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A STUDY OF THE PLEIOTROPIC EFFECTS OF THE
DOMINANT GENE N
IN THE NEW ZEALAND ROMNEY SHEEP

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presented for the degree
of Doctor of Philosophy in the
University of New Zealand

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Massey Agricultural College
University of New Zealand

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Summary

Research on the causes of medullation of the fibres from the New Zealand Romney sheep by Dry (1940), lead to the description of a dominant gene, N, causing a high abundance of halo-hairs in the birth coat of the lamb. Sheep showing this characteristic were called N-type sheep.

This thesis has been concerned with the possible pleiotropic effects of this gene and with their relationships, both to the economic potentialities of N-type sheep and to their possible use in research on genetic and phenotypic correlations.

The investigation involved lambs from matings made in two consecutive years. Those from the first year were used primarily for a study of lamb's growth and a general survey of the problem, while the second year's lambs were used to examine hypotheses which arose from the first year's results and which concerned the relationships between birthcoat type, body growth and the hogget fleece characteristics.

The results, which are based on statistical analysis, can be summarised as follows:

1. The hypothesis of a single dominant gene was not disproved.
2. Growth in the first year showed
 - (a) There were no differences of weight or body size at birth attributable to the presence of N in the genotype.
 - (b) Differences in body weight occurred at 30 days of age, N-type sheep being lighter than the ordinary Romney. These differences were proportional in the sub-groups of sex and birth rank (single or twin lamb)
 - (c) These differences were confirmed at the mean ages of 67, 100 and 144 days. For these ages the differences were greater between the groups of single lambs than between the groups of twin lambs, being of the order of ten or more pounds for single lambs at the final age.

- (d) These later differences were probably to a large extent the result of those already present at 30 days and this initial effect was found to be the more important when the data was analysed in terms of relative growth.
 - (e) Differences of weight could not be attributed to differences in the skeletal size of the animals.
 - (f) Effects may have been present, associated with the homozygous animals (NN) that were not the sole result of the gene N, but were also the result of possible inbreeding and selection associated with the development of these animals for the production of carpet wool.
3. Examination of the carcasses of ram lambs from this experiment indicated no differences not associated with those of weight corrected for age.
 4. These results were not confirmed in the second year when no effect of the gene N on growth was detected in a comparison of heterozygous (N+) and ordinary (++) lambs.
 5. The major difference between the two years' experiments being one of environment, it is suggested that there is an interaction between the genotypes containing N and the environment. Comparison of the growth curves of the ordinary lambs for the two years and consideration of the different conditions suggests that this interaction may well be one of climate conditions and birthcoat type.
 6. The long dorsal spines of the thoracic vertebrae of N-type sheep appeared to be associated with the presence of horns, although further information is required on the early development of both the horns and these spines.

Fleece Characters:

7. When corrected for body weight, the greasy fleece weight of N-type lambs and hoggets was greater than that of ordinary animals. The difference was greater for twin than for single lambs.

In the first year:

8. Wool from ewe hogget twins had a greater staple length and more 'hairiness' (benzol test) than single lambs (70 lambs)
9. There was a negative association between body weight at 30 days of age and the percentage of coarse continuously medullated fibres in the hogget fleece. In heterozygous animals a greater density of halo-hairs at birth was associated with more coarse fibres in the hogget fleece.
10. Medulla diameter at constant fibre diameter was found to decrease with greater body weight (or faster growth) in both years.
11. Results in the first year suggested penalisation of the secondary follicle population in N-type sheep following the poor growth of the lamb with the resulting coarse fleece of low density. This was shown, for instance, in the coarser fleece with longer staple length of twin animals. This hypothesis formed the basis for the major part of the second year's work.

The second year's work: *

12. Ordinary lambs had more fibres per unit area (density) at birth and at 25 weeks of age.
13. The lower fibre density of N-types at birth was interpreted as the result of the higher density of halo-hairs, as a high proportion of halo-hairs was found to be associated with a low birthcoat density of all fibres.
14. N-type twins had a higher halo-hair density than N-type single lambs, and larger animals (measured by the height at withers) had a lower total density. These results were assumed to follow from the different skin expansions in the last few weeks of pre-natal life. This, with a suppressing effect of large primary follicles on the formation of (or production of fibre from) new secondary follicles, could account for the observed density differences and associations at birth.
15. The variance amongst N-type lambs of halo-hair density was not fully accounted for and it is suggested that other unknown factors, genetic or otherwise, may affect the number of primary follicles which are originally of sufficient size to produce halo-hairs.
16. The fleece density at six weeks of post-natal age would depend on the density at birth, the skin expansion and the number of new fibres added. The results for different relative skin expansions were:
 - (a) Skin expansion less than two (times birth area): the number of new fibres were penalised by high birth fleece density or by many halo-hairs.
 - (b) Skin expansion greater than two for N-types and 2.5 for ordinary lambs: fibre numbers added were independent of initial densities and, in addition, at expansions greater than 2.5, the N-types added more fibres per unit area than did the ordinary lambs.
 - (c) Skin expansion greater than four for N-types and three for ordinary lambs: a maximum of about 6000 fibres added to an initial square centimetre for N-types and of about 3000 fibres for ordinary lambs, is reached.
17. The results under section 16 above are similar (with additions) to those obtained by other authors and suggest penalisation of secondary follicle formation or of fibre growth from these follicles (no actual follicle counts were available) under the circumstances detailed.

