cent works with grass of comparatively low toxicity, we find some animals show signs of facial eczema liver damage, although they have eaten comparatively small amounts of grass compared with others which show no liver damage. In other words, there appears to be much variation in susceptibility judging from the few results available. I would like to hear Mr. Hancock's opinion as to whether these progeny of 599 were just a few cases among a number of cases of facial eczema occurring at that time.

MR. HANCOCK: Unfortunately they were run on a hill which was our worst facial eczema paddock, so if any sheep on the farm would have been affected by facial eczema these lambs had the greatest chance. That does not, of course, preclude the possibility that the progeny of 599 had an inherited tendency to be affected with facial eczema, but I think that is rather dubious. We actually had other lambs that year affected with facial eczema.

BREEDING N-TYPE SHEEP

by

F.W. DRY, MASSEY AGRICULTURAL COLLEGE.

N is the first letter of a name very familiar to members of this Society. N-type sheep are named in gratitude to the Romney stud-breeder who was the donor of the foundation ram of my oldest stock. He was somewhat apologetic over that lamb, but in view of tentative commercial interest that N-type sheep have attracted the time may come when the full name will be used with complete freedom.

N-type sheep have coats packed with large birthcoat kemps, the biggest of which are halo-hairs, on the main area of the body, or most of it, as well as on the extremities, where they are very plentiful on some non-N lambs. The birthcoat kemps on shedding are often followed by later kemps, frequently succeeded by a series of kemps grown one after the other; or the successors of the birthcoat kemps may largely be persistent fibres, mostly very hairy. The biggest persistent fibres of the birthcoat are hairy, generally very coarsely so, in the region grown in the early months after birth. The total hairiness of the full year's N-type fleece varies greatly. Many are supremely hairy in either or both of the two ways just distinguished.

N-type sheep came to dominate my breeding work with sheep of Romney type because I followed a trial whither it led. In the early days our thoughts were much on hairiness. Halo-hairs are very hairy, and when present are the first fibres to begin to grow. It was logical to study the inheritance of their abundance. This was done in matings made on gradings for halo-hair abundance which had been made as soon as the sheep about to become parents had themselves been born. In the early experiments the abundance of halo-hairs on the back varied none to about a tenth that characteristic of N-type. Abundance proved to be strongly inherited. After two years N-type was encountered, and since then I have become more and more engrossed with it. At the outset I was acting on the time-honoured principle of breeding something deemed bad in pursuit of knowledge to be used to defeat it. Then interest came to be centred on the fundamental genetics of N-type. And recently the products of these sheep have attracted notice as potentially ornamental or useful, but what the profit and loss will be remains to be ascertained.

N-type is inherited in three different ways: multifactorial, simple dominant, simple recessive. Such a story of inheritance would win notice in the Mouse or Drosophila. It is surprising to encounter such a situation in a large domestic animal.

Multifactorial-N: Starting with sheep with comparatively modest numbers of halo-hairs, a small stock that consistently

produces full N-type has been built up by selection, gradually but quickly. From the origin of this stock, and from the get of some of the rams used when they have been mated with non-N type sheep, it is concluded that a small number of different factors are interacting to produce N-type. Three pairs of genes seems a likely number. It appears probable that these factors multiply one another's effects, so that they interact in geometric, in contrast with additive or arithmetic fashion. In building up the Multifactorial stock the generations have been rotated rapidly on the male side, five rams having been used in seven years, each after the first the son of his predecessor. Dickerson and Hazel have drawn attention to the part likely to be played in livestock advance by rapid rotation of the generations accompanied by straight selection without progeny testing.

Dominant-N: The N-type ram lamb donated in 1931 turned out to be heterozygous for a dominant gene for N-type. It was realised, a little slowly in truth, that in matings with non-N ewes of varying halo-hair abundance he had got about half his lambs N-type, half non-N. Various N-type rams descended from him have given 1:1 ratios in out-crosses, and matings between N-types all having one parent non-N have given 3:1 ratios. Several rams with both parents N-type have shown themselves to be homozygous, getting all their offspring N-type (or near-N) with whatever ewes they were mated.

