New Zealand Society of Animal Production online archive

This paper is from the New Zealand Society for Animal Production online archive. NZSAP holds a regular annual conference in June or July each year for the presentation of technical and applied topics in animal production. NZSAP plays an important role as a forum fostering research in all areas of animal production including production systems, nutrition, meat science, animal welfare, wool science, animal breeding and genetics.

An invitation is extended to all those involved in the field of animal production to apply for membership of the New Zealand Society of Animal Production at our website www.nzsap.org.nz

<div style="text-align:center">

View All Proceedings   **Next Conference**   **Join NZSAP**

</div>

The New Zealand Society of Animal Production in publishing the conference proceedings is engaged in disseminating information, not rendering professional advice or services. The views expressed herein do not necessarily represent the views of the New Zealand Society of Animal Production and the New Zealand Society of Animal Production expressly disclaims any form of liability with respect to anything done or omitted to be done in reliance upon the contents of these proceedings.

Genetic and environmental relationships between liveweight change over the summer in Perendale ewes and the lifetime live weight profiles of their progeny

R.M.W. SUMNER*, C.A. MORRIS, S.M. HICKEY and A.M. SHEPPARD

AgResearch Ruakura, Private Bag 3123, Hamilton 3240, New Zealand
Corresponding author: roland.sumner@xtra.co.nz

ABSTRACT

Multi-generation data from 1985 to 2002 were analysed from a 200-ewe Perendale flock to investigate genetic and environmental relationships between ewe pre-mating liveweight change and live weight of their progeny at birth, weaning, and 1, 2, 3, 4 and 5 years of age. The flock was managed at Whatawhata Research Centre and then at Winchmore Research Station, with selection for either increased or decreased wool bulk at one year of age. A total of 162 rams were used in a single-sire system. Numbers of resulting dam-offspring pairs ranged from 3,510 for progeny birth weights, to 369 for daughter 5-year-old live weights. Genetic and environmental correlations of progeny trait on dam trait, and the derived genetic (b_G) and environmental (b_E) regressions, were obtained from a restricted maximum likelihood animal model with a relationship matrix, after adjustment for known fixed effects. The b_G estimates were all non-significant, with 14 of the 20 estimates tending to be negative. Three of the 20 estimates of b_E were significant, with values ranging from 0.7 to 1.3% of mean progeny weight per kg dam gain. The estimated environmental relationships were of insufficient magnitude to impact on the flock's productivity in the short term.

Keywords: genetic relationship; environmental relationship; dam; live weight change; progeny; live weight profile.

INTRODUCTION

The expression of a characteristic in an animal is regulated by its genotype and the direct action of the environment to which the animal is exposed. Biologically based characteristics are passed from parent to offspring through the action of single or groups of genes (Turner & Young, 1969) with intergenerational genetic relationships between pairs of characteristics, reflecting the commonality in genes regulating the characteristics, being expressed as a genetic correlation (r_g). Genetic correlations are calculated by comparing the performances of parents and their offspring. In a similar manner it is possible, using the same basic model, to derive an estimate of intergenerational environmental relationships between characteristics.

Increasingly, biologists are finding that a proportion of the non-genetic variation acquired during the life of an organism can sometimes be passed on to their offspring (Bocock *et al.*, 2009), a phenomenon that is referred to as epigenetic inheritance. Rosefeld (2010) has presented a series of definitions of epigenetics derived from previous authors, back to Waddington's (1939) original definition of "…any causal mechanisms that act on genes to govern a resulting phenotype…". Recent studies on human cohorts exposed to famine or excess nutrition have shown that the nutritional status of the mother preceding ovulation affects mechanisms in the resulting individual that control central regulatory mechanisms of energy intake and expenditure at different stages during the life of that individual (Ravelli *et al.*, 1999). The potential impact of an epigenetic effect on production characteristics in farmed livestock is unknown.

This paper compares estimates of the intergenerational genetic and environmental effects associated with differential nutrition of grazing ewes in the summer, as reflected in ewe live weight change between weaning and her next joining period, on the lifetime liveweight profile of her progeny.

MATERIALS AND METHODS

Sheep

Liveweight data collected between 1985 and 2002 from a flock of approximately 200 individually identified Perendale breeding ewes, aged 2 to 5 years, maintained at Whatawhata Research Centre and relocated to the Winchmore Research Station in 1997, were used. The flock was maintained to study the inheritance of wool bulk, with half the flock consisting of a line selected for decreased wool bulk and the other half consisting of a line selected for increased wool bulk (Sumner *et al.,* 2007). Replacement yearling ewes for each line were selected from within that line, with no rams from outside their line being used after 1988.

