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Genetic progress in a Romney Group Breeding Scheme

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ABSTRACT

The Auckland Romney Development Group was established in 1968 and its aims continue to be to test and select rams for Group Members, and to breed rams for sale under conditions relevant to farming in the greater Auckland district. Breeding objectives include increased litter size (NLB), weaning weight (WWT), yearling live weight (YLW), yearling greasy fleece weight (YFW), and also increased facial eczema (FE) tolerance. Each year until 1993, members received selected nucleus-bred 15-month rams for use at home, and the next cut of nucleus rams and some elite homebred rams were offered as breeding stock for sale. From 1993, restricted maximum likelihood methods were introduced to calculate breeding values, and across-age ram selection was applied. At the same time, the nucleus ewes were re-distributed across all Members' flocks, and between-flock and between-year genetic links were maintained by movement of sires for mating.

Estimates of total genetic progress by birth-year (obtaining data from Animalplan files, which were only available from 1986) were: WWT (1986-97) 1.83 ± 0.17 kg (7.8% of the mean), YLW 2.76 ± 0.24 kg (6.4%), YFW 0.23 ± 0.01 kg (7.3%) and NLB (1986-95) 0.029 ± 0.015 lambs (1.8%), and all flocks have contributed to the long-term genetic changes. Annual genetic trends over the period were approximately linear, except for YLW which appeared to show an increasing response rate. This is probably related to the extensive progeny testing carried out since 1994 to study sire families which appear to be elite for YLW, using progeny-test matings of rams to outside tester ewes. Segregation tests for a possible major gene have been carried out. Some evidence of bimodal distributions for YLW within sire was found, with a gene whose effect was +9% of the mean, in heterozygotes. Since 1993, secondary selection decisions based on FE have been complicated by across-flock selection, but genetic progress for this trait appears to be linear, with a heritability estimate for log (gamma glutamyltransferase; GGT) of 0.34 ± 0.09 . Over the birth years 1981-1997 there was genetic change in GGT by a factor of 0.71 (29% improvement), compared with a factor of 0.30 (70% improvement) over the same time period in the *single-trait* FE selection lines at Ruakura (Resistant versus Control lines).

Keywords: sheep; facial-eczema; genetic-selection; yearling-weight; major-gene.

INTRODUCTION

The Auckland Romney Development Group (ARDG) was established in 1968, and has continued since then to test and select rams for use by Group Members, and also to breed rams for sale, under conditions relevant to farming dual-purpose sheep in the greater Auckland district. Breeding objectives include production traits (described below) and also, since the late 1970s, increased facial eczema (FE) tolerance. Each year until 1993, Members received selected nucleus-bred 15-month rams for use at home, and the next cut of nucleus rams and some elite homebred rams were offered as breeding stock for sale. From 1993, reference sires were used for genetic links across flocks, and all flocks contributed to the pool of potential rams for breeding.

A group of related ARDG rams which were elite for yearling live weight (YLW) was identified in 1993, and extensive progeny-testing has been carried out subsequently to study the segregation of a possible major gene. There were 21 such rams progeny-tested since 1994, using matings to outside unrelated tester ewes. The present paper reports estimates of the Group's genetic trends in four production traits and in FE tolerance. The response to selection for FE tolerance using a selection index is compared with single-trait selection against FE in experimental flocks at Ruakura. The paper also describes the progress achieved in testing for segregation of a major gene for YLW.

MATERIALS AND METHODS

Group structure

Seven breeders with recorded Romney flocks established the original ARDG structure in 1968, by setting up a recorded and jointly-owned central nucleus. Recorded ewe numbers in the Group totalled about 2750 per year in the 1970s (currently about 3000), with a central nucleus of 450 elite ewes screened in from Members' flocks, mainly on litter size (NLB) as 2-year-olds. Young stock in the nucleus were recorded for production traits, followed by a performance test for FE carried out on production-selected young nucleus rams. Three of the original 7 flocks still survive in the Group today, and the Group now includes 3 other flocks whose owners joined in the 1970s.

The central-nucleus structure continued until 1993, at which time restricted maximum likelihood (REML) methods (Johnson & Thompson, 1995) were introduced to rank individual animals on breeding value (BV), and across-age ram selection was applied. At the same time, the nucleus ewes were re-distributed to the six Members' flocks, and between-flock and between-year genetic links were then maintained by movement of rams for mating.

