Investigation into the possibility of a major gene for fleece weight in screened sires

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ABSTRACT

Progeny test mating was carried out for 7 high fleece weight (HFW) and 5 random control (RC) sires from the Woodlands breeding flocks in 1987, and for 4 HFW sires in 1988. In 1990, 8 of the surviving HFW sires were backcross mated to their daughters (born in 1987 and 1988). There was no evidence for any of these sires being heterozygous, or for any of the sires involved in the backcross being homozygous, for a major gene which affects either fleece weight or liveweight.

Keywords: progeny, major gene, fleece weight, romney, backcross.

INTRODUCTION

A high fleece weight Romney flock (HFW) was established at Woodlands Research Station by intensively screening ewe and ram hoggets from commercial flocks in the early 1980's. The average selection differential of the screened ewe flock was 3 standard deviations (SD), equivalent to 1 kg of fleece weight or 40% of the mean. Twenty two rams were screened from 25,000 rams and used for breeding in the initial 2 years (averaging 19.4 progeny per ram), while 5 sires from HFW were used in each of the following seasons. At the same time a random control flock (RC) was established from the same base animals. Progeny distributions of two rams in the first season indicated that they could be heterozygous for a major gene affecting fleece weight and/or live weight (Hawker *et al.*, 1988). A series of progeny evaluations for these sires or their relatives, together with other outlier sires, was undertaken during 1987 -1990 in order to confirm or dismiss this hypothesis.

MATERIAL AND METHODS

Progeny test matings

Tests for major genes on the 1985 progeny in the HFW wool selection (WS) flock at Woodlands showed that sire 830256 (20 progeny) was significant ($p<0.01$) for both hogget fleece weight (FWT) and hogget live weight (SLW), and that sire 830217 (19 progeny) was significant ($p<0.05$) for FWT. The putative major genes had estimated effects of 1.1 kg (sire 830256) and 0.8kg (sire 830217) for greasy fleece weight (GFW) and 12.4 kg for SLW (Hawker *et al.*, 1988). A series of progeny tests was conducted to further investigate these results.

The first progeny test was carried out in the 1987 breeding season, and included 3 high breeding value (FWT and SLW) sons of each of these sires. Because 830256 died, 830217 was the only original 'carrier' ram included. Each ram was mated with 125 ewes. Simultaneously, 5 RC rams were each mated with 25 ewes as a progeny test control. All test sires were randomly mated with an unrelated Perendale ewe flock at Waiora farm. The second test mating was carried out in the 1988 season for 4 rams, 2 being repeat sires from the 1987 test mating and 2 being the highest FWT breeding value rams from the 1986 HFW progeny. Each was mated with 100 Perendale ewes by artificial insemination (AI).

The ewe progeny generated from the 1987 and 1988 test matings were sorted into their sire groups for mating to their sires (backcross) in the 1990 season. Seven of the 9 previously tested rams (2 of whom were repeat tested), along with 310 1987 born and 170 1988 born ewes were present for mating. Of the ewes whose sires were unavailable, one sire group was mated to a 1/2 sib, while the other was mated to a 1/4 sib taken from the 1987 HFW progeny.

Animal management and records

All matings were in single sire groups for one oestrous cycle (17 days), ewes were colour coded for the assigned sire and rams were harnessed with a coloured crayon marker, while ewes for AI were synchronised for oestrus using CIDRs. Ewes were grazed in one mob with progeny of those being marked by a follow-up being excluded. Only ewe lambs were retained from the 1987 and 1988 drops whereas both sexes of the backcross progeny were retained in the 1990 season. All these progeny test (PT) lambs were identified by sire group with ear tags.

Birth date, birth rank (except in 1988), weaning weight (WWT), hogget FWT, SLW, 2-tooth autumn fleece weight (2thFWT) and liveweight (2thLWT) were recorded. The back fat depth (BF) was measured only for progeny born in 1987.

