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Genetic formulas for the colour in the *Texel*, the *Dutch* and the *Zwartbles* sheep in the Netherlands

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Summary

The *Texel* sheep of the Netherlands, as well as the common sheep we have called *Dutch*, are usually white. Their most frequent formula for the three loci of coloration *Agouti* (*A*), *Extension* (*E*) and *Irregular Spotting* (*S*) is $A^{wh}A^{wh}E^{+}E^{+}S^{+}S^{+}$, where A^{wh} is a gene for light tan or white.

The blacks segregating in *Texel* are given by the recessive *a* (black) in *Agouti*.

The black sheep found in *Dutch* sheep, on the contrary, are usually $A^{wh}A^{wh}E^{d}E^{+}$ (or $E^{d}E^{d}$) $S^{+}S^{+}$. The black pigmentation being due to the dominant E^{d} allele in *E* which is epistatic on *Agouti* genotypes.

The *Zwartbles* which is black with white stripe in head, white socks and white tip of tail (HST) has a formula which is probably $A^{wh}A^{wh}E^{d}E^{d}$ (or $E^{d}E^{+}$) $S^{b}S^{b}$ where S^{b} is the allele for HST or *Bizet* design.

The frequency of *a* in *Texel* sheep is around .018 that of E^{d} in *Dutch* sheep lies between .015 and .030.

Introduction

According to HAGEDOORN and HAGEDOORN (1914) the black coloration segregating in white flocks in the Netherlands was due to a gene recessive to a gene for white.

Nevertheless a note by KALSBEK (1963) seemed to indicate that a dominant type of inheritance for the black was also present in the sheep of the Netherlands and this was confirmed by HOOGSCHAGEN (1963).

Later on data were collected among breeders in the Netherlands (HOOGSCHAGEN, 1964) and presented in two articles: one of which was devoted to hereditary

transmission of white markings on black background (HOOGSCHAGEN, 1966) and the other had to do with the two types of black (recessive and dominant), HOOGSCHAGEN (1967).

Since that time additional information has been presented concerning the transmission of coat color in Sheep. In this article a consideration will be given to a more accurate interpretation of the inheritance of coat colour in the Netherland sheep.

I. — Material and methods

A. — *The breeds*

According to the May-census there were in 1977 about 800 000 heads of sheep in the Netherlands, thereof about 330 000 mature ewes and 450 000 lambs.

We have considered three breeds of the Netherlands: the *Texel*, the *Dutch* and the *Zwartbles* sheep.

The *Texel* is a registered white breed originating from the Texel island, with about 60 000 ewes registered.

The *Dutch* sheep is the name we propose in this article to the non-registered common sheep. It presents many similarities with the *Texel* as many *Texel* rams are among its progenitors. The number of *Dutch* sheep can be estimated on 250 000 ewes, most of them are white, about 10 to 15 000 are black.

The so-called *Zwartbles* breed gathers flocks of black sheep deriving from *Dutch* populations and wears the white design sometimes called HST (white head, spotted socks, white tail tip). The number can be estimated between 1 000 and 2 000. It is in extension with the need for black wool for handicraft.

B. — *The observed colorations*

The color standard of the *Texel* is a white, which presents some melanisation on the muzzle and around the eyes (fig. 1a).

The black animals in *Texel* or in *Dutch* sheep are usually totally black. There are some cases of HST in *Dutch* sheep and even of more extended piebaldness (fig. 1b.c.d).

The *Zwartble* sheep are black with HST, as said before (fig. 1c).

C. — *The data of segregation*

The data are those already presented by KALSBEK (1963) and HOOGSCHAGEN (1963, 1966, 1967) plus those resulting from a survey in pure *Texel* Sheep and others recently gathered by one of us (P. H.).

In order to measure the economical importance of breeding black sheep in the Netherlands we have checked the observations of the *Netherlands Wool Board* (*Coöperatieve Nederlandse Wolfederatie G.A.**) which commercializes more than 50 p. 100 of domestic wool.

