GENETICS OF COLOUR IN WENSLEYDALE LONGWOOL SHEEP

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INTRODUCTION

This study examines colour variations in black, blue-grey and silver Wensleydale sheep. Colour breeding records are examined in order to identify the alleles responsible for the different colours and to assess whether these are at the same or different loci. The results are discussed in relation to the detailed research published by the eminent geneticist Dr. F. W. Dry in the 1920's and current knowledge of sheep colour genetics. Health problems, believed to be associated with silver-grey Wensleydales are also discussed.

Description of the Breed

The Wensleydale is a British longwool sheep of great size. The usually white-fleeced animals have a distinctive deep blue skin colouration to head and ears, a pigmentation which can also extend to other parts of the body. Wensleydales are one of the largest British Breeds, mature rams weighing over 130 kg and shearling ewes about 90 kg. They have a rapid growth rate and possess the ability to produce heavy lean carcasses. They are prolific, good milkers and rarely have lambing problems.

The traditional role of the breed is as rams for cross-breeding with ewes of hill and mountain breeds. They are well known as the original sire of the Masham, a widely used and popular commercial cross-bred ewe. Over the years they have been used as foundation stock in other commercially important breeds including the Blue-faced Leicester and the Bleu de Maine.

The Fleece

An important feature of the breed is the uniquely purled and lustrous fleece which is said to be the finest and most valuable lustre longwool in the world. The staple length measures 20 to 30 cm with a Bradford count of 44 to 48 (approximately 33 to 35 micrometers).

An unusual feature of the birth coat of Wensleydale lambs is that the central primary follicles which in most breeds produce the coarsest kempy fibres, in Wensleydales produce some of the finest fibres. This characteristic, first described by Burns[1] as "central checking" is most pronounced in Wensleydales but is also believed to be found in most other longwools. As a result of central checking, the breed has a uniquely characteristic array of wool follicle producing a completely kemp-free fleece in pure-bred sheep. This attribute is passed on in high degree to cross-bred offspring; hence the description "kemp-killers"[2].

Origins and History

The early history of the Wensleydale breed can be traced to North Yorkshire in 1839 when the ram "Bluecap: was born[3]. This ram was the progeny of a cross between a large Leicester ram and the so-called "Mug", the local longwool breed. Mugs were a spotted-faced longwool sheep, not unlike and undoubtedly the predecessor of the present-day Teeswater. Bluecap was clearly a remarkable ram: He is said to have been an extremely wild and active sheep in spite of weighing

32 stones (over 200 kg) as a two shear; he possessed a very dark blue head, while his skin was nearly black, although covered with fine white lustrous wool. Bluecap was stated to be the best ram in the North of England, in his day[3]. He was widely used, transmitting his unique qualities together with his distinctive blue skin colouration to his progeny. The descendants of Bluecap continued to be bred as a uniform type of sheep and by 1876 the breed was established having adopted the name "Wensleydale". A flock book society was started in 1890, and the "Wensleydale Longwool Sheepbreeders' Association" continues to register and promote Wensleydales today.

The number of Wensleydale flocks was at its greatest in the early years of this century and reached a peak of about 180 registered flocks in 1920. In the late twenties and thirties numbers began to drop and by the sixties there were only 18 registered flocks. Fortunately, renewed interest in old and rare breeds in the late seventies and eighties resulted in many new flocks being formed and the numbers of Wensleydale flocks have continued to increase until the present day. It is interesting to note that Wensleydales have always been kept in relatively small flocks, the average flock size at the height of the breed's popularity was less than 15 ewes.

"Black" Wensleydales

Throughout the history of the Wensleydale breed, black lambs are known to be occurred in flocks of white Wensleydales. In the 1920s Dry5 made a study of Wensleydale flock records and was able to show that black was inherited as a simple recessive to white and that the proportion of black lambs at that time was about 15 to 20 percent. More recently, as a result of selection against black, the percentage of black lambs born into white flocks has decreased.

Although the incidence of black lambs has been known and accepted as a familiar, if unwelcome, facet of the Wensleydale breed, until recently, black lambs have not been accepted for registration by the Wensleydale Association; rules from the early Flock Books clearly indicated that breeding from blacks was prohibited by the Association[4]. The policy of the majority of breeders was to cull black lambs at birth or to sell them out as fatstock. Records indicate that black ram lambs met with a very ready sale for crossing purposes, sometimes making more money than white ram lambs[3].