* Note: The wool samples were from ^{the} standard loin position, being carried out in duplicate for the determination of sampling and other errors.

18. The density of the hogget fleece, sampled at about 25 weeks of age, after shearing, depended on that at six weeks and the intervening skin expansion. Only a small proportion of new fibres were added to the fleece over this period.
19. Weighted mean fibre diameters were inversely proportional to the fleece density at each sampling time except for the ordinary lambs at birth. N-types showed a greater diameter for a given density and in addition, for both types of hogget, the diameter at constant density was greater for a faster growing animal.
20. At birth higher halo-hair density was associated with a smaller mean diameter of the unmedullated fibres.
21. When the component fibre types (A, B & O; after Burns 1953) from which the overall mean weighted diameters were calculated were examined, it was found that there was a large increase after birth, this being proportional to the maximum diameter, which was attained at six weeks. It should be emphasised that the mean diameter frequently used in work on fleece characteristics may be based on a trimodal skewed distribution and this does not reflect the true pattern of diameters.
22. There was a tendency for the fibre diameter mean and variance to be reduced in the N-types at 25 weeks of age and the means of the N-type and ordinary lambs tended to converge at this age.
23. Unmedullated fibres (O types) from N-type hoggets were smaller than those from ordinary hoggets.
24. It was reasonable to suppose that halo-hairs were generally followed by coarse medullated fibres and the importance of these in the hogget fleeces depended on the original halo-hair density and the number of other fibres added to the fleece. Consequently the hogget fleece characters depended in turn on the early growth of the lamb.
25. An examination of fibre diameters at the thinnest pre-natal portion and at six weeks for both N-type and ordinary sheep and the various fibre types from them, indicated that the proportional reduction in diameter was similar in both types of sheep. Fibres had a reduction in pre-natal diameter which was proportional to the diameter at six weeks.
26. It was suggested that the 'pre-natal check' and the fibre type array phenomena are in part the morphological end point of the different pre-natal and post-natal fleece densities, the lambs' growth at the two periods and the distribution of potential fibre sizes which can be produced by the follicles. Consequently further investigation in these terms and in terms of follicle ratios and measurements are likely to be profitable.
27. The relationships between medulla diameter, fibre diameter and body weights were similar for the hoggets from both years' work. There was a greater medulla diameter for

a given fibre diameter at birth and at six weeks than at the hogget stage. Differences in 'Hairiness' observed in the fibre type arrays would be the result of the fibre diameters which in turn would depend on the factors in sect. 25 above.

From these results a suggested plan of the pleiotropic effects of the gene N has been constructed.

If the initial action is one producing large primary follicles, then it is possible to account for the results obtained above. Some confirmation is naturally required on various points by repeated or more detailed work, but the general plan seems clear. These large follicles will produce the halo-hairs and in addition affect the formation of secondary follicles or the growth of fibres from them. The effects which follow this show considerable variation as a result of interactions with other genetic effects or with the environment. The environmental interactions are shown markedly by the differences between twin and single lambs in the various characteristics and also by the different results of the growth experiments in the two years. The various factors affecting the fleece density at six weeks will also be dependent to a considerable extent on the environment, and on other genetic factors. These interactions are included in this plan of pleiotropy which can thus follow various paths. These paths are not, however, discrete/and separate, but form the pattern of continuous variation observed in the hogget fleeces. Thus by establishing connections between the growth of the lambs and the fleece characteristics, much of the variation in the N-type hogget fleece can be accounted for. In addition, some overlapping between the characteristics of N-type and ordinary

hogget fleeces found in particular in the first year is explained although there is a gene difference with marked phenotypic manifestation at birth.

The thesis concludes with a discussion on the possible research uses of N-type sheep and suggests various investigations in which they could be of use. The important research use lies in the possibility of producing two groups of lambs of very different wool types from one group of ewes, it being known that this difference is a genetic one and that all maternal and similar effects are randomised amongst the two groups. Some suggestions for an N-type experimental flock and for its part in sheep and wool research are made.

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Dry, F.W. (1940) Nature 145: 390

Burns, M. (1953) J. Agric. Sci. 43: 422

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