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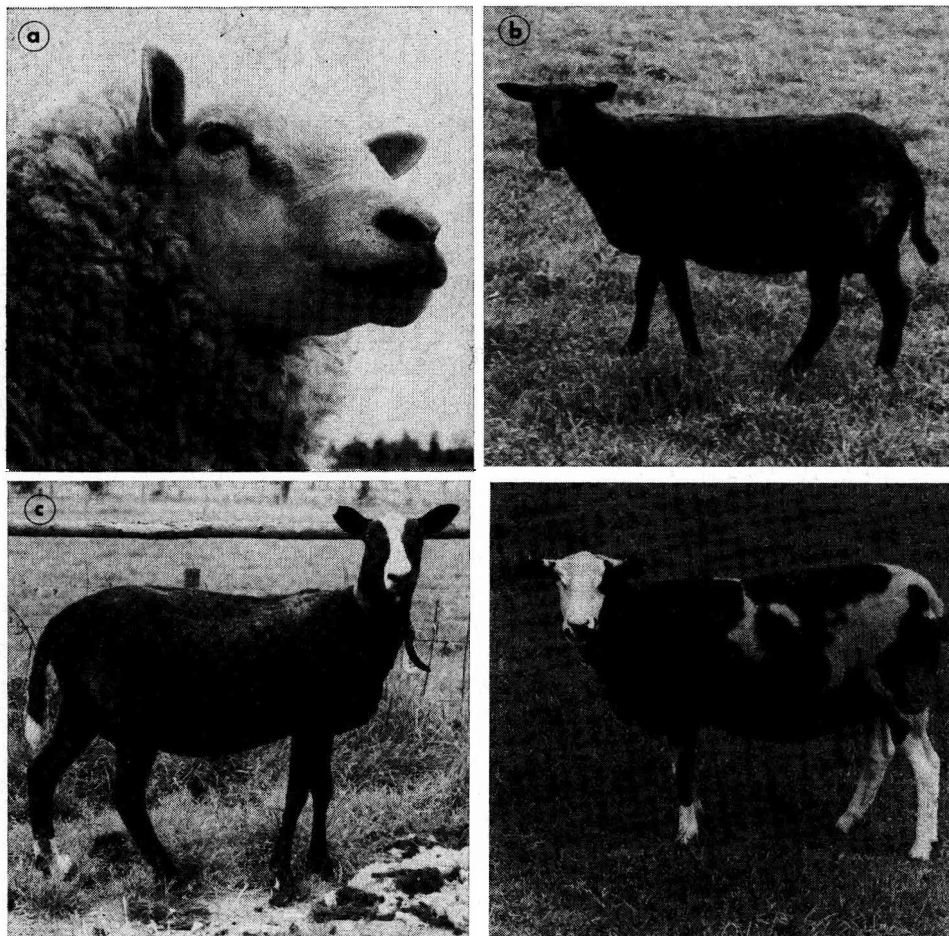


FIG. 1. — *Observed coloration*

- a) Head of a white *Texel* ewe — one can see the melanisation on the muzzle and around the eye.
- b) Black ewe as observed in *Dutch* Sheep.
- c) HST design observed in *Zwartbles* and in some black *Dutch*.
- d) Extended piebaldness sometimes seen in black *Dutch* sheep.

FIG. 1. — *Les couleurs observées*

- a) Tête d'une brebis *Texel* blanche — on distingue la mélanisation sur le museau et autour de l'œil.
- b) Brebis noire en race *Dutch*.
- c) Le dessin HST du *Zwartbles* et de quelques *Dutch* noirs.
- d) Extension de la panachure quelquefois rencontrée chez les *Dutch* noirs.

II. — Results

The results of crossings are presented in table 1 and 2. Table 1 is devoted to the analysis of black versus white, table 2 to the segregation of piebaldness.