It is known, however, that there were in the early 1900s a few unregistered all-black Wensleydale flocks kept principally for ornamental purposes[5]. These flocks were comparatively large (one of 40 ewes) when compared with the average white Wensleydale flock size at that time and also the largest black flocks found today.

About 10 years ago, the Wensleydale Association approved registration of coloured Wensleydales. The first coloured register appeared in the 1985 Flock Book and listed 10 black females. A census in 1990 revealed 56 coloured females and 16 registered coloured rams. Total registered white females at this time was approximately 1000.

Colour Variation and Pattern

Robinson[3] in his paper on Wensleydale sheep for the Royal Agricultural Society in 1923 noted that "a proportion of black and silver-grey lambs are born ever year". Dry[5] also noted that the "blacks" differed from thoroughly black to silver grey, having a mixture of black and white fibres. He found a complete range exists from deep black to light silver-grey and also noted variability in individual animals and lightening of colour with successive shearing.

Terminology: Although the descriptive terms used by present-day breeders of coloured Wensleydales are "black", "blue-grey" and "silver", occasional animals of intermediate shades also occur. Therefore in this stud the term "silver-grey" (as used by Dry[5]) will be used to describe all sheep born either grey or silver. The term "black" will describe animals born black.

The Upper Mill Flock

The Upper Mill flock was founded in 1986 with the purchase of 2 black Wensleydale ewes and an unrelated ram, all born into white flocks. A further 5 coloured females and 3 whites, known to be heterozygous for black were added to the flock in 1987. Subsequently 3 unrelated black rams have been introduced. The ewe population is now maintained at about 12 and it is one of the largest black flocks.

METHODS

Assessment of Fleece Colour

Samples of fleece were taken from lambs at approximately 1 week, 3 months, 6 months and 1 year of age after which annual samples were taken from adult animals. The routine specimens were taken from the shoulder of the animal although fleece samples were also taken at other sites where, for example, variation of colour was obvious. For analysis of the specimen, a staple slice of approximately 1 mm or less was made across the basal end of the staple of the sample. The cut fibres from these were mounted directly in glycerol on a microscope slide, teased and spread, and viewed with a light microscope at a magnification of x 50. Pigmented and non-pigmented fibres were counted in random total counts of 500 fibres. Percentages of pigmented and non-pigmented fibres were calculated and recorded.

The original wool evaluation work on central checking in Wensleydales was carried out on white lambs only. Fleece samples from coloured Wensleydale lambs were therefore taken for fibre array analyses.

Genetics of Colour

A detailed examination of "colour" breeding records from individual animals and a study of "colour" pedigrees from the Upper Mill and other black Wensleydale flocks was undertaken. In the Upper Mill flock black rams were used routinely although occasional individual crosses were made using silver-grey rams. Results from colour crosses within the Upper Mill flock and those carried out by other breeders were noted. Clearly, with a total breed population of around 50 females in about 20 flocks spread throughout the British Isles a true statistical analysis was inappropriate and impractical.

RESULTS

Colour Variation and Pattern

Dry's description[5] is broadly consistent with the colour found in Wensleydales today; colour can vary considerably; many lambs are born black and remain so or nearly so throughout their lives. Others although born apparently black, exhibit a graying with age; the body fleece may appear charcoal grey by first shear at 15 to 18 months and ewes of 3 or more years of age may appear quite pale grey due to the gradual appearance of white fibres among the black. The fleece colour

of head and legs however, remains dark. Occasional lambs are born a light silver or blue-grey, in some cases with dark head and legs. Silver animals exhibit some reduction of pigmentation with age, but this is less obvious than in the blacks.

The occurrence of white head spots which can be associated with a white tip to the tail have also been noted. In the Upper Mill flock 4 out of a total of 94 black lambs (born in the years up to 1993) were born with small white head spots. Two of these also had a white tip to the tail. The ewes which produced black lambs with white head spots were all from the group of black ewes which, at other lambings, had produced silver-grey lambs.

One silver-grey lamb, born dead at full term from a silver x black cross, had a large white head spot. Other silver-grey lambs had pale silver fleece "topknots".

The blacks can also vary in colour over the body; a grey neck ruff is not uncommon and they may also exhibit a general uneven patchiness of black and grey.

Dry[5] observed that small white patches are occasionally found on black sheep. In the Upper Mill flock only one individual was born with a patch of more than about 2 to 3 cm^2. This ewe had several white patches covering a total area of approximately 150 cm^2 on her right side. She was also unique in having black irises to her eyes.

