COLOUR INHERITANCE IN SHEEP
III. FACE AND LEG COLOUR

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1. Introduction.

During the past four years the writer has had the opportunity of conducting experiments on the inheritance of colour in sheep and a part of the conclusions that have emerged up to the present time have been published in a series appearing in this *Journal* (1924, 1926). It is hoped in this way to bring together the results obtained in these experiments as well as the results of other workers and so eventually to add a chapter to the study of coat colour in mammals, a study that has led to fruitful hypotheses, and in particular to more or less physiological conceptions of genetic action. The writer feels that some such explanation is required to preface this paper, which is mainly an attempt to systematise a portion of the field and to analyse further the results obtained by Wood (1905, 1909), and only includes a few casual original observations. Unfortunately, there is little prospect at present of the carrying out of any further experiments on the inheritance of face colour, so that it may be justifiable to analyse as far as possible the results already obtained and to fit them into the general scheme.

2. The Rationale of Variations in Face and Leg Colour in Sheep.

Amongst the mammals about which something is known regarding the inheritance of variations in coat colour, sheep occupy a rather special position, this being due to the peculiarities in the make-up of the coat. Primitive sheep, that are considered to resemble closely the ancestors of the domesticated breeds, possess two clearly defined coats, a coarse outer protective coat, and a fine inner warmth-retaining coat. Most modern sheep have the inner coat greatly developed at the expense of the outer coat which, in most cases, has become reduced to a covering of short

stiff hairs on the face and legs, to a remnant of varying but usually small amount in the body of the fleece known as kemp, and to a birth-coat sometimes present in the new-born lamb which is soon lost. For the sake of simplicity, it is convenient to visualise a threshold for the formation of pigment. An ordinary white sheep represents almost complete restriction, a black one almost complete extension. Associated with this and other variations is the occurrence of dilution which turns the black into brown or light red. Between the extremes of self-black and white many intermediate conditions are found. For example, the writer (1924, 1926) has investigated what is probably a series of quadruple allelomorphs; the top of the series is white, then come badger-face pattern, reversed badger-face pattern, and black. In this case the intermediate condition may be visualised as a pattern of black and white, the threshold for pigment formation being reached in certain areas but not in others. Other patterns, such as the piebald pattern described by the writer (1926) or that of the black-headed Persian sheep, are similar, in that colour is confined to certain areas irrespective of the type of fibres involved. Another intermediate condition is of an entirely different kind. In this second type the threshold for pigment formation is reached in the case of the derivatives of the primitive outer coat but not at all, or only to a slight extent, in the case of the derivatives of the inner coat. An excellent example of this type of restriction is the Suffolk sheep, which has been fully described from this point of view by Nichols (1927). In the Suffolk sheep the face and leg hair, the kemp in body of the fleece and the portion of the birth-coat derived from the outer coat are black, while in the case of the wool fibres only the tip is pigmented, the pigment being present in such small quantity that its contribution to the gross colour of the sheep is negligible. In the adult, moreover, as tips do not occur except in regenerated fibres, even this slight pigmentation is almost absent. It is this type of colouring, where pigment is practically confined to derivatives of the outer coat, that will be considered in this paper. It should be noted that a consequence of this type of pigment formation is that there is an almost perfect correlation between amount, distribution, and dilution of colour on the face and on the legs respectively, so that when face colour is mentioned it will be understood that leg colour is also included in the description.

It is possible to extend the scheme further and to separate the variations in face colour into three groups.

1. Variations in the relative proportion of pigmented and unpigmented areas and their distribution.

2. Variations in dilution.

3. Variations in grades of completeness of restriction of pigment in the white sheep.

A few words of explanation are required with reference to group 3. This group covers variations in the nature and amount of the small quantities of pigment found on the bare skin of the nose, on the hoofs, as well as spots on several regions chiefly round the nose, about the eyes and ears, and on the scrotum. This pigment is mainly confined to the skin, the hairs being white, but occasionally the pigment spreads into the hairs too.

There are several lines of evidence to show that variations of group 1 type and of group 3 type are rightly separated. It will be shown that variations in the characteristics determined by factors of group 1 are inherited in a definite way and that white-faced sheep are homozygous for that character. Their genetic constitution is the same in respect to group 1, although they may vary considerably as regards the precise degree of restriction of pigment on the extremities. For example, sheep with pink noses and white hoofs and almost complete absence of pigment are in respect of factors of group 1 identical with sheep with black noses and hoofs which also show little spots of black round the muzzle and on the ears. Another line of evidence pointing to the same conclusion is that where there is considerable dilution of the colour on the face as determined by factors of group 2, the pigment on the nose and the scattered coloured spots are not necessarily diluted correspondingly. For example, the Welsh Mountain sheep has a broken-coloured face, the patches being light red, but the nose and small spots round the nose and in the ears are dark.

The various breeds of sheep can be grouped as regards their face colour in accordance with the scheme. The following breeds are distinguished by whole colour on the face subject to increasing degrees of dilution:

Suffolk—black.