Both selection lines were managed as a single flock except over mating and lambing. The ewes were single-sire joined for two cycles beginning in mid to late March after oestrus synchronisation. Ewes within each selection line were re-randomised to mating groups annually, avoiding half-sib or

dam-offspring matings. To prevent errors in "mothering-up" across selection lines at lambing, ewes in the two selection lines were lambed in groups based on the genotype of the dam and the lines combined together again at docking.

Measurements

Meteorological records

Rainfall and daily soil water deficit (mm) over the spring and summer at the Whatawhata and Winchmore Meteorological Stations were extracted from the National Institute of Water and Atmospheric Research (NIWA) national weather database. The soil water deficit was calculated cumulatively as rainfall minus an estimate of the potential evapotranspiration rate derived using the Penman model (Burman & Pochop, 1994).

Dam live weights

Ewes were weighed each year at weaning in December and pre-joining in late February / early March, and the liveweight change over this period (dam weight gain: DWG) calculated. For rising two-year-old dams (first parity), subsequently referred to as "juvenile" as they were still actively growing, the DWG was calculated as the gain or loss between shearing at one year of age and the subsequent pre-joining live weight. This was a longer period than was the case for the adult, 3- to 5-year-old ewes (second to fourth parity). This makes the juvenile versus adult ewe age groups difficult to compare, for reasons of time period of weight change, and also active growth in the juveniles.

Progeny live weights

Lambs were individually identified, weighed and the identity of their dam recorded within 24 hours of birth.

At weaning, all lambs were weighed and then shorn as a group in December at about 90 days of age, and again weighed and shorn at one year of age in the following spring. While at Whatawhata, the yearling rams were shorn in late August and the yearling ewes shorn in mid-October. After the flock was transferred to Winchmore all yearlings were shorn in mid-September. All rams, other than those selected for breeding, were culled from the flock following the yearling shearing. Rams retained for breeding were managed differently to the breeding ewes.

During the period of this study the ewes were weighed and shorn annually in late July / early August, approximately six weeks prior to the commencement of lambing. The July live weight was used as an indicator of the effect of increasing ewe age at a consistent point in the yearly management cycle.

Statistical analysis

Animal-model restricted maximum likelihood bi-variate analyses were carried out with a relationship matrix including all pedigree data (Gilmour *et al.*, 2006), to estimate heritabilities and genetic and environmental correlations between dam liveweight gains and offspring live weight. The data set was divided into four parts. These were: two sexes of progeny, ewe and ram; by two age groups of dam, juvenile (rising 2-year-olds that were possibly still maturing) and adult (3- to 5-year-olds). The statistical model was as follows for mixed-age dams:

$Y = X\beta + Zp + Zu + e$, where

Y = the vector of two traits, dam liveweight gain and progeny live weight with the model repeated for progeny live weight at each specified age, and for the two sexes separately;

β = the vector of fixed effects (Progeny: year of birth, age of dam, birth rank, with a covariate for date of birth within year. Dams: year of record, age of ewe (3 to 5 years), and number of lambs reared (0, 1 or 2) at the previous weaning time);

p = the vector of permanent environmental effects across parities;

u = the vector of additive-genetic animal effects;

X and Z = incidence matrices relating observations to fixed-effects levels and individuals respectively, and

e = the vector of residual effects.

The model for juvenile dams was similar to the above, but with no permanent environmental effect across parities, no fixed effect for previous lamb rearing outcome, and no age of ewe (3 to 5 years).

Genetic and environmental effects

The b_G values were calculated as the genetic coefficient multiplied by the ratio of genetic standard deviations of progeny weight/DWG, and b_E values were calculated as the environmental coefficient multiplied by the ratio of environmental standard deviations of progeny weight/DWG.