Testing and selection practices

Breeding objectives determined by the Group since 1968 include increased NLB, weaning weight (WWT), YLW, yearling greasy fleece weight (YFW), and also (since the late 1970s) increased FE tolerance. Index

selection of yearling rams born in the nucleus was applied to these 4 production traits, using weightings as in Animalplan (Johnson *et al.*, 1989), followed by performance testing of the top-ranked 90 rams (approx.) for FE tolerance, and selecting from amongst these. Since 1993, the top 15 rams (approx.) from each of the 6 flocks were selected as yearlings on the same Animalplan production index using across-flock REML, and these animals were then performance tested for FE tolerance. (Although selecting equal numbers per flock may not be optimal, it encourages all Members to remain in the Group because they continue to supply rams to, and receive rams from, the pool available for potential use each year). The FE-test result was obtained from a blood sample taken 21 days after dosing with the FE toxin, sporidesmin, and the sample was analysed for serum gamma-glutamyltransferase (GGT) as an indicator of sporidesmin-induced liver injury. Final selection rankings for rams of all ages were made by giving equal weight (when expressed on a genetic standard deviation basis) to the production index and to log GGT (negative log GGT BVs being desirable for greater resistance to FE). Performance data for genetic-trend analyses were available from the Animalplan records of all animals born in 1986 and subsequently (although earlier ancestry was available and included). Data on GGT have been recorded since the 1981 birth year, and all years of GGT data were included in the trend analyses.

Progeny testing for live weight

Progeny-test results for adjusted yearling live weight (YLW_a) from one ram (S), siring 86 lambs in 1992, suggested that a major gene could be segregating (by comparison with YLW_a data of 670 contemporary progeny by 7 other sires). After the results became available in spring 1993, ram S and four of his 1992-born sons were used in 1994 for outbred matings, generating 267 progeny (2 sites). Next, within-ARDG matings were set up to test some possible heterozygote (carrier) sires further for YLW_a, but they failed to clarify the mode of inheritance. Possibly, copies of the favoured allele were now also being transmitted to progeny through ewes. Therefore, four more rams which were possible carriers were used in 1997 for outbred matings to 100 ewes (approx.) each (1 site), with a further 12 rams mated similarly in 1998 (2 sites). The 1994-, 1997- and 1998-born lambs of both sexes were recorded for WWT and through to March (6 months of age), uncullled. All female lambs were retained and recorded for YLW. The weight data for the 1994- and 1997-born lambs are complete, but so far data from the 1998-born lambs are only complete to the WWT stage.

Data analyses

Performance data from the nucleus and the 6 Members' flocks were analysed using REML (Gilmour, 1997) animal-model methods, with a full pedigree matrix and a log transformation for traits WWT, YLW and YFW. Fixed effects for lamb traits included contemporary group (year-sex-mob), age of dam, birth type and a covariate for date of birth, whilst for NLB the fixed effects were contemporary group when lambing, and age of ewe. Similar REML analy-

ses were carried out for log_eGGT, fitting fixed effects for contemporary group (year-location) and age of dam. For all traits, means for Member-flock x year of birth combinations were obtained from the REML solution files, to summarise genetic trends.

Analyses of variance for YLW_a and earlier weights were used to test whether variability was greater in the progeny of carrier sires than other sires. Distributions were also plotted, all on a within-sire basis, to test for evidence of bimodality in the progeny data from carrier sires. Segregation analyses were undertaken using the 'Findgene' (Kerr and Kinghorn, 1996) and 'Maggic' programmes (Janss *et al.*, 1995), in an attempt to classify the genotypes of all animals for the putative major gene.

RESULTS

Genetic trends

Table 1 shows the estimates of total genetic change achieved for four production traits over the time period from 1986 to the present day, and for FE from 1981 onwards. Expressed relative to the trait means, these genetic changes were 6.4 to 7.8% for the weight or fleece weight traits (0.6-0.7% per year), and 1.8% for NLB (0.2% per year). Animal-model REML heritability estimates are also shown, which can be compared with estimates obtained from a large file of Romney research data (Morris *et al.*, 1996). For log_eGGT over the 16-year period 1981-97, the estimate of genetic change was -0.339 log_e i.u./l, equivalent to a factor of 0.71 on conversion back to the units of measurement. This indicated that GGT had changed (reduced) by 29% over the 16-year time period measured; alternatively the GGT mean before selection was 1/0.71 or 40% above the mean after selection. The REML estimate of heritability was 0.34 ± 0.09 with a phenotypic standard deviation (σ_p) of 0.70. There was no indication that the GGT selection response rate had altered after the change in ARDG group structure in 1993, although thereafter secondary selection decisions on FE had to be made across flocks.

TABLE 1: Total genetic change achieved in production traits and facial eczema, relative to the means.

Item (Units)	WWT ¹ (kg)	YLW (kg)	YFW (kg)	NLB (lambs)	FE (log i.u./l)
Birth years analysed	1986-97 ²	1986-97 ²	1986-97 ²	1986-95	1981-97
Total genetic change,					
estimate	1.83	2.76	0.23	0.029	-0.34
s.e.	0.17	0.24	0.01	0.015	0.05
% of mean	7.8	6.4	7.3	1.8	-29
Heritability,					
estimate	0.42	0.35	0.36	0.061 ³	0.34
s.e.	0.01	0.01	0.02	0.009	0.09
research flock ⁴	0.11	0.37	0.39	0.08	0.45 ⁵

¹For trait definition, see text.

²Analysed after log transformation.

³Repeatability = 0.096 ± 0.008.

⁴From Morris *et al.* (1996): "High" Control flock.

⁵From Morris *et al.* (1995): Ruakura FE flocks.