All coloured Wensleydales seen today and those observed by Dry in the 1920s appear to be either black or varying shades of grey. Moorit or brown individuals have not been reported. However the weathering effects of sun, wind and rain often cause the exposed staple to become bleached to a golden brown or honey-beige colour, resulting in a remarkable range of colours.

Health and nutrition have also been observed to affect fleece colour. A manufacturing error in the diet formulation of feed for ewes in-wintered prior to lambing resulted in several ewes loosing condition and slipping fleece on their backs. As the fleece resumed growth beyond the break, it was obvious that it was substantially more intensely pigmented. Ewes born black but which had become grey with age remained predominantly grey but with an area of intense pigmentation along the dorsal midline. Counts made of fleece samples taken from the area of fleece slip revealed that the percentage of non-pigmented fibres before the fleece break was 56 percent and after the fleece break 14 percent. The modified areas gradually loose the darker pigmentation with time.

A second unfortunate incident was the occurrence of an abscess, initially undetected under the fleece of a ewe in early summer. When discovered, this had discharged its contents over the ribcage and was seething with minute blowfly larvae. The area was trimmed and cleaned and the wound healed. However, when the fleece resumed growth over the area of skin damage it was clearly substantially more pigmented than the adjacent areas of fleece.

Skin Pigmentation

The characteristic blue skin pigmentation of the white-fleeced Wensleydale is replaced with a jet black skin in black Wensleydales. Colour is noticeably less intense in individuals born with silver-grey fleece. The skin pigmentation, although most intense over head and ears, can also extend to the main fleece-bearing areas of the body. Generally, areas between and under the forelegs and hind legs and surrounding the anus are devoid of pigment.

Central Checking

The consistently fine quality of fleece in coloured Wensleydales indicates the probably presence of central checking. Examination of lamb fleece samples by Dr. Burns confirmed this likelihood although she reported that "many of the checked fibres had been lost either by breakage of the tips (in older samples) or loss or failure to see the extremely short and fine tips in 4-day samples."

Colour Crosses

The results of crosses between white, black, and silver-grey Wensleydales are shown in Table 1. A number of non-routine health problems were encountered particularly when breeding with certain silver-grey and black sheep. For this reason, information on viability and lamb health is included in addition to details of colour.

Table. 1

RESULTS OF CROSSES BETWEEN WHITE, BLACK AND SILVER-GREY WENSLEYDALES								
MATINGS:	RAM COLOUR	BLACK	S/G	BLACK	S/G	BLACK	S/G	TOTAL
	EWE COLOUR	WHITE	WHITE	BLACK	BLACK	S/G	S/G	
MATNGS: TOTAL NO:		12	7	40	12	6	1	78
NO. EWES ABORTED:		2	3	1	4	-	-	10
LAMB COLOUR	**LAMB HEALTH**	**NUMBER OF LAMBS**						
WHITE	NORMAL	10	3					13
	POOR	0	0					0
	ABORTED	2	1					3
	TOTAL	**12**	**4**					**16**
BLACK	NORMAL	5	1	50	6	2		64
	POOR	0	1	11	2	0		14
	ABORTED	2	5	5	4	0		16
	TOTAL	**7**	**7**	**66**	**12**	**2**		**94**
S/G	NORMAL			6	2	3	1	12
	POOR			1	0	3	1	5
	ABORTED			0	3	0	0	3
	TOTAL			**7**	**5**	**6**	**2**	**20**
LAMBS: TOTAL NO. PRODUCED		**19**	**11**	**73**	**17**	**8**	**2**	**130**
					TOTAL = 25			
% WHITE LAMBS		63.2%	36.4%					
% BLACK LAMBS		36.8%	63.6%	90.4%	56			
% S/G LAMBS				9.6%	44			

Health Problems

A number of lambs were born dead (for no obvious reason) and several ewes aborted their lambs from a gestational age of about 100 days. Four of these abortions took place in 1989 to ewes served by a silver-grey ram. (Two other ewes served by the same silver ram and two served by a

black ram lambed normally in 1989). Veterinary investigation, which proved negative for enzootic abortion and Toxoplasma, revealed Campylobacter organisms in the stomach mucosa of 2 foetuses.

All abortions involving white lambs (3) also involved one coloured female lamb. Although most categories indicated approximately equal numbers of male and female lambs, only 4 out of the 20 silver-grey lambs born were female.