A second stock of Dominant-N sheep, that has been kept separate, traces to a ram born in an early experiment at the College. It is simplest to postpone discussion of his origin until certain breeding work has been carried further. From preliminary tests it is likely that the Dominant-N genes in the two stocks are the same.

Recessive-N: An N-type ram born in 1935, from non-N parents, was mated with non-N ewes and got thirty lambs. Not one of them had more than very moderate numbers of halo-hairs, and most had few or none. Mated with his own daughters he sired offspring half of them N-type, half non-N, and other breeding results have demonstrated simple recessive inheritance.

Relation between Dominant-N and Recessive-N: Breeding work is in progress to test the hypothesis that Dominant-N. non-N, and Recessive-N form a series of multiple allelomorphs. Certain breeding results suggest that the Recessive-N gene can change into the Dominant-N gene. Ideas on the relation between the two genes are taken from the Drosophila workers. Testing the suspicion that a change in a gene takes place in the production of one germ cell in a hundred is an exacting matter with slow-breeding animals that live, not in cages or milk-bottles on the shelves of laboratories, but in paddocks out-of-doors.

Horns: Almost all N-type rams, of all three genetic types, have horns curving in a wide spiral, though a few are not horned. In Dominant-N I at first supposed that horns were conditioned by a different gene from the N gene, but linked with it rather closely. I thought that in the original ram the gene for N-type and the gene for horns were on the same chromosome, and that an occasional N-type ram without horns, or a non-N ram with horns, were to be explained by crossing-over. My present belief is that any gene or combination of genes giving an N-type coat in a ram ordinarily also causes him to grow horns. An odd N-type ram is completely polled. A few have scurs, and some have small horns. Non-genetic accidents are a possible explanation of the absence of horns, but there is some evidence that modifying genetic factors can restrict or prevent the growth of horns. If N-type should ever be in demand, attempts to render stocks polled by breeding may have to be considered, but it might prove difficult to do so without reducing hairiness.

In Dominant-N ewes there are good grounds for concluding that homozygotes usually have horns, up to seven inches long, heterozygotes rarely. We can thus go a long way in recognizing

heterozygotes by inspection. Horns may thus prove more than an oddity by speeding the building of stocks homozygous throughout. There appears little risk in accepting as homozygous, without the delay of a breeding test, a ram by a proved homozygous sire out of a horned dam whose parents have both been N-type.

It will thus be observed that horns in Dominant-N are inherited as a sex-influenced character, as Wood found in early Mendelian times in breeding experiments beginning with the cross between Dorser Horn and Suffolk.

A few further details about horns may be reported. Multifactorial-N ewes are often horned. Recessive-N ewes have so far never had horns. Non-N rams carrying the Recessive-N factor have small horns so often that we may indeed think of the Recessive-N factor as producing a sex-influenced dominant effect in causing these horns to grow.

Poor Expression of N Genes: Some animals which there is convincing reason for classing as genetically Dominant-N or Recessive-N have birthcoats only Borderline-N or Near-N, with, say, a tenth of full N-type halo-hair abundance. Modifying factors have something to do with this failure of the N gene to come to complete expression. This is shown most clearly by the frequency of Near-N in the offspring of N-type ewes mated to Southdown rams. In a few genetically Dominant-N animals the place of many of the halo-hairs of the N-type complement has been taken by sickle-fibres with very large sickle-ends.

It is probable also that the Dominant-N factor sometimes fails completely to raise the abundance of halo-hairs. The coats of several lambs likely for certain reasons (including the presence of large-ended sickle-fibres) to be genetically Dominant-N, though not yet proved to be so, have only few halo-hairs on the back, or even none. This is a complication calling for investigation parallel with that of the relation between Dominant-N and Recessive-N.

Inheritance of Variation in N-type: Near-N has just been mentioned. In all Near-N lambs there are far fewer halo-hairs on the withers and side of the neck than on the main part of the back. In N-type proper full abundance of halo-hairs may be maintained all over the body, or there may be a greater or less reduction at the anterior end. The analysis of observations recorded at birth shows that genetic factors have at least something to do with this kind of variation.

In about half the N-type lambs bred there have been brown fibres, on the back of the neck, from just a few intermingled with the white fibres up to a large brown patch. Brown on the neck is common in all the N-type stocks. Occasionally brown spots or even large areas are present elsewhere on the body. Genetic factors are concluded to affect the presence and amount of brown.