Hampshire Down—black, but not quite as dark as the Suffolk.

Oxford Down, Shropshire, Dorset Down } brown.

Southdown—mouse colour.

The following breeds are examples of white faces with varying degrees of completeness of restriction of colour as determined by factors of group 3:

Merino
Dorset Horn } very white.
Ryeland

Longwool breeds, *e.g.* Border Leicester—white with dark or mottled nose and varying amounts of small dark spots.

The following breeds have broken colour on the face:

Kerryhill—coloured areas on face not as dark as black of Suffolk.

Scotch Blackface—whole black or broken black.

Welsh Mountain—coloured areas light red or tan.

A special complication exists in the case of Wensleydales and Leicesters, which are characterised by blue faces, the blue appearance being due to the growth of white fibres on a dark skin. This complication is not considered further in this paper.

It is a most remarkable fact, and one that apparently has escaped comment, that sheep with whole-coloured faces or white faces breed entirely true for these features, whereas breeds with broken colour on the face most emphatically do not breed true for the grade of speckling desired, or even sometimes for broken colour at all. Similarly, constant selection is required to maintain the desired degree of dilution of colour and the desired grade of restriction of colour on the nose. These facts suggest that inheritance of variations of group 1 type is not complicated and suggests, further, that whole-coloured faces and white faces depend upon a homozygous condition. It is a point of some interest that "white pattern," a white spot on the top of the head and a white tip to the tail, as described by Adametz (1917) and the writer (1924, 1926), among others, is not expressed in sheep with coloured faces, although it seems to be established that the factors responsible occur generally amongst coloured breeds and also in white ones. In the latter case, however, they cannot be expressed.

3. A Further Analysis of the Results of Wood.

The only thorough piece of genetical research on this subject was carried out by Wood (1905, 1909), who made reciprocal crosses between Suffolks and Dorset Horns, raising an F_2 generation of 73. The Suffolk, as already mentioned, has an intensely black face, while the Dorset Horn represents almost the extreme in reduction of pigment. The F_1 animals had speckled faces of a more or less uniform kind, with some tendency to the formation of a pattern round the nose and eyes. An F_2 generation of 33 individuals was raised and their characterisation was described as follows:

3 pure black faces.
3 pure white faces.
3 white faces with black noses.
3 white faces with black round eyes.
3 white faces with black round eyes and black noses.
1 with large irregular patches of black on the face.
17 with more or less uniformly speckled faces.

33

A speckle-faced F_2 ram was mated to speckle-faced F_1 ewes, the result being given as follows:

No pure black faces.
2 pure white faces.
26 speckled faces or faces showing pattern.

28

A white-faced ram from this mating was crossed to Dorset Horn ewes and gave nine lambs with pure white faces. Wood suggested that the evidence for segregation is clear and that three characters are probably involved representing white, black, the patterns and speckling, some characterisations depending upon the heterozygous condition. He did not attempt any further analysis, but after the lapse of eighteen years it is perhaps possible to do this.

Questions of dilution do not enter appreciably into this cross. Suffolks have been selected for an extreme of darkness for generations, though it would appear that some diluting factors were introduced by the Dorset Horn because Wood mentions the fact that some of the hybrids exhibited a distinctly tan colour. Dilution can therefore be ignored and attention concentrated on the action of factors of group 1.

The true breeding character of the parents suggests that they represent a homozygous condition. The extracted white from the $F_1 \times F_2$ mating was also a true breeding parental type. The proportions of blacks and of whites in F_2 are strongly suggestive of a dihybrid ratio, the whites and the blacks being the homozygous parental forms. If it is assumed that sheep with two dominants, one or both heterozygous, are speckle-faced, and that sheep with one dominant, either homo- or heterozygous, show the patterns, the constitutions and characterisation of the F_2 are as follows:

1 *AABB*—black face.
2 *AABb*, 2 *AaBB*, 4 *AaBb* } speckle face.
1 *AAbb*, 2 *Aabb*, 1 *aaBB*, 2 *aaBb* } patterns.
1 *aabb*—white face.

A comparison of the expected figures on this hypothesis and those actually obtained is as follows:

	Black	Speckled	Pattern	White
Expectation	2·1	16·5	12·3	2·1
Obtained	3·0	17·0	10·0	3·0

The F_2 ram used for crossing with the F_1 sheep was of the F_1 type and as, in addition, he gave the double recessive type, his constitution can be assumed to be that of the F_1, viz. *AaBb*. Adding together the figures for this cross and the F_2, and considering together the figures for speckled face and the patterns, as these are not given separately, the comparison between expectation and theory becomes:

	Black	Speckled and Pattern	White
Expectation	3·8	53·4	3·8
Obtained	3·0	53·0	5·0

The correspondence between the expected figures and those obtained can only be regarded as remarkably close and goes far towards justifying the hypothesis advanced. It is only to be regretted that the test of crossing the various F_2 types to the white-faced parent cannot be made. This would not only provide a complete test for the hypothesis, but would also enable a further analysis to be made by which it would be possible to recognise the contribution of each factor in the homo- and heterozygous condition, both alone and in combination.