Notes on Table 1

1. Health of lambs is divided into normal healthy animals (NORMAL), poor or persistently unthrifty animals (POOR), and lambs aborted or born dead at full term (ABORTED). Note: Accurate identification of colour (black or silver-grey) of aborted coloured lambs was difficult.
2. All white ewes were known to be heterozygous for black.

A number of coloured lambs failed to thrive in spite of intensive management and feeding. Several of these were silver-grey (including light and dark variation). The poor black lambs were invariably from the group exhibiting early graying. Apparent problems were variable but mostly alimentary or respiratory in nature. A contributory factor in several of these lambs was a persistent loss of cud.

Some infertility was evident. Results from barren ewes were not included in Table 1. These were: one light silver ewe who proved barren after mating to three different black rams for three successive years, and one black and one white ewe barren one year after mating to silver-grey rams. (Both had lambed normally the previous year and did so subsequently.) Testicular development of ram lambs was occasionally uneven and in one silver-grey ram lamb, absent at 9 months. Two black rams were found to be only intermittently fertile.

DISCUSSION

Genes for Colour in Wensleydales

The presence of genes responsible for black and silver-grey fleece in Wensleydales is well established[5,6]. The present study shows that there are additional genes present which are responsible for white head and tail spots and for black eyes, both apparently recessive. The head and legs of sheep invariably remain dark while the main fleece-bearing area exhibits graying with age; this may indicate the presence of a gene for head and leg colour that is dominant to the factors causing graying with age.

Nature of Pigmentation

The graying of black sheep with age due to an increase in non-pigmented fibres, has frequently been demonstrated[5,7,9,10]. The increase in fleece pigmentation following an illness resulting in a fleece break has also been described[10]. The focus on such an increase in pigmentation to a specific area of fleece-slip and to an area of skin damage shown in this study demonstrates that this effect can be quite localized; melanocytes in the specific areas have clearly been activated. Greying with age in Wensleydales can be relatively rapid or may take place over a period of several years; it may also vary over the animal. Thus melanogenesis can be seen to slow at a variable rate but, as demonstrated, can also be stimulated, demonstrating a transient nature to the pigmentation.

Skin Pigmentation

Much of Dry's early work[5,7] in analyzing records of the Underley flock concentrated on the blue face and ear colour of white-fleeced Wensleydales. He was able to show that a high percentage of animals with "good blue skin colour" were also heterozygous for the "black" gene (now known as A^a, the nonagouti allele of the Agouti locus)[11] but this is frequently misinterpreted to suggest that the blue skin colour is a heterozygous expression of this black gene[12]. White Wensleydale sheep possess the intense blue skin colour of the breed; a skin pigmentation gene must be responsible for this colour[13] and it would appear to be dominant since most Wensleydale-cross lambs retain the face and ear pigmentation of the pure Wensleydale.

There are known to be many white Wensleydale flocks with this characteristic skin pigmentation but which never produce black lambs (personal communication). However, when the black gene is known to be present, as indicated by the occasional appearance of black lambs, the presence of the "black" gene is found to enhance the blue skin colour, i.e. there is an epistatic effect of the black gene on the blue skin colour gene. Since dark skin pigmentation is a desirable feature of the breed, this can lead to the selection of breeding stock, particularly rams, which have the black gene. Dry demonstrated a parallel situation in the early years of the century; although blacks were never bred from, the high percentage of sheep heterozygous for 'black' was perpetuated by a preferential selection of heterozygous rams[14].

Colour Crosses

Dry[6] working on coloured Wensleydales in the twenties, concluded that "white, silver-grey and black form an epistatic series, white dominant to silver-grey and silver-grey dominant to black". His conclusions were based on both his own color crossing experiments and other information available to him:

1. He was assured by the breeders of ornamental black flocks of that time that "black Wensleydales mated to black produce nothing but black lambs."
2. He found that black mated to silver-grey produced either black or silver-grey lambs.
3. He mated silver-grey to silver-grey and produced mostly silver-grey but some black lambs.

However, in the Upper Mill flock, and also in other more recently established coloured Wensleydale flocks (personal communication), crosses between two blacks have been shown to produce occasional silver-grey lambs (Table 1). if black were a simple recessive to silver-grey as postulated by Dry, this would not be possible. Clearly, the results of Dry's work in the twenties and the results of the present study appear incompatible. In view of the dramatic drop in the Wensleydale population during the years between these studies, it was necessary to consider whether the two populations were genetically similar, and if so how such apparently contradictory results could be reconciled.

