

## COLOUR INHERITANCE IN SHEEP.

### V. DOMINANT BLACK.

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#### I. THE BLACK OF THE BLACK WELSH MOUNTAIN BREED.

IN the first paper of this series (1924) a description was given of this breed and of an  $F_1$  resulting from a cross with ordinary white sheep. A black ram of this breed crossed to white ewes gave:

23 blacks,

and black ewes crossed to a white ram gave:

5 blacks and 2 whites.

An  $F_2$  generation was raised, the result being:

18 blacks and 2 whites<sup>1</sup>.

Three of the  $F_1$  females used were actually from a black badger-face<sup>2</sup> mating. In view of the results given in a later section of this paper it is justifiable to include them, the crosses actually being black  $\times$  non-black.

In view of the wide divergence between the figures for the  $F_2$  generation and the expected 3 : 1 ratio, it was decided to back-cross the  $F_1$  females to white. The result was:

28 blacks and 22 whites<sup>3</sup>.

As already explained, it is possible to treat a black badger-face cross as black  $\times$  non-black, so that the result of a black badger-face back-cross given later can be added. The total result now becomes:

39 blacks and 29 non-blacks.

<sup>1</sup> Full tables of the various matings have been prepared and are being deposited for reference at the British Museum (Natural History).

<sup>2</sup> For description of badger-face pattern see papers I and IV of this series.

<sup>3</sup> These sheep were taken over by a private breeder. Totals only were recorded each season. Additional results 1930—4 blacks and 8 whites.

The back-cross ratio is fairly normal, but the slightly larger class is still the black one. The possibility that there is more than one factor that results in dominant black is considered in the next section.

## II. THE OCCURRENCE AND INTER-RELATIONSHIP OF DOMINANT BLACKS.

Dominant black, *i.e.* a black dominant to white, is one of the best known colour types in sheep. The black of the Karakul breed has been described by Adametz (1917), Duck (1921, 1922), Wassin (1928) and others, and shown to be dominant to white. It is also known in other breeds of mid-Asia. One of the writers in the second paper of this series (1926) described experiments demonstrating the existence of a dominant black in the Piebald breed of sheep, a number of flocks of which breed are in existence in Great Britain. In this case the black is turned into piebald by the presence in the duplex state of a recessive pattern factor. A rather similar case is that of the Somali and the Persian Fat-tail. In these breeds, as shown by the results of Henseler (1913) and Davy (1927), the dominant black is turned into a pattern in which the head and neck only are pigmented. This is due to the presence of a factor in the duplex state; in the simplex state the factor turns colour into a variety of piebald. Wassin states that this pattern also occurs in Mongolian sheep. He explains the results of Henseler and Davy on the above basis, and also gives the results of his own experiments confirming that conclusion.

The origin of the dominant black of the Black Welsh Mountain breed is a question of considerable interest. The breed is a small one and the history usually obtained is that it arose by the selection of black individuals from ordinary white Welsh Mountain flocks. It is perhaps not inconceivable that the dominant black is the result of the introduction at some time of black Asiatic sheep, or, of course, crosses with the Piebald breed could have introduced it. An Asiatic origin appears to be very unlikely because in those breeds the sheep, in addition to the black factor, often carry a factor for dominant brown (which factor only expresses itself in the absence of dominant black). Dominant browns do not occur in the Black Welsh breed. Heterozygosity in this breed is a marked feature, but the recessives appearing are white. The possibility of the black being introduced owing to crosses with the Piebald cannot be so easily dismissed. This must be regarded as a perfectly reasonable theory. Perhaps the most probable explanation is, however, that dominant black does occur amongst English breeds, though as the various breeds have been improved it would tend to disappear. In

ordinary commercial flocks in which a few blacks are to be found there is often a history of these sheep having had black mothers. There seems to be no reason why in certain cases the dominant black cannot still occur, being handed down in an unbroken succession of blacks. Although a black ram would not be used in many commercial flocks, no attempt would be made to get rid of black ewes.