TABLEAU I

Crossing between black and white Sheep of Texel and Dutch breed
Résultats de croisements entre moutons Texel et Dutch noirs et blancs

Crossing No	Parents	Progeny	Place, time, references
1	White pure bred <i>Texel</i>	Some black are seen from time to time	HAGEDOORN and HAGEDOORN (1914)
2	White pure bred <i>Texel</i>	Four black lambs among about 13 000 births	Survey in <i>Texel</i> pure bred flocks in <i>Texel</i> island (1977)
3	Black <i>Dutch</i> ♂ × white <i>Dutch</i> ♀♀	22 black, 0 white	KALSBEEK (1963)
4	Black <i>Dutch</i> ♂ × white <i>Dutch</i> ♀♀	Only black	In De KRUIF flock, de Bilt (Utr.), (1977)
5	Black <i>Dutch</i> ♂ × white <i>Dutch</i> ♀♀	About the same number of white and black	HOOGSCHAGEN (1967)
6	White <i>Dutch</i> ♂♂ × black daughters of 5	About the same number of white and black	HOOGSCHAGEN (1967)
7	White <i>Dutch</i> ♂♂ × black daughters of 6	About the same number of white and black	HOOGSCHAGEN (1967)
8	Black <i>Texel</i> ♂ × <i>Zwartbles</i> ⁽¹⁾ ♀♀	17 black, 1 white	In Van den BURG flock, Jelsum (Friesland) HOOGSCHAGEN (1967)
9	Black ♂ from 8 × black ♀♀ from 8	7 black, 2 white	Id. 8
10	Black <i>Texel</i> ♂ × white ♀ from 8	1 black, 1 white	Id. 8
11	Black ♂♂ from 8 × white <i>Texel</i> ♀♀	38 black, 32 white	In C. HOOGSCHAGEN's flocks, Julianadorp (North Holland) HOOGSCHAGEN (1967)

(¹) Black with HST markings.

The frequency of black wools in the Netherlands for the years 1971 to 1976 is given in the table 3.

Discussion

A. — Recall of the genetics of white and black in Sheep

1) White

The existence of two black factors: one acting as a dominant, the other as a recessive towards white, has been described for years in the Sheep (see RAE, 1956 for a review). For a geneticist in mammalian coloration it is rather puzzling

TABLEAU 2

Segregations of HST markings among black animals in different crosses with the test of HST being due to a recessive gene⁽¹⁾

Ségrégation du dessin HST parmi les animaux noirs dans différents croisements et test de l'hypothèse d'un récessif donnant HST

Cross No	Parents		F 1				χ ²	Flocks
	♂♂	♀♀	Solid black		HST			
			Ex-pected	Ob-served	Ex-pected	Ob-served		
1	Solid black <i>Texel</i> S+ S+	<i>Zwartbles</i> S ^b S ^b	17	17	0	0	0 NS	Van den BURG, Jelsum (Fr)
2	Solid black from 1 S+ S ^b	White <i>Dutch</i> S+ S+	38	38 ⁽¹⁾ (2)	0	0	0 NS	C. HOOGSCHAGEN Juliana- dorp (N.H.)
3	Solid black from 1 S+ S ^b	<i>Zwartbles</i> S ^b S ^b	4.5	6	4.5	3	1 NS	WENNEMARS, Dalisen (Ov.)
4	Solid black from 1 S+ S ^b	Solid black from 1 S+ S ^b	5.25	5	1.75	2	0.47NS	Van den BURG, Jelsum (Fr.)

⁽¹⁾ Data from HOOGSCHAGEN, 1966.

⁽²⁾ Some animals have a few white hair or a little white spot on the forehead.

as, usually, black may not be obtained by alleles of loci giving white designs as these genes act only as suppressors of any kind of pigmentation (SEARLE, 1968). Moreover it is hardly to admit a dominant black as well as a recessive one being at the same locus.

Nevertheless it has been shown that an allele in *Agouti* may play the role of a white gene. This is the case for the allele A₁ of ADALSTEINSSON (1970) further on (1974) named A^{wh} by the same author. This factor induces a tan pigmentation (black or brown eumelanin being suppressed) which at its turn may turned offset, giving pure white. This offsetting is apparently due to modifier genes which may lead to pure white breeds.