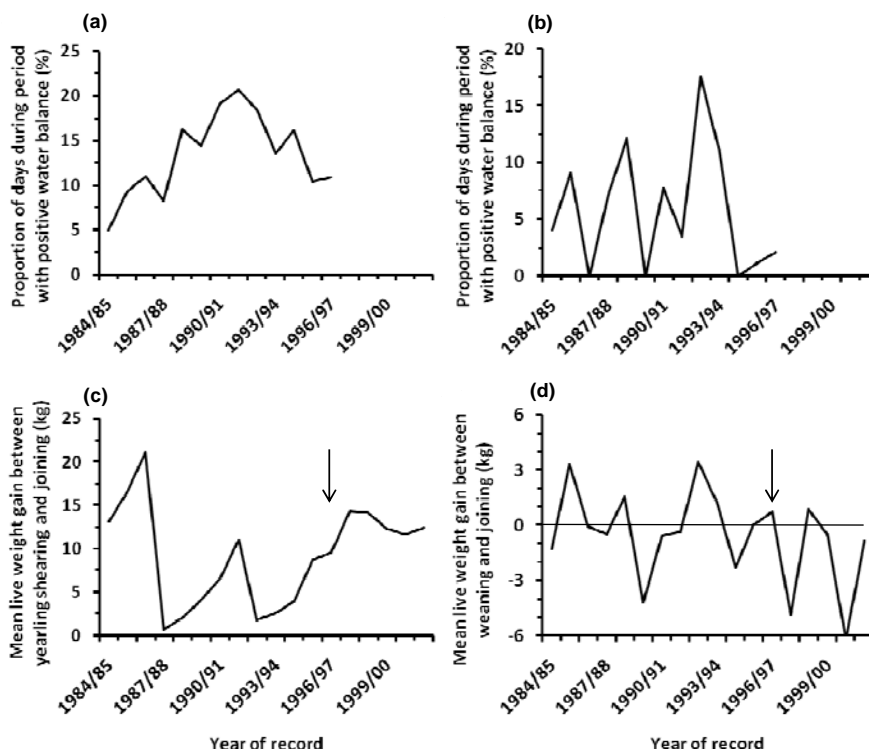## RESULTS

Seasonal effects on ewe weight gains

The mean interval between weighing the juvenile ewes at one year of age and pre-joining was 172 ± 20 days with a range from 147 to 210 days at Whatawhata, and 214 ± 17 days with a range from 194 to 240 days at Winchmore. In the case of the adult ewes the mean interval between weighing the ewes at weaning and pre-joining was 96 ± 11 days with a range from 80 to 121 days at Whatawhata, and 130 ± 8 days with a range from 121 to 142 days at Winchmore.

The proportion (%) of days each year with a positive soil water balance between the DWG dates for the juvenile and for the adult ewes, while they were grazing at Whatawhata under semi-intensive conditions, are shown in Figures 1a and 1b respectively. The annual mean DWG for the two age groups of ewes are shown in Figures 1(c) and (d) respectively. In the case of the actively growing juvenile ewes (Figure 1c) there was a non-significant correlation ($r = -0.36$; df = 13) between DWG and the percentage of time there was a positive water soil water balance, whereas in the case of the adult ewes (Figure 1d) there was significant correlation ($r = 0.75$: df = 13) between DWG and the percentage of time there was a positive water soil water balance. There was no significant relationship between DWG and soil water balance at the Winchmore meteorological site. Up to approximately 90% of the Winchmore Research area was available for flood irrigation during the summer, with no records maintained of the actual paddocks grazed by the Perendale flock used for this study.

FIGURE 1: Year of record plotted against the proportion (%) of days over the weight gain period where there was a positive soil water balance while the sheep were grazing at Whatawhata in (a) juvenile ewes (from September at one year of age to pre-joining in February/March), and (b) adult ewes (from weaning in November/December to pre-joining); and year of record plotted against mean liveweight gain over the same time periods in (c) juvenile ewes, and (d) adult ewes, with the time of relocation from Whatawhata to Winchmore indicated by an arrow.

Live weights and regressions

Weight data from the trial comprised a total of 575 juvenile ewes producing 725 progeny with weights, and a total of 881 adult ewes with 1,924 lambings from which 2,785 progeny with weights were produced (Table 1). Overall there were 162 sires of ewes. Results are tabulated for two sexes of progeny and two dam-age groups. Heritability estimates for DWG were 0.42 ± 0.14 for the juvenile dams and 0.07 ± 0.04 for the adult dams; the repeatability estimate for DWG in adult dams across years was 0.36 ± 0.05. The heritability estimates for progeny weight traits are also shown in Table 1, with genetic correlations, and genetic (b_G) and environmental (b_E) regression coefficients of progeny weights on DWG. The heritabilities of progeny weights ranged from 0.05 to 0.68; three-quarters of the estimates were in a narrower range from 0.22 to 0.54. Six of the 20 estimates of b_G were positive in sign; none of the b_G estimates of either

sign were significantly different from zero. In contrast, all but one of the 20 environmental regression estimates (b_E) were positive (Table 1). Three of the 20 estimates of b_E were significantly different from zero (P <0.05), but they were small relative to the progeny mean for the trait. The significant b_E values were between 0.7% and 1.3% of the progeny mean, per kg DWG.