Considerable variation exists in the kind and size of curl in the birthcoat. At one extreme the halo-hairs and associated fibres form a solid mass, not divided into tufts, and scarcely relieved by waving. Some birthcoats show waving rather than curling, and to some this waving appeals, but in the pursuit of the ornamental it is well-rounded curls that are being favoured. If beauty is most seriously sought the skins are likely to be clipped to produce a variegated effect somewhat like broadtail. Clipping would simplify matching, for skins that have well marked curling may look the same after clipping when one has had the halo-hairs well bedded in the curls, while in the other some halo-hairs project in straggly fashion. It is possible to say that genetic factors play some part in determining curl type, and it seems likely that breeding for a preferred kind of curl would not be unduly difficult.

Variation in the abundance of kemp amongst the fibres grown in the follicles that have shed birthcoat kemps has been mentioned earlier. Again genetic factors appear to be at work. As published elsewhere, Miss Janet M. Ross has achieved good success in correlating differences in the characterization of the fibre types of the birthcoat and in the freedom of shedding of the birthcoat fibres with the abundance of later kemp. Shedding is regarded as the expression of vigorous action on the part of the follicle, which is looked upon as working so energetically that it is compelled to take a rest. The "toughness" of the birthcoat, as judged by the stoutness of certain pre-natal structural features, is also regarded as revealing early vigour. Variation in these characters that, we believe, give the measure of early activity in the skin, allows us to foretell with substantial success how much later kemp will be grown. On our interpretation, higher or lower later follicle vigour, related to earlier degree of vigour, plays a large part in determining the greater or less freedom of shedding of the fibres grown by the follicles that have shed birthcoat kemps, that is, in deciding whether those succeeding fibres are kemps.

CONCLUSION: In seeking to understand the inheritance of N-type a variety of genetic phenomena have been encountered or suspected. Sex-influenced inheritance of horns has long been known. Geometric interaction of multiple factors has gained prominence rather recently. The poor penetrance of a gene, ordinarily dominant, is a confusing happening liable to occur in the human subject. Inheritance of the same character as a simple dominant and as a simple recessive is known in Drosophila (Eyeless) and in Man (Retinitis pigmentosa). In each of these cases the two genes are allelomorphs, so that, with the gene for normalcy, they form a series of three multiple alleles, and we wonder whether this is true also of Dominant-N, non-N, and Recessive-N. N-type, too, by way of variety, is inherited in multifactorial fashion, the three different modes of inheritance of the same character giving genetic standing to the sheep. The suspicion that the Recessive-N gene, and indeed the Dominant-N gene, too, may be unstable, brings us into the company, as country cousins, of the Drosophila workers.

In our observational "hair-splitting", accompanied by a preliminary study of pre-natal development, we have sought understanding of the mode of working of the Dominant-N gene, with some thought to that of postulated modifying factors adding or subtracting vigour. In fundamental terms our fibre type work may be said, too, to explore the architecture of the fleece. On the practical side our concern in the fibre type work is largely with early recognition, with prophecy of the future of the fleece. Early recognition is a matter of much consequence in scientific livestock breeding. Hope is entertained that, in addition to forecasting abundance of later kemp, we shall be able to declare, very early, the degree of hairiness of the persistent fibres, that is, the non-kemp hairiness of the fleece. For some purpose extreme hairiness may be wanted.

DISCUSSION ON DR. DRY'S PAPER:

DR. McMAHON: I wish to pay a tribute to Dr. Dry for his patience in carrying out this work with an animal as wellbred as the sheep and discovering some information which is really of important fundamental application - this question of the mode of action of genes in relation to the geometrical and arithmetical idea is really a very fundamental idea, and to have demonstrated that in sheep is a very great achievement. I would also pay a tribute to Dr. Dry's patience in the breeding of young geneticists. Although I am not a geneticist, I do owe a lot of my genetical training to the patience of Dr. Dry in the early days. I would like to ask two questions: What is the relationship of N-type in weight of fleece? Secondly, what is the story about the direction of curl of the horns? Is it the