In order to test the relationship of the black of the Welsh Mountain breed to that of the Piebald breed, crosses were made. The  $F_1$  lambs were all blacks. An  $F_1$  ram was mated to white ewes, the result being:

23 blacks, 2 piebalds and 1 white.

As the piebalds are genetically blacks, this result is really:

25 blacks and 1 white.

No doubt is possible in the case of the one white. This was co-twin to a black, and in addition the characteristics of the Piebald breed are so distinctive that the lambs of the  $F_1$  ram could readily be distinguished from any others in the whole countryside.

It is difficult to explain these figures. It was thought that one of three results would be obtained:

- (1) That the factors would be identical and the result all blacks.
- (2) That the factors would be different, giving a result of 3 blacks to 1 white.
- (3) That one parent of the  $F_1$  ram might have been heterozygous, and not have handed on the black factor, giving a result of 1 black to 1 white.

Taking these figures, however, in conjunction with the abnormal  $F_2$  ratio given in the preceding section, the possibility is undoubtedly raised that there may be more than one dominant black factor. If there were two black factors in the Black Welsh and a third in the Piebald, the  $F_1$  ram might be a triple heterozygote, the expectation in a cross with white being 7 blacks : 1 white. However, this can only be a speculation and the question must be left an open one. Nevertheless, taking the result of this section and that of the preceding one together, it does seem possible that more than one dominant black factor is involved.

These experiments, together with those previously recorded, indicate that the piebald factor is not of very rare occurrence amongst ordinary white sheep. The question arises as to why piebald lambs are not sometimes born, an occurrence that must at the best be extremely rare. It is, of course, possible that the piebald factor does not express itself in the case of recessive colour; but only in the case of dominant colour.

It is probably, however, not necessary to make this assumption. Given random mating, if

$$m = \text{percentage heterozygotes in the parental generation,}$$

and  $x = \text{percentage recessives appearing in the filial generation,}$

$$x = \frac{m^2}{400}.$$

If 10 per cent. of a sheep population were heterozygous for the inhibitor, 0.25 per cent., or 1 in 400 recessive blacks would appear amongst the lambs.

If, however, the characterisation depended upon the simultaneous presence of two recessive factors, the proportion occurring is greatly reduced. The formula now is

$$x = \frac{m^2 n^2}{16 \times 10^6},$$

where  $x = \text{percentage of double recessives in the filial generation,}$

$m = \text{percentage heterozygotes as regards one factor in the parental generation,}$

and  $n = \text{percentage heterozygotes as regards the other factor in the parental generation.}$

Assuming a heterozygosity as high as 10 per cent. for the piebald factor as well as for the white inhibitor, the percentage piebalds appearing would only be 0.0006 per cent., or 1 in 160,000. If a 5 per cent. heterozygosity is assumed for both factors, the proportion of double recessives appearing would be only 1 in 2,560,000.

### III. THE RELATIONSHIP OF DOMINANT BLACK TO RECESSIVE BLACK AND TO BADGER-FACE AND REVERSED BADGER-FACE PATTERNS.

In the first paper of this series the  $F_1$  of a cross between dominant black (Welsh Mountain) and badger-face was described. A black ram crossed to badger-face ewes gave:

12 blacks and 1 white.

Black ewes crossed to a badger-face ram gave:

3 blacks and 1 badger-face.

The occurrence of the single white is discussed in a subsequent section.

A black  $F_1$  ram from the above mating was back-crossed to badger-face ewes, the result being:

11 blacks, 3 whites and 4 badger-faces.

This is a close approximation to the expected 2 : 1 : 1 ratio on the basis of a two-factor difference. The black sheep possess the white inhibiting factor as well as the black factor.

Reversed badger-face sheep (see fourth paper of the series) were also crossed to dominant black, the ram used in this case being a Piebald. The result was:

5 blacks.

The same Piebald ram crossed to badger-faces gave:

3 blacks.