Pedigrees

For the 21 rams progeny-tested in 1994, 1997 and 1998, 8 traced back 4 generations to S's sire (A), and 11 traced back 4 generations to a common ancestor B; A and B had a common male ancestor born 7 generations earlier in 1972, and a common female ancestor born in 1977. A grandsire of B was well known in the Group to be a very large ram, as well as being FE-resistant. The 21 rams accounted for 20% of the rams used in all ARDG matings in the three years 1994, 1997 and 1998.

Evidence for a major gene

In the original analysis of 1992-born lambs for YLWa, there was significantly greater variability in ram S's male progeny than in those of the 7 other contemporary progeny groups ($P < 0.05$), although the same did not apply to daughters' data. Culling had already been applied to females, but not to males, by yearling weighing time (December in females and August in males). The size of the effect on YLWa was about 5kg in heterozygotes, or 9% of the mean. There was also evidence of significantly greater variability for WWT and for YFW (taken in August), within S's progeny of both sexes than in the other 7 groups.

From ram S and his four sons, all of which were tested by outcrossing in 1994, the within-sire distributions for YLWa were bimodal in 3 out of 5 progeny groups, with an effect of about 4kg (12%) between the modes. The other two sires were selected as low YLWa controls, and were not expected to be heterozygotes. Results from the Maggic analyses of all YLW data up to and including 1994-born lambs indicated an additive effect (a) of 10.5% of the mean, for the putative major gene, with complete dominance (d ; with $d = a$). The gene apparently accounted for 73% of the additive genetic variation in YLWa, but we failed to get the computer program to converge when used later with the additional progeny born in 1995 and 1996. The most logical explanation for this is that none of the models fitted was completely adequate for the data structure. The Findgene analysis up to the 1994 lamb crop gave values of 6 and 3% for a and d respectively, with the heterozygote expected to perform 9% above the non-carrier value for YLW. So to this stage it appeared that a major gene with an effect of at least 9% in the heterozygote was segregating, probably completely dominant, but that it was not possible to show it segregating when dams were possibly contributing copies to the population as well. From the further rams then tested by outcrossing, it was concluded from the distributions both for YLWa in the 1997 progeny tests, and for WWT in the 1997 and 1998 progeny tests, that one (maybe two) out of 4 sire groups in 1997 and at least 4 of 12 in 1998 appeared to show bimodality.

DISCUSSION

Genetic trend

Although the genetic trends for production traits were at the lower end of those expected for selection in Animalplan flocks (Callow *et al.*, 1986), these traits only accounted for half of the selection applied at ARDG, be-

cause of the FE trait. In examining the genetic trends for Members' flocks separately (results not shown), it appeared that all flocks were contributing to genetic progress. The underlying heritabilities for ARDG production traits were similar to the research flock for YLW and YFW, but higher for WWT (although possible maternal effects were not estimated in either resource), and slightly lower for NLB which could help to explain the lower NLB responses achieved.

In addition to the production traits, a trend of about 2% per year was estimated for GGT overall. For comparison, the difference in back-transformed GGT between the Ruakura Resistant line (established in 1975; Morris *et al.*, 1995) and its Control line was a factor of 0.30 over the last 16 years (a 70% reduction, or over 4% per year), and the flock had a higher heritability (0.45 ± 0.04) and σ_p (0.90) than estimated in the ARDG data. Calculating the actual selection intensity applied to FE at ARDG compared with the Ruakura lines (from the heritability, σ_p and realised response, all assuming similar generation intervals), it was concluded that selection intensity applied in the Ruakura flock was 2.07 times as high as in the ARDG flock. This shows the difference between the selection intensity achievable with a single trait rather than with multiple traits.

Evidence for a major gene

The results of testing for a major gene appear to be inconclusive so far, although an extra 12 progeny tests as far as YLW are expected in September 1999. Many of the sires tested by outcrossing were also used within the Members' flocks, but perhaps the resulting progeny data suffered from the limitation that ewes could also be supplying copies of the putative major gene to progeny. Maternal effects or imprinting could complicate such analyses.

If the major gene is confirmed, our difficulty in demonstrating its existence by formal testing explains why it has not been identified earlier accidentally, by casual inspection of data. The size of the putative effect (at least 9%) is such that it would be agriculturally important if it could be characterised. A series of productive, reproductive and disease traits, plus measures of food intake, have also been recorded on the progeny of the same sires, so that the costs/returns of any side-effects can be estimated. Results, as yet unpublished, suggest that there should be net economic advantages in using the putative carrier sires in dual-purpose flocks, although the mode of inheritance is not clear to us yet. Although other major genes for growth have been identified before in farm animals, we believe that all previous examples have been for smaller size (such as dwarfism) rather than for greater size.

ACKNOWLEDGEMENTS

We wish to thank the members of the Auckland Romney Development Group for access to data, and for permission to publish results; also staff at AgResearch Tokanui and Whatawhata for data collection from the outcross matings of 1997 and 1998. The major-gene search was funded by a "Technology for Business Growth" grant from Technology New Zealand.

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