The estimated b_E values appeared to be similar in magnitude for the ewe and ram progeny, during the period whilst the ram progeny remained in the flock. Similarly there appeared to be no differences between b_E values obtained from juvenile versus adult dams, for each of the measured progeny traits. There was an incomplete data set of regression coefficient data for the ram progeny as they were culed routinely at one year of age after the replacement sires to be used at the next joining had been selected. The estimated b_G and b_E values between DWG over summer and the lifetime live weight profile of their ewe progeny born to juvenile and adult ewes, are plotted in Figure 2, with a line of "best-fit" added to indicate the shape of the response with increasing progeny age.

TABLE 1: Relationships between dam premating trait and the weights of ewe and ram progeny at up to 7 stages (birth, weaning, and annual weighings at 1, 2, 3, 4 and 5 years of age). Premating traits of dams were weight change from October to February, for juvenile (rising 2-year-old) ewes and weight change from weaning (December) to February, for adult (3- to 5-year-old) ewes. Genetic regressions were per unit genetic change in the dam's premating trait; environmental regressions were per unit non-genetic change in the dam's premating weight. Significant regressions (P <0.05) are shown in bold print; SD = Standard deviation; SE = Standard error, h^2 = Heritability; r_g = Genetic correlation.

Progeny trait	Dam age	Progeny sex	Number of progeny	Progeny mean (kg)	Progeny phenotypic SD (kg)	Progeny h^2 ± SE	r_g ± SE	Genetic regression ± SE	Environmental regression ± SE
Birth wt	Juvenile	Ewe	387	3.7	0.7	0.14 ± 0.13	0.23 ± 0.44	0.02 ± 0.05	0.01 ± 0.03
		Ram	338	3.9	0.8	0.38 ± 0.17	0.12 ± 0.34	0.03 ± 0.08	-0.03 ± 0.05
	Adult	Ewe	1,398	4.0	0.8	0.31 ± 0.06	-0.09 ± 0.27	-0.05 ± 0.15	0.01 ± 0.01
		Ram	1,387	4.2	0.8	0.36 ± 0.07	0.12 ± 0.42	0.13 ± 0.45	**0.04 ± 0.02**
Wean wt	Juvenile	Ewe	340	20.1	2.8	0.44 ± 0.14[a]	-0.64 ±0.39	-0.38 ± 0.23	0.27 ± 0.16
		Ram	285	21.8	3.6	0.33 ± 0.19	-0.72 ± 0.46	-0.78 ± 0.58	0.30 ± 0.19
	Adult	Ewe	1,234	20.6	3.2	0.28 ± 0.06	0.17 ± 0.29	0.37 ± 0.65	0.08 ± 0.06
		Ram	1,184	22.5	3.4	0.14 ± 0.06	1.05 ± 0.46	2.42 ± 1.97	0.02 ± 0.07
1-yr-old wt	Juvenile	Ewe	305	37.1	4.4	0.30 ± 0.18	-0.61 ± 0.36	-0.58 ± 0.34	**0.48 ± 0.23**
		Ram	257	40.3	5.5	0.68 ± 0.21	-0.33 ± 0.34	-0.72 ± 0.80	0.49 ± 0.31
	Adult	Ewe	1,099	37.9	4.4	0.50 ± 0.07	-0.07 ± 0.26	-0.26 ± 1.00	0.13 ± 0.09
		Ram	1,058	41.2	5.0	0.22 ± 0.07	0.31 ± 0.46	1.43 ± 2.49	0.16 ± 0.11
2-yr-old wt	Juvenile	Ewe	127	46.7	5.0	0.15 ± 0.32	-0.11 ± 0.64	-0.09 ± 0.48	0.29 ± 0.32
	Adult	Ewe	573	47.7	4.9	0.28 ± 0.09	-0.41 ± 0.37	-1.40 ± 1.47	**0.33 ± 0.13**
3-yr-old wt	Juvenile	Ewe	123	53.5	5.4	0.05 ± 0.30	-0.48 ± 1.99	-0.23 ± 0.53	0.37 ± 0.34
	Adult	Ewe	467	54.0	6.1	0.27 ± 0.10	-0.85 ± 0.43	-3.66 ± 2.70	0.26 ± 0.18
4-yr-old wt	Juvenile	Ewe	101	56.8	6.7	0.54 ± 0.36	-0.41 ± 0.41	-0.75 ± 0.73	0.52 ± 0.39
	Adult	Ewe	353	57.6	6.0	0.30 ± 0.13	-0.45 ± 0.44	-1.94 ± 2.12	0.20 ± 0.20
5-yr-old wt	Juvenile	Ewe	77	58.0	5.8	0.43 ± 0.53	-0.29 ± 0.51	-0.44 ± 0.74	0.46 ± 0.48
	Adult	Ewe	292	59.3	6.3	0.50 ± 0.14	-1.18 ± 0.52	-8.29 ± 6.51	0.14 ± 0.22