Later on LAUVERGNE (1976) studying in France various crosses between deep red *Solognot*, white *Berrichon*, black with HST *Bizet* and a black and tan HTS *Finish* ram has shown that, in this situation, a modifier gene for obtaining pure white from a red allele in *Agouti* was the piebald HST gene called S^b

TABLEAU 3

Frequency of black wool in percentage of total weight commercialized by the Netherlands Wool Board
Fréquence des laines noires aux Pays-Bas en pourcentage du poids total commercialisé par l'Office
néerlandais de la laine

Provinces	Years						
	1970	1971	1972	1973	1974	1975	1976
Groningen		3	3	3	2	2	1
Friesland		4	3	3	2	2	1
Drenthe		4	3	4	3	2	1
Overijssel		3	3	3	3	2	1
Gelderland		3	2	2	3	2	1
Utrecht		4	4	3	3	2	2
North-Holland		1	1	1	1	1	1
South-Holland		4	5	5	5	4	2
Zeeland		1	1	1	1	0	0
North-Brabant		3	3	2	2	1	1
Limburg		1	1	1	1	0	0
All country	2,02	2,46	2,21	2,12	1,99	1,50	0,98

(ADALSTEINSSON'S 1974 s). Whose behaviour was very different according the pigmentary background. This red allele was named A^{wh} but one can wonder if it is the same as ADALSTEINSSON'S one.

2) Recessive black

White being explained by an allele in *Agouti* the recessive black is, as in many Mammals, the recessive term of this allelic series.

3) Dominant black

Reviewing previous works, specially those by ROBERTS (1924), ROBERTS and WHITE (1930) and ZOPHONIASSON (1934) and taking account of the homology between colour loci in Mammals RENDEL (1957) was the first author to consider the dominant black gene in the Sheep to be an allele at the *Extension* (E) locus. This interpretation supposes that E^a is not only dominant upon E^+ but also epistatic on any kind of allelic combination in *Agouti* locus. Recently one of us (LAUVERGNE, 1976) has analysed data with the two type genetic factors for the black, with that scope in mind.

B. — Interpretation of our data

1) The white colour and the recessive black

According the above considerations the white of *Texel* could result of the action of an allele in *Agouti* dominant towards the recessive black a . As the blacks segregating are solid black the gene for HST S^b is apparently absent from the breed.

One can admit that the *Agouti* allele for white is A^{wh} , as in Iceland, provide one considers that, in some cases this factor for tan may allow some black pigmentation on the muzzle and around the eyes as in the white *Gotland* sheep described by LÖFVENBERG and JOHANSSON (1952).

The formula of white *Texel* becomes $A^{wh}A^{wh}S^+S^+$ or $A^{wh}aS^+S^+$, as some recessive blacks aaS^+S^+ are sometimes produced. The formula of white *Dutch* is probably identical to that of white *Texel*.

2) *The dominant black*

The crosses no 3, 4, 5, 6, 7 and 11 demonstrate the existence of a dominant black, the black parents being homozygotes as in 3 and 4 or heterozygotes as in 5, 6, 7 and 11 (resp. $A^{wh}A^{wh}E^dE^d$ and $A^{wh}A^{wh}E^dE^+$).

The crosses 8, 9 and 10, show that the two genes for black, dominant and recessive, are definitely non allelic.

3) *The white marks on black background*

The hereditary transmission of HST among pigmented animals appears monofactorial recessive as tested in table 2: $s^b < S^+$. Some very thin dominance (white hair on the forehead) may be detected in some heterozygotes.

These interpretations concerning heredity of pigmentation and of white markings are summarized in table 4.

TABLEAU 4

Genetic formula proposed for the various phenotypes observed in Dutch, Texel, and Zwartbles sheep in the Netherlands

Formules génétiques proposées pour les divers phénotypes observés en races ovines Dutch, Texel et Zwartbles aux Pays-Bas