Statistical (segregation) analyses

To test for a major gene we assume that the Perendale dams were all non-carriers of the putative gene. We require matings where the gene is segregating. This will be the case for half-sib families when the sire is a heterozygous carrier, half of his progeny would be expected to be heterozygous carriers, and the other half would be non-carriers. An appro-

priate test would detect such a sire provided heterozygous carriers and non-carriers had different means and there were enough progeny; i.e. a dominant or codominant allele, but not a recessive allele.

A gene would also be segregating in half-sib families if the dams are all heterozygous for the putative gene. This would be the case for the backcross progeny if the HFW sire was a homozygous carrier, all these progeny would be carriers - half would be expected to be homozygous and half heterozygous. A test would then be appropriate provided the gene was not dominant.

The progeny born in 1987 and 1988 were used to test whether their HFW sire was heterozygous for a major gene that is not completely recessive. The backcross progeny were used to test if the sire was homozygous for a major gene that is not completely dominant.

In both cases the progeny groups were tested to see if they were the equal mixture of two normal distributions (with known and equal variances but different means) using the test described in Hawker *et al.*, (1988). The likelihood under this model is compared with that under the assumption that the data come from a single normal distribution with the specified variance. Segregation is then tested by comparing twice the difference between the log-likelihood for the mixture of two normals and the log-likelihood for the single normal with a χ^2_1 distribution. Simulations indicate that this procedure is conservative and that its power for detecting a gene of size 2 phenotypic standard deviations at the nominal 1% significance level is 41% and 86% for progeny groups of sizes 20 and 50 respectively. The data were adjusted for birth date, birth rank, age of dam, flock and year (if this information was available) prior to applying the test.

RESULTS AND DISCUSSION

The three sets of progeny test results are given in Table 1. The analyses for sires used in 1987 showed little evidence that any of these were heterozygous for a major gene in the traits recorded. Sire 850300 had the highest standard deviation (SD) in progeny FWT, but the data did not appear to be a mixture of two normal distributions, and the major gene test was not significant. Sire 850069 produced a significant result for BF, but in view of the number of tests performed, this was not considered strong enough evidence to warrant further investigations.

The differences between progeny test sires and control sires in 1987 were 0.19 (SED 0.07), 0.61 (0.44), 0.58 (0.71), 0.11 (0.50), 1.43 (0.72) and 0.44 (0.11) for FWT, WWT, SLW, BF, 2thLWT and 2thFWT respectively. Estimates of the differences in additive genetic merit of these two groups are double these.

The second test, in 1988, showed no evidence of a major gene segregating in any of the four progeny groups. Although the progeny FWT distribution for one sire (850069) appeared to be bimodal, this was not the case for the 2thFWT distribution and may have been influenced by unadjusted birth rank differences in the progeny.

The backcross progeny information showed no strong evidence that some of their sires were homozygous for a major gene for any of the traits analyzed. The only sire significant for the test was 850129 for FWT (for his nine backcross progeny). This was not confirmed by the 2thFWT results, although only ewe progeny were retained to this age. If this sire is a homozygous major gene carrier, then we might expect the distribution for his progeny resulting from half-sib mating to be more variable than on average. This is not the case (data not shown).

In the backcross there are other types of gene action which are not directly tested by the model used here. For example the backcross progeny of a sire heterozygous for a recessive gene, would consist of two distributions in the ratio of 3:1. However such a scenario is expected to increase the SD in the progeny, and this is not the case.

Combined analyses for two sires that had progeny in both the WS and PT flocks is summarised in Table 2. Although the major gene test for FWT in WS for sire 850300 was close to significance ($p<0.08$) the tests in the PT flocks and the combined analysis did not support this result. The combined analysis for sire 850069 showed no evidence of a major gene for any of the traits of interest except for BF. Similarly the significant result for WWT in WS was not supported by the PT results.

The objectives of the extreme screening procedure used to create the HFW flock were firstly to rapidly create genetically divergent animals for subsequent physiological study and secondly to concentrate any rare genes with a major effect on fleece weight that may be present in the population. This study involved the second of these by investigating the possibility that at least one of the 20 initial rams used contained such a major gene.