[a] Apparent confounding encountered between sire groups and a fixed effect. A reduced model used.

DISCUSSION

Pasture growth rate over the warm months of the year in New Zealand is principally dependent on soil moisture levels (Rollo *et al.*, 1998) with animal production of semi-intensively grazed livestock being dependent on the quantity and quality of the available herbage (Webby & Bywater, 2007). Within the Whatawhata data set reported here, there was a significant correlation of 0.75 between DWG of adult ewes over the summer and the soil water balance. There was however no significant relationship between these measurements over a longer period approaching five months in the spring and summer for young actively growing ewes who were offered a higher feed allowance than the adult ewes as part of a normal farm management procedure to encourage body growth and overall maturation prior to their first mating. No supplementary feed was offered to either stock class.

Dry conditions were experienced in the springs of 1987/88 and 1992/93, and the summers of 1986/87, 1989/90 and 1994/95 with moist conditions during the summer of 1985/86, 1988/89 and 1992/93. These variations in climatic conditions resulted in a difference of up to 6 kg in liveweight gain, equivalent to approximately 12% of their mean weight, over the summer period. The magnitude of the variation in liveweight gain in ewes over the 13 summers of data recorded at Whatawhata, can be considered indicative of the variation to be expected during normal seasons on hill country on the west coast of the North Island of New Zealand. Under such conditions the farm manager has limited scope to directly influence liveweight gain of ewes over the summer. The situation on the Canterbury Plains where irrigation and supplementary feeding are possible potentially enables liveweight gain in ewes to be controlled more directly by the farm manager.

The measures of variability for the live weight data showed that males were more variable than females and, disregarding birth weight, females generally had higher heritabilities for live weights than males consistent with Clarke *et al.*, (1998). The same trend has also been observed in cattle data (Baker *et al.*, 1987). Live weights are generally moderately heritable. The seven traits comprising the present progeny data were consistent with other publications in this respect (e.g., Clarke & Johnson

FIGURE 2: Estimated genetic and environmental regression coefficients, with their respective standard errors, between pre-mating liveweight change in the dam and the lifetime live weight profile for ewe progeny born to (a) juvenile ewes and (b) adult ewes. The error bars for the environmental regression coefficients fall within the marked data points. A polynomial line of "best-fit" has been overlaid on each data set to indicate the shape of the response over the lifetime of the progeny.
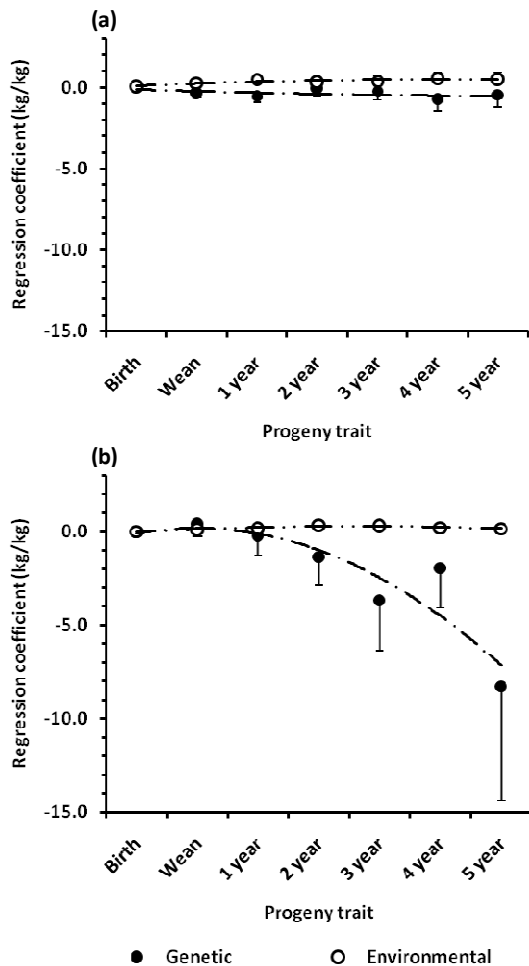
(1994) in New Zealand, and Safari *et al*. (2005) in Australia). The low heritability estimated for liveweight change in adult dams (0.07 ± 0.04) suggests that this characteristic is almost entirely influenced by environmental effects. Some of these effects on ewes are likely to be permanent, on account of the moderately high repeatability (0.36 ± 0.05) of this trait over seasons. The authors are unaware of any published data reporting heritability estimates for liveweight change in adult sheep. In contrast, the heritability estimate for liveweight change in juvenile ewes (0.42 ± 0.14) was also moderate to high. This trait has the potential to include a contribution from any change in weight associated with maturing of the juvenile female.