Dr. Dry conducted his studies in the early part of this century when the Wensleydale population was at its peak. The population began to decline from the twenties and the trend continued until the mid sixties when the population was at a level of only about 200 breeding females[4]; one of the largest flocks at that time was the Islebeck flock of Mr. Sidney Weighell, with about 40 ewes. Since the origins of nearly all the present-day blacks can be traced back to the Islebeck flock[15], it was pertinent to establish the origins of the Islebeck sheep: The first entry for Mr. Weighell is in the 1931 Wensleydale flock book which records the founding of the flock with the purchase of 4 gimmer lambs from the flock of Mr. George Wood who, in turn was found to have purchased his foundation sheep from the Underley Flock, the very flock on which many of the observations of

Dry were based. This direct link between the Underley and Islebeck flocks provides an indication that the present study and that of Dry in the twenties are probably based on genetically related population, although the broad genetic background of the flocks of the two periods my well be different.

It is interesting to note that one line of black Wensleydales in the present study did not produce any silver-grey lambs. A very black ewe of "Islebeck" origins was purchased in 1988. This ewe and her twin daughters when born, were intensely black and exhibited very little graying with age compared with other ewes. None of these ewes produced silver-grey lambs although they were on several occasions put to black rams capable of producing silver-grey lambs; the original black "Islebeck" ewe also produced a black lamb sired by a silver ram.

Observations on the Upper Mill flock suggest that the black sheep capable of producing silver-grey and also some known to be bred from silver-grey seem to exhibit a more pronounced graying with age than some other blacks not known to be associated with the silver-grey gene. The trend to select only "very black" animals for breeding in present-day flocks could explain the fact that silver grey lambs are rare. This may also explain the non-appearance of silver-grey lambs in the all-black ornamental flocks kept in the early ears of this century, evidence used by Dry that crossing blacks gave only black lambs[6]. It would be reasonable to suppose that the flock owners selected the "blackest" ewes and rams available when setting up their ornamental flocks, a not unlikely choice as really black Wensleydales are of quite stunning appearance. Certainly there would have been many excellent black sheep to choose from as the white Wensleydale flocks were in those days throwing 15 to 20 percent black lambs and the numbers of silver-greys were low[16]. A selection for "blackness" by the flock owners could have meant that not only were no silver-greys chosen but that few or no black ewes carrying silver-grey were selected. Thus, only black lambs would be born in these flocks.

It is known that grey fleece colour in sheep can be due to a number of different genes both at the Agouti and other loci (reviewed by Adalsteinsson[17]). Dry's proposal that white, silver-grey and black form an allelic ("epistatic") series (at what is now known as the Agouti locus) is untenable in the light of current information. The more obvious conclusion is that, although self-colour black (A^a) is recessive to white (A^{wt}) the silver-grey is more likely to be caused primarily by a gene at a separate locus.

Health Problems

Total number of coloured Wensleydales are extremely low and the numbers of crosses carried out are relatively few; the problems must be subject to further veterinary and genetic investigations. However, a number of unexplained health problems were encountered in this study and these were frequently found to be associated with silver-grey sheep, particularly when a silver-grey ram was used for breeding. Similar unexplained lamb deaths have also been reported in other coloured Wensleydale flocks (personal communication).

Veterinary reports on the aborted lambs in 1989 indicated that *Campylobacter* may have been associated with these abortions; regrettable the strain was not identified. However it is known that there are several strains of *Campylobacter*, some of which may not o their own cause abortions but could be contributory agents when associated with other factors.

While considering these contemporary losses, it is interesting and revealing to re-examine Dr. Dry's paper[6]. The results of his crossing experiments between silver-grey Wensleydales and between silver-greys and blacks, are tabulated and divided into two sections: "Animals living at least three months" and "Animals dying very young". Dr. Dry gives no explanation for this but on

can only assume that he also experienced "health" problems and losses when attempting colour breeding experiments. The numbers of lambs he lists as "dying very young" were 8 out of a total of 32 lambs born from the silver to silver crosses (25%) and 16 out of a total of 60 lambs born from the silver to black experiments (27%%), not insignificant losses. In both groups the losses included both black and silver-grey lambs.