In a homogenous breed such as the Romney, where selection for fleece weight has been practised (directly or indirectly) for a considerable period, major genes affecting fleece weight are likely to be rare as otherwise they would rapidly increase to near fixation under such selection. The chances of detecting rare major genes could be markedly improved by screening for 'outliers' from a large base population. In this experiment 20 rams were selected from 25000 measured. The effectiveness of such a screening program depends on the magnitude and frequency of the major genes affecting the trait in the population. A major gene with frequency less than 0.001 and an effect of 2 phenotypic standard deviations would be concentrated 130 to 160 fold. Such a gene would contribute less than 1% to the phenotypic variance (Smith, 1984), or less than 3% to the additive genetic variance for a trait with a heritability of 0.3. For example if the frequency of the gene was 0.001 in the population we would expect 5 of the selected rams to be heterozygous at that locus. Therefore the progeny group sizes in these experiments (approximately 20 for HFW in 1985 and 1986; Hawker *et al.*, 1988, and approximately 50 for PT) had sufficient power to detect possible major genes of this magnitude and frequency.

Such intense screening procedures have been used previously to concentrate rare loci with a major effect. In sheep the Inverdale gene (Davis *et al.*, 1991) was identified using a screening procedure for fecundity almost identical to this study. Insect resistance to insecticides identified from field populations are also often under monogenic control, probably a result of the selection by using doses that kill all but a

TABLE 1: Significance tests and estimated effects[1] of major genes for productive traits

Year/ Sire	n[2]	FWT P[3]	FWT effect	WWT P	WWT effect	SLW P	SLW effect	n[4]	2thFWT P	2thFWT effect	2thLWT P	2thLWT effect	BF P	BF effect
1987														
830217	71							71						
850069[5]	86							83					.030	3.00
850129[6]	54	.817	0.12			.771	1.41	53	.790	0.12				
850282[5]	73							73						
850288[6]	76	.798	0.14			.889	0.96	73			.382	3.29	.802	1.01
850300[6]	64	.415	0.25			.369	2.37	64	.132	0.27	.293	3.33		
850320[5]	78	.830	0.12			.293	2.56	76						
SD used			0.32		3.00		3.10			0.28		4.40		2.40
1988														
850069	47	.757	0.21			.480	3.29	47			.556	3.48		
850300	58	.790	0.16					59	.734	0.13				
860227	45							44						
860297	42	.525	0.29			.516	3.30	43	.892	0.09	.687	2.93		
SD used			0.36				4.0			0.26		5.0		
1990[7]														
850069	67			.118	3.10	.282	4.37	36			.511	3.97		
850129	9	.006	1.21					4						
850129[8]	38	.716	0.26					14						
850282	38							22						
850300	61	.749	0.21			.853	1.79	30	810	0.13	.492	3.94		
850320	25			.267	3.23			16			.826	2.72		
860227	16	.450	0.51	.858	1.40	.087	8.84	8	.295	0.42	.198	9.61		
860297	11	.615	0.44	.644	2.65	.598	4.51	6						
870079[9]	46							18	.537	0.24				
SD used			0.42		2.9		5.0				0.25	5.0		

[1] not shown where the maximum likelihood gave a single distribution (i.e. effect=0)
[2] number of progeny; also approximate number for WWT, SLW, BF
[3] Significance probability.
[4] number of progeny; also approximate number for 2thLWT.
[5] Sons of 830256.
[6] Sons of 830217.
[7] Backcross progeny except where noted.
[8] Maternal grandsire: 830217 (1/2 sib mating).
[9] Maternal grandsire: 850288 (1/4 sib mating).

TABLE 2: Significance tests and estimated effects of major genes for productive traits for two putative major gene carrier rams used in several flock/ years

Sire	Flock	FWT n[1]	FWT P[2]	FWT effect	WWT P	WWT effect	SLW P	SLW effect	n[3]	2thFWT P	2thFWT effect	2thLWT P	2thLWT effect	BF P	BF effect
850069	WS	48	-[4]		.004	4.40	.303	3.97	51					.206	1.07
	Combined[5]	181	-		.148	2.21	.261	2.44	140	-		-		.01	2.29
850300	WS	35	.075	.55	-		-		36					-	
	Combined[5]	157	.149	.29	-		.246	2.58	123	.141	.22	.371	2.78	-	

[1] number of progeny; also approximate number for WWT, SLW, BF.
[3] Significance probability.
[3] number of progeny; also approximate number for 2thLWT.
[4] not shown where the maximum likelihood gave a single distribution (i.e. effect=0).
[5] WS, PT87, PT88.

tiny proportion of individuals. Laboratory investigations have investigated this aspect and found polygenic responses at low doses and monogenic responses at high doses as predicted by theory (McKenzie *et al.*, 1992).

