-breed differences and whilst breed differences in young rams have been identified (Land and Sales, 1977; Kilgour and Winfield, 1977 and Louda et al., 1981) these can be interpreted to be largely a function of differences in physiological maturity. Hultnas

(1959), in a study of bull libido and mating performance, found inbreeding affected performance, and whilst differences between levels of inbreeding in the studs from which the D flock lines were derived could be expected, quantification of this parameter was not possible.

In none of the serving capacity measures analysed was the sire source of variance significant, and negative sire components of variance were obtained for all except the second test index score. These negative sire variance components reflected large within-sire variances associated with a relatively small range of sire mean values, a situation which arose due to the extreme skewness of the distributions. Transformations which attempted to "normalise" the frequency distribution by transformation into classes with more equal frequencies or which treated serving performance as an "all or none" trait, also failed to produce any evidence of significant between-sire variances.

4.5.3. Repeatability of serving capacity

Despite the serving performance of the entire group of 837 rams in the two one-hour pen tests being moderately repeatable (0.54), this value, to a large degree, reflects the perfect repeatability of the 317 animals which failed to achieve service in either test.

Examination of the performance of rams which did display serving ability revealed lower repeatability of performance. The group of 91 rams achieving four or more serves in the first test and classified as being of high serving capacity, did not maintain that performance and their repeatability did not differ from zero. Those rams of low serving capacity in the first test (one or two serves), whilst showing an overall improvement, also displayed a wide range of performance in the second test.

These results, taken together with the fact that during pen-testing, a substantial number of rams began to show sexual activity but did not serve, suggest that these young rams had not attained a stable state of serving performance. It would therefore seem likely, that pen-test serving capacity of rams, at this age and level of heterosexual experience, would not accurately predict subsequent paddock mating performance The estimate of repeatability of 0.77 reported by Kilgour (1980) for serving capacity of mature rams, suggests that with further experience more repeatable performance could be expected from the rams of the D flock.

4.5.4 Genetic parameters

The absence of additive genetic variation in measures of serving capacity in these 20 month-old rams contrasts with the findings of similar studies with other species and is contrary to indications from one sheep investigation. Blockey et al. (1981) have found serving capacity in young beef bulls to be highly heritable whilst Benoff and Siegel (1977) succeeded in producing, by selection, two lines of cockerels differing in serving frequency. There are many other examples in laboratory animals of behavioural traits showing evidence of additive genetic variation (reviewed by Goddard, 1980). In Merino sheep, Mattner et al. (1974) reported that sons of high "libido" rams had significantly higher mean "libido score" than sons of low "libido" rams although specific details of this finding have not been published.

In the light of the above findings, the absence of additive genetic variation in serving performance of the young rams in this study, reinforces the often stated qualification which pertains to estimates of genetic parameters. That is, they are relevant only to the population from which they are derived and to the environment to which the population has been subjected. Thus, these estimates of heritability refer only to the Merino population from which this composite flock was derived, and more importantly, they refer only to the serving ability of young Merino rams precluded from having heterosexual experience prior to their exposure to oestrous ewes in pen-tests.

The relatively unstable serving performance of the group suggests that due to a conditioning or learning process, repeated tests of performance at this stage of development of sexual behaviour may not be multiple measurements of what is genetically the same character. Thus, variation within individual rams may not be purely environmental and the variance between the means of individuals may therefore be supplemented by an additional variance due to an interaction between genotype and time of measurement. Falconer (1960) suggests that an increase in the proportion of additive genetic variance arising from multiple measurements cannot be relied upon until the genetic identity of the character measured has been established. Such a situation in ram serving capacity may not develop until paddock mating experience stabilises the expression of libido and mating dexterity.