In the original Dutch study that investigated the long term effects on offspring born to famine-affected mothers in 1944/45 (Ravelli *et al.*, 1976), there was greater obesity in offspring born to mothers affected in the first half of pregnancy, and less in offspring exposed in the last trimester. The present study aimed to identify whether there was any relationship between an offspring's growth and the level of nutrition, as described by DWG, experienced by the dam before she conceived the fetus. With the derivation of 20 estimates of b_E as listed in Table 1, testing at the 5% level would be expected, on the base of chance alone, to identify one estimate as significantly different from zero. In this data set three regression coefficients were significantly different from zero, and all three were positive in sign. We did not have any prior expectation about the sign of such regressions in sheep. However, taken at face value, it appears that if these regressions are describing a real phenomenon, the pre-conception nutrition of the dam may affect progeny growth in a positive manner. That is, higher maternal pre-conception weight gains than those of the contemporaries in the flock, within the range studied, were associated with greater weight-for-age in the progeny. However significant b_E estimates were small relative to the flock mean for that trait at between 0.7 and 1.3% of the mean, for a 1 kg increase in ewe weight gain. Apart from birth weight, there was a tendency for the b_E values to be higher in the juvenile dam x progeny pairs than in the adult dam x progeny pairs, suggesting that in this flock a nutritional stress to a juvenile dam may have had a more serious consequence for progeny development than when it occurred in a mature dam. The authors are unaware of any published data reporting the lifetime productivity of lambs born to one-year-old ewes in comparison with lambs born to adult ewes that would validate this interpretation.

Without any definitive molecular genetic data being available from the sheep in this flock to support the contention, it could be suggested that the progressively decreasing b_G, as the progeny of adult ewes age, shown in Figure 2, may be interpreted as the progressive expression of an epigenetic effect allied to the situation reported for humans where epigenetic effects tend to show when progeny attain older ages (Wadhwa *et al.,* 2009). To date, no single locus and corresponding phenotype that is sensitive to diet, has been identified in humans (Rosenfeld, 2010).

Even though the relationships estimated in this study were small in relation to the mean of the characteristic, epigenetic inheritance associated with live weight change in the dam could still exist between a dam and her progeny. However, the lack of a significant effect may suggest that epigenetic effects of practical significance did not occur under the normal New Zealand sheep farming conditions

under which this flock was run. In New Zealand, animal welfare issues are a prime concern to the sheep farm manager such that they aim to feed their sheep to avoid either extreme over- or extreme under-nutrition throughout the year. Assuming that the management of the flock in this study reflected that on a "normal" North Island hill country property the results of this study, with a power based on 1,450 juvenile and adult ewes and their replacement progeny, suggest that the "normal" nutritional conditions imposed on ewes over the summer period before joining seem to be insufficiently severe to initiate an epigenetic response of sufficient magnitude to be detectable in the live weight profile of their progeny. In this data set climatic conditions resulted in a difference of up to approximately 12% of the mean weight of ewes over the summer period. Severe droughts and feed shortages can result in greater changes than this when it is not possible to either reduce the number of sheep grazing the area or provide adequate supplementary feed. Notwithstanding, even under normal farming conditions physiological thresholds may be set in the epigenome of the resulting individual such that they may initiate a response when the resulting individual is itself subjected to a severe stress late in life. Elucidation of an effect at the epigenome level requires an alternative research approach to that followed here. As an example, possible confounding of pre-ovulation with post-ovulation effects was not tested here, nor could it be tested realistically with just 19 years of field data, but it could be tested in a designed epigenetic trial imposing different nutritional regimens pre- and post-ovulation.