These results are of interest in view of the information they provide as to the relationship of dominant to recessive black. As regards ordinary visual inspection no distinction in appearance can be made out, and Wassin (1928) states that the rate of bleaching with hydrogen peroxide is the same for black wool taken from sheep of both kinds. While, however, the factors for badger-face and reversed badger-face patterns turn recessive self-colour into the corresponding pattern, they produce no effect at all on dominant black. If, following Ouslow (1915), white colour is regarded as being due to the presence of an inhibiting enzyme, dominant black colour cannot simply depend upon an anti-inhibitor, because if this were the case the result of a dominant black-badger-face cross would be badger-face. It is more probable that the effect of the dominant black factor is to intensify the processes resulting in the formation of black pigment, and this to such a degree that neither the inhibitor nor the two pattern factors can produce any effect.

#### IV. MODIFICATIONS OF BLACK COLOUR.

A brief note on the modifications of black colour, apart from the effect of main pattern factors such as badger-face, was given in the fourth paper of this series.

One of the largest modifications is the case where lambs are born grey owing to an admixture of white hairs with the black. Dry (1924, 1927) describes such a type, which he calls silver-grey, and shows it to be due to the action of a single dominant factor. Wassin (1928) describes a similar modification also due to the effect of a single dominant. Dry's sheep were recessive blacks, while Wassin only discovered this factor amongst the dominant blacks of southern and south-eastern Russia, nevertheless it is possible that both observers are dealing with the same factor. This modification was not observed during the course of the experiments.

On the other hand a type of greying was observed amongst the heterozygotes, this process not occurring to any extent until the animal is mature, and increasing gradually with age. Black Welsh sheep are naturally selected for a deep uniform black, so it is not to be expected that such a modification will be of wide occurrence amongst them. It was in all probability introduced by the white parents. Wassin describes the probable existence of two factors causing a greying later in life, one of them, however, causing a profound change in about six months when in the homozygous condition. No *ad hoc* experiments were carried out by the writers on this problem, so the existence of the modification in the experimental sheep is simply recorded.

It is often observed that lambs that are born black turn brownish later, the tips of the wool fibres especially appearing to bleach. Many degrees of change may be observed, but one special case occurred during the experiments that appeared to be of a more definite character. It was stated in the second paper of the series (1926) that the pigmented areas of the Piebald sheep of the flock from which were drawn the experimental animals rapidly lost the original very dark colour and became a definite dark fawn. It was noted that in the self-black  $F_1$ 's resulting from crosses with this breed the process did not occur. Ten lambs were born in connection with a back-cross of the  $F_1$  to Piebald. At the time the above paper was written it was decided that the lambs should be observed for a further period, and the result as regards the bleaching of the fleeces is now given. This was:

- 4 blacks (like ordinary blacks);
- 5 bleached (like Piebald breed);
- 1 doubtful—this animal had brownish shoulders and dark hind-quarters.

There is thus the suggestion that in this case a single recessive factor may be responsible for the marked modification. It is possible that this is the same factor as that described by Wassin—also recessive—that turns black into brown.

#### V. AN ANOMALOUS RESULT.

In the first paper of the series (1924) it was recorded that the dominant black ram used, when mated to white ewes, sired 23 blacks, and when mated to badger-face ewes, 12 blacks and 1 white. He thus gave 35 blacks and 1 white. It was decided to test further the single anomalous white. Mated to white ewes this anomalous ram gave:

7 whites.

Mated to badger-faces he gave:

10 whites.

Apparently, therefore, he was not even heterozygous for the white inhibitor, although his mother was a badger-face and could not have possessed it.

This lamb was co-twin to a black. The possibility of a double fertilisation by two rams may be ruled out. Not only is it practically impossible that a strange ram could have broken into the field without the knowledge of the shepherd, but the black ram was an animal of such ferocity that he would undoubtedly have killed such an intruder. One possible explanation is that an event occurred which is known to happen in the sheep, although owing to the care of the shepherd the chance is extremely remote in this particular flock, viz. that the ewe just before parturition took away the lamb of another sheep.