There were some technical difficulties involved in these trials. Large progeny groups are necessary to detect a major gene. An uneven sire distribution of the backcross progeny was generated due to a high rate of infertility in 2th ewes of 1990. The poor grazing conditions resulted in the animals being well below their potential wool production so that 2th fleeces were also collected. In addition the trait under investigation (GFW), can be strongly influenced by the environment.

Furthermore, fleece weight is a collective term for a wool production measure that has at least four components, namely fibre cross sectional area, fibre length, fibre numbers per unit area and fibre growing surface of a sheep. The major genes relating to wool successfully identified are the N gene of Drysdale sheep (Dry, 1955) and black colour whereas lustre, bulk and follicle ratios were also under investigation by various researchers.

The chances of finding any existing major genes for a productive trait by using genetic markers is high. This method is much more powerful than segregation analyses, as used here, and provides the opportunity to detect genes with smaller effects. Lande (1981) estimated that on average 5 to 20 genes are involved in influencing a quantitative trait. The usefulness of markers in plants has been shown (Paterson *et al.*, 1988) and modeled for livestock (Fernando and Grossman, 1989), while recent research suggests that the best approach to search for a major gene influencing a productive trait is to construct an experimental population and conduct gene mapping approaches, which involves evaluating large number of animals for the quantitative traits of interest and genotyping them for a number of markers (Mackinnon, 1992).

In conclusion, there was no strong evidence for any of these sires being heterozygous, or for any of the sires involved in the backcross being homozygous, for a major gene which affects either fleece weight, liveweight or another of the measured traits. It is unlikely, then, that there were any genes for fleece weight of magnitude 2 phenotypic standard deviations or greater at a frequency of at least 0.001 in the population sampled. Should the search for such major genes be attempted in the future, we recommend focusing on the fleece production components and their possible special effects on fleece weight.

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REFERENCES

Davis G. H.; McEwan J. C.; Davis G. H.; McEwan J. C.; Fennessy P. F.; Dodds K. G. and Farquhar P. A. 1991. Evidence for the presence of a major gene influencing ovulation rate on the X chromosome of sheep. *Biology of Reproduction* **44:** 620-624.

Dry F. W. 1955. The dominant N gene in New Zealand Romney sheep. *Aust. J. Agric. Res.* **6:** 725-769.

Fernando R.L. and Grossman M. 1989. Marker assisted selection using best linear unbiased prediction. Genetics, Selection, Evolution 21:467-477.

Hawker H.; Dodds K.G.; Andrews R.N. and McEwan J.C. 1988. Production and characteristics of wool from the hogget progeny of sheep intensively screened for fleece weight. *Proceedings of New Zealand Society of Animal Production* **48:** 207-212.

Lande R. 1981. The minimum number of genes contributing to quantitative variation between and within populations. *Genetics* **99:** 541-553.

Mackinnon M.J. 1992. Use of genetic markers in genetic improvement programmes. *Proceeding of Australian Association of Animal Breeding and Genetics* **10:** 245-251.

McKenzie, J.A.; Parker, A.G. and Yen, J.L. 1992. Polygenic and single gene responses to selection for resistance to Diazinon in *Lucilia cuprina*. *Genetics* **130:** 613-6120.

Paterson A.H.; Lander E.S; Hewitt J.D; Peterson S.; Lincoln S.E. and Tanksley S.D. 1988. Resolution of quantitative traits into Mendelian factors by using a complete linkage map of restriction fragment length polymorphisms. *Nature* **335:** 721-726.

Smith C. 1984 Ultilization of major genes. *In* Genetics of reproduction in sheep Eds Land and Robinson Butterworths 151-158.