4. Some Further Observations.

About three years ago the writer had the opportunity of examining some F_1 and F_2 sheep of a Suffolk-Cheviot cross, bred by the late Dr Douglas, of Auchlochan, Lesmahagow. These sheep had been bred with a commercial purpose and the F_1 was a selected one. The observations that it was possible to make were in perfect accordance with those of Wood. There were some differences that were to be expected when the distinction between the Cheviot and the Dorset Horn is borne in mind. Nearly all Cheviot sheep are white-faced at the present time, but in commercial flocks sheep with broken tan on the face are sometimes

seen. This was responsible for a certain variability in the F_1 which the writer did not have the opportunity of examining fully because the F_1 sheep had been selected for the uniform speckling. In the F_2 the parental types, white and whole colour, appeared. There was much more dilution, however, some of the whole-coloured sheep as well as the broken-coloured ones having faces of a peculiar sickly kid-glove shade.

The writer also had the opportunity of examining a Kerryhill-Merino crossbred lamb which is a cross of considerable interest in connection with the general hypothesis. On this hypothesis the speckle-faced Kerryhill sheep should possess both dominants, at least one in the heterozygous condition. The Merino is white-faced. The lamb had a dark pattern on the nose exactly similar to the three F_2 sheep described by Wood. It is not an unreasonable assumption to make that the lamb was probably a homozygous recessive as regards one factor and heterozygous as regards the other. In any case, this piece of evidence is entirely in favour of the position assigned to the speckle-faced Kerryhill breed.

Blackface ewes, which have broken-coloured or whole-black faces, are often mated to Border Leicester rams, which have white faces. The face colour of the lambs from this cross is in entire agreement with the two-factor hypothesis. Some lambs are speckle-faced, a large number have lighter faces with a pattern involving mainly the nose, and occasionally a white face is seen.

5. Conclusion.

The analysis of Wood's figures, supported by the observations mentioned in different parts of this paper, justify the adoption, as a working hypothesis, of the scheme outlined in the first part of the paper. There is reason to suppose that the variations in face colour of the white-fleeced breeds of sheep can be classified according to the three groups postulated. Further, there is good evidence that with regard to variations of the first group—those affecting the distribution of white and coloured areas—the differences found in the pure breeds and crosses between them can be explained in terms of two factors. Of course, the possibility must not be excluded that other factors also exist that modify the action of those main factors.

With regard to dilution and extreme restriction nothing is known, but the multiplicity of grades that exist suggest the interaction of many factors.

One practical conclusion of interest is that in cases where breeders of sheep characterised by broken colour on the face find it difficult to

maintain their ideal type, they have probably based that ideal type upon a heterozygous condition.

6. Summary.

1. A type of pigmentation in sheep is found in which the derivatives of the primitive outer coat—face and leg hair, kemp, and birth-coat—are coloured and the body of the fleece practically free from colour.

2. Variations in face colour fall into three groups:

(1) Those affecting the relative proportions and distributions of coloured, and white fibres.

(2) Those affecting the dilution of this pigment.

(3) Those affecting the precise degree of restriction of pigmentation in the white-faced sheep; this pigment being mainly confined to the skin.

3. A further analysis of the results of T. B. Wood in his crosses of Suffolk and Dorset Horn sheep shows that these results can be explained on the basis of a two-factor difference, the variations in this case being of group 1.

4. As a working hypothesis, it is suggested that the above classification, together with the recognition that variations of group 1 are mainly due to the different states of two factors, affords a reasonable explanation of the variations in face colour found in the white-fleeced breeds of sheep and in their crosses.

7. REFERENCES.

Adametz, L. (1917). "Studien über die Mendelsche Vererbung der wichtigsten Rassenmerkmale der Karakulschafe bei Reinzucht und Kreuzung mit Rambouillet." *Bibl. Gen.* I. 1–258.

Nichols, J. E. (1927). "On the Occurrence of Dark Fibres in the Suffolk Fleece with Particular Reference to the Birth Coat of the Lamb." *Jour. Text. Inst.* XVIII. 395–417.

Roberts, J. A. F. (1924). "Colour Inheritance in Sheep. I. Black Colour and Badgerface Pattern in Welsh Mountain Sheep." *Journ. of Gen.* XIV. 367–374.

—— (1926). "Colour Inheritance in Sheep. II. The Piebald Pattern of the Piebald Breed." *Journ. of Gen.* XVII. 77–83.

Roberts, J. A. F. and Jenkin, T. J. (1926). "A Preliminary Note on Reversed Badgerface Pattern in Sheep." *Welsh Journ. Agric.* II. 70–73.

Wood, T. B. (1905). "Note on the Inheritance of Horns and Face Colour in Sheep." *Journ. Agric. Sci.* I. 364–365.

—— (1909). "The Inheritance of Horns and Face Colour in Sheep." *Journ. Agric. Sci.* III. 145–154.