#### VI. A BRIEF SUMMARY OF COLOUR INHERITANCE IN THE SHEEP.

A brief summary of what is known at present of the inheritance of coat colour in the sheep may not be out of place. Sheep may be of five fundamental colour types:

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|---------------------|----------------------|
| (1) Dominant black. | (4) Recessive black. |
| (2) Dominant brown. | (5) Recessive brown. |
| (3) White.          |                      |

Each factor in the duplex or simplex state prevents the appearance of any characterisations lower in the series. The exact relation of the two bottom members of the series must remain doubtful for the present; they may be allelomorphic.

The main known modifications of these basic colours are as follows:

1. A recessive piebald factor which in the duplex state turns dominant black into piebald. Its effect on the other colours is not known. It has probably no effect on white.

2. A factor which in the duplex state turns dominant black or dominant brown into black-headed pattern; in the simplex state into a form of piebald. Its effect on the recessive colours is not known.

3. The badger-face factor, which in the duplex or simplex state turns recessive black and probably recessive brown into badger-face pattern. It has no effect on white or the dominant colours.

4. The reversed badger-face factor, which in the duplex or simplex state turns recessive black or recessive brown into reversed badger-face.

It can only be expressed in the absence of the badger-face factor. It has no effect on the dominant colours or on white.

In addition to the above, other factors are known which produce less profound effects, while in yet other cases the genetics of the modifications are not fully known. Wassin may be consulted for a fuller account.

The most important of these modifications about whose genetics something is known are as follows:

1. A white patch on the top of the head and a white tip to the tail is a modification that appears to crop up amongst all coloured sheep. Adametz (1917) considered it to be based on the presence of a recessive factor, but Wassin gives data which show that it is a dominant. Many white sheep carry this factor, which in them cannot of course be expressed. Many of the coloured sheep in the writers' experimental flocks exhibited this pattern.

2. Wassin describes a pattern prevalent amongst the black Romanov sheep and also observed by him in other recessive blacks. This pattern involves varying amounts of white on the face and legs. It is possible that the sheep exhibiting a little white only may be identical with those showing the white pattern described above, but by no means certain in view of the relationship to dominant black. The various grades of this pattern appear to depend upon a series of multiple factors. Wassin assumes five in order to explain his results. It is very probable that these factors do not affect dominant black.

3. A dominant factor which in a coloured sheep produces a white collar. This characterisation and its inheritance are described by Wassin. It may be expressed in dominant or recessive blacks.

4. Data were given in the third paper of the present series regarding the probable existence of two pairs of factors which affect the amount and distribution of pigment on the face and legs of white-fleeced sheep. These factors do not affect coloured sheep.

5. A dominant factor which turns black into grey. Lambs are born grey. This modification is fully described by Dry, and may be identical with the similar factor also fully described by Adametz and by Wassin.

6. Greying later in life is more complicated. Wassin tentatively suggests the existence of two factor pairs with a different effect, but the data are scanty as yet.

7. The definite bleaching of black to brown is described in the present paper. A single recessive factor may be responsible in the case quoted. This may be identical with the factor described by Wassin.



8. Agouti coloration is described by Wassin, and probably depends upon a single recessive factor which exerts its influence in the presence of certain colour combinations. The white factor appears to be necessary for its exhibition. The very interesting relationship of this factor to the other colour factors has not yet been fully worked out.

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#### VIII. SUMMARY.

1. Further data are given on the inheritance of the dominant black of the Black Welsh Mountain breed.
2. Results are given that have a bearing on the question of the origin of dominant blacks and the inter-relationship of the dominant blacks of various breeds. It is possible that more than one factor exists that can produce dominant black.
3. It is shown that in the presence of the dominant black factor the factors for badger-face pattern and reversed badger-face pattern cannot be expressed.
4. A brief account is included of some of the modifications of black colour.
5. A very brief summary is given of the present state of knowledge regarding the genetics of coat colour in the sheep.

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