The results of this study indicate that while "epigenetic" relationships in farmed sheep may be broadly similar in concept to that in humans they appear to be of insufficient magnitude to impact on the flock's commercial productivity in the short term, under the conditions evaluated.

ACKNOWLEDGEMENTS

REFERENCES

Baker, R.L.; Carter, A.H.; Morris, C.A.; Johnson, D.L.; Hunter, J.C. 1987: Reciprocal crossbreeding of Angus and Hereford cattle. 1. Growth of heifers and steers from birth to the yearling stage. *New Zealand Journal of Agricultural Research* **29:** 421-431.

Bocock, P.N.; Aagaard-Tillert, M.D. 2009: Animal models of epigenetic inheritance. *Seminars in Reproductive Medicine* **27(5)**: 369-379.

Burman, R.; Pochop, L.O. 1994: Evaporation, evapotranspiration and climatic data. *In*: Developments in Atmospheric Science, Number 22. Elsevier Amsterdam, The Netherlands. p. 81.

Clarke, J.N.; Johnson, D.L. 1994: Lessons from New Zealand sheep selection experiments. *In*: Proceedings of the A.L. Rae Symposium on Animal Breeding and Genetics, Massey University, Palmerston North, New Zealand. p. 52-68.

Clarke, J.N.; Nicoll, G.B.; Mowat, C.M. 1998: Genetic parameters for liveweight and live animal ultra-sound fat and eye muscle dimensions in a synthetic terminal sire breed. *Proceedings of the New Zealand Society of Animal Production* **58**: 140-142.

Gilmour, A.R.; Gogel, B.J.; Cullis, B.R.; Thompson, R. 2006: ASReml User Guide Release 2.0, VSN International Ltd., Hemel Hempstead, Hertfordshire, UK.

Ravelli, A.C.J.; van der Meulen, J.H.P.; Osmond, C.; Barker, D.J.P.; Bleker, O.P. 1999: Obesity at the age of 50 y in men and women exposed to famine prenatally. *American Journal of Clinical Nutrition* **70(5)**: 811-816.

Ravelli, G.P.; Stein, Z.A.; Susser, M.W. 1976: Obesity in young men after famine exposure in utero and early infancy. *New England Journal of Medicine* **7:** 349-354.

Rollo, M.D.; Sheath, G.W.; Slay, M.W.A.; Knight, T.L.; Judd, T.G.; Thomson, N.A. 1998: Tall fescue and chicory for increased summer forage production. *Proceedings of the New Zealand Grassland Association* **60**: 249-253.

Rosenfeld, C.S. 2010: Animal models to study environmental epigenetics. *Biology of Reproduction* **82:** 473-488.

Safari, E.; Fogarty, N.M.; Gilmour, A.R. 2005: A review of genetic parameter estimates for wool, growth, meat and reproduction traits in sheep. *Livestock Production Science* **92**: 271-289.

Sumner, R.M.W.; Clarke, J.N.; Cullen, N.G. 2007: Effect of divergent selection for wool bulk on live weight and wool characteristics in Perendale sheep. *Proceedings of the New Zealand Society of Animal Production* **67**: 180-185.

Turner, H.N.; Young, S.S.Y. 1969: *Quantitative Genetics in Sheep Breeding*. Macmillan, Melbourne, Australia. 332 pp.

Waddington, C.H. 1939: Introduction to Modern Genetics. George Allen & Unwin Ltd., London, England.

Wadhwa, P.D.; Buss, C.; Entringer, S.; Swanson, J.M. 2009: Developmental origins of health and disease: brief history of the approach and current focus on epigenetic mechanisms. *Seminars in Reproductive Medicine* **27(5)**: 358-368.

Webby, R.W.; Bywater, A.C. 2007: Principles of feed planning and management. *In*: Rattray, P.V., Brookes, I.M., Nicol, A.M. eds. Pasture and Supplements for Grazing Animals. New Zealand Society of Animal Production, Hamilton, New Zealand. Occasional Publication Number 14, pp.189-220.