"Silvering" or "graying" genes which have lethal (including prenatal lethal) or semi-lethal effects have been reported in a wide variety of mammalian species from mice to cattle[18]. and unthriftiness in light self-colour varieties of certain British sheep breeds has also been noted[19]. A possible parallel to the situation in Wensleydales might be the well documented "lethal roan" found in the Russian fur-sheep, the Karakul and other breeds (see reviews of Rae[9] and Searle[18]) where a dominant silvering gene (Rn^{Rn}) causes silvering of the normally dominant black (E^{D}) of the Karakul, resulting in grey lambs. Lambs homozygous for this gene can often be distinguished from the heterozygous individuals by their paler colour. The lethal effects are associated with the homozygotes but are not manifest until about 3 months of age; deaths are mostly associated with various abnormalities of the digestive tract. There are many differences between the situation in the Karakul and the initial results presented here in Wensleydales. But there are similarities, and it is not unknown for similar or related genes or alleles to act on genetically very different breeds to produce different but comparable results[18].

HYPOTHESES

The results of the work of Dry and those of the present study can be reconciled if we consider the following possibilities:

1. The black colour of Wensleydales is primarily the result of the action of the self-colour allele A^{a} of the Agouti locus in homozygous state.
2. The "background" black colour can be modified by a dominant "silvering" gene at another locus. This gene, which I propose to call Sv^{Sv}, causes a reduction of the number of pigmented wool fibres and also reduces the overall skin pigmentation; expression is very variable, in both the heterozygous and homozygous state. Phenotype could vary from "black" (those that show relatively rapid greying with age?) to light silver (possibly with a predominance of the lighter silver animals being homozygous?) Some sheep phenotypically "black" at birth may in fact be genotypically "silver-grey". The recessive wild type allele at this locus Sv^{+} would have no effect on the black colour of the A^{a} allele of the Agouti locus. Some black sheep, homozygous for both recessive genes ($A^{a}A^{a}$, $Sv^{+}Sv^{+}$) would be very black and remain relative black, (as in flocks selected for "blackness"?) Matings within these blacks would not produce silver-grey lambs.
3. The variable expression of this proposed Sv^{Sv} gene could be a result of influences of one or more unknown genetic or environmental factors or possibly the expression of more than one allele at this locus.
4. Preliminary results indicate that it is possible that this proposed "silvering" gene Sv^{Sv} has a pleiotropic effect, being responsible for certain lethal or semi-lethal health problems. Alternatively, the effects may be due to an association with a gene responsible for these problems.
5. It is likely that this proposed silver-grey gene would also be found in white Wensleydales but in the absence of pigment no "silvering" would be seen to occur and its presence would not be easily detected.
6. The above hypothesis assumes that crossing the silver-greys can result in occasional black lambs, as shown by Dry[6]. However, there is some discrepancy between the definitions of silver-grey of Dry and the present study. Dry's definition includes dark

grey animals (25 percent non-pigmented fibres); these animals are nearer in color to the "blacks which show rapid greying" in this study than those considered to be silver-grey. A silver-grey to silver-grey cross has been achieved only once in the present study (Table 1) and resulted in two silver-grey lambs. Further crossing experiments within the silver-greys of the present-day will establish whether occasional black lambs can be produced. If, however, only silver-grey lambs are produced, the interpretation of the evidence would change: "Sv^{Sv}" would become a recessive gene, but having some effect in the heterozygote, resulting in a relatively rapid greying of a "black" sheep.

CONCLUSIONS

The object of this study has been to stimulate interest in and shed new light on a unique and long-neglected breed. The wide range of colour and pattern found in black and silver-grey Wensleydales is indicative of a very complex colour-genetic picture, undoubtedly involving a number of different genes, probably combined with the epistatic effects of several others. It is indeed remarkable that such an apparently wide range of coloured genes should have been perpetuated in the white Wensleydales for so many years. Breeders would have been unaware that their random selection of these genes concealed by the dominant white allele may well have contributed to their preservation.

Coloured Wensleydales are now becoming more popular. As numbers increase, the results of further matings within the breed and from crossing with other breeds should prove extremely interesting. If future breeding information confirms a genetically linked health problem associated with silver-grey Wensleydales, breeding policies can be formulated to eliminate this undesirable trait. Certainly both black and silver-grey Wensleydales are fine and distinctive sheep, possessing the remarkable property of central checking. Like their white counterparts they have not been fully exploited as a breed for radically improving the quality of wool.

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