Breed	Agouti locus <i>A</i>	Extension locus <i>E</i>	Irregular spotting locus <i>S</i>	Formulas given by HOOGSCHAGEN, 1963, 1966, 1967
<i>Texel</i>	$A^{wh}A^{wh}$ or $A^{wh}a^{(1)(2)}$	E^+E^+	S^+S^+ or $S^+S^b^{(2)}$	$WW\ zz$ or $Ww\ zz$
Black segregating in <i>Texel</i> flock	aa	E^+E^+	S^+S^+ or $S^+S^b^{(2)}$	$ww\ zz$
White <i>Dutch</i>	$A^{wh}A^{wh}$ or $A^{wh}a^{(1)(2)}$	E^+E^+	S^+S^+ or $S^+S^b^{(3)}$	$WW\ zz$ or $Ww\ zz$
Black <i>Dutch</i>	$A^{wh}A^{wh}$ or $A^{wh}a^{(2)}$	E^dE^d or E^dE^+	S^+S^+ or S^+S^b	$WW\ ZZ$ or $WW\ Zz$
<i>Zwartbles</i> (HST)	$A^{wh}A^{wh}$ or $A^{wh}a^{(2)}$	E^dE^d or E^dE^+	S^bS^b	$WW\ ZZ\ nn$

(1) When they gave black lambs.

(2) Rare.

(3) Rather rare.

It may seem strange that the black is due in two closely related breeds in the same country to different genetical formulas. This is apparently due to the fact that only white *Texel* rams are raised and sailed out, which prevents the spreading out of the recessive black *a*. On the other hand in *Dutch* breed it is easier to obtain black offspring with a ram wearing a dominant black.

C. — Comparison with previous interpretations

An hypothesis with two independent factors for the black was already brought by one of us (HOOGSCHAGEN, 1963) : W/w (w = recessive black) and Z/z (Z = dominant black). For statistical tests there is no difference between this hypothesis and the present interpretation. But, if the alternative W/w fits well with A/a , the dominant black Z upon a white z does not correspond exactly to the new interpretation. The relationship of E^a towards white, as a matter of fact, is not of dominance but of epistasy. The allele E^a gives a black coloration whichever the formula in *Agouti* may be and is dominant on E^+ whose behaviour is simply to allow the normal expressivity of genotypes in *Agouti* locus.

For the piebald gene giving HST there is a close corresponding between HOOGSCHAGEN'S n (1966) and s or S^b (ADALSTEINSSON 1974, LAUVERGNE 1976).

D. — The frequency of different alleles for the black color

With the data of the survey in pure *Texel* breed (4 in 13 000) one can estimate the frequency of the gene a : ($q_a = 0.018$ in that breed).

The data of table 3 show that the frequency of pigmented wool is about 2 p. 100 (established on seven years). According the experts this value must be majored of at least 1 point, as a greater part of black wool is not checked by the *Wool Board*, as it is used for handicraft.

If all the black sheep on *Dutch* breed are homozygote the frequency of the gene E^a is 0.03. In case all are heterozygotes the frequency is only 0.015. The frequency lies probably somewhere between these two figures.

Conclusion

Two genetical types of black do exist in the sheep in the Netherlands. One is given by the recessive a allele in *Agouti*; the other by a dominant allele E^a in *Extension*, which is epistatic on *Agouti* genotypes.

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Résumé

Formules génétiques pour la couleur des moutons, Texel, Dutch et Zwartbles aux Pays-Bas

Le mouton *Texel* des Pays-Bas, au même titre que le mouton commun de ce pays que nous avons appelé *Dutch*, est généralement blanc. La formule la plus fréquente aux trois loci de coloration *Agouti* (A), *Extension* (E) et *Panachure Irrégulière* (S) est $A^{wh}A^{wh}E^+E^+S^+S^+$ où A^{wh} est le gène pour le fauve ou le blanc.

Les animaux noirs ségrégant en *Texel* portent l'allèle récessif *a* (noir) en *Agouti*.

Les agneaux noirs qui naissent dans la race *Dutch* sont, au contraire, généralement $A^{wh}A^{wh}E^a E^+$ (ou E^aE^a) S^+S^+ . La pigmentation noire est due à l'allèle dominant E^a au locus E , allèle qui est épistatique sus les génotypes en *Agouti*.

Le *Zwartbles* qui est noir avec une liste blanche en tête, des socquettes et le bout de la queue blancs (dessin blanc dit HST) a probablement la formule $A^{wh}A^{wh}E^aE^a$ (ou E^aE^+) S^bS^b , S^b étant l'allèle pour le dessin HST ou *Bizet*.

La fréquence de *a* en race *Texel* est aux alentours de 0,018 celle de E^a du mouton *Dutch* est comprise entre 0,015 et 0,030.

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