Colour inheritance in sheep

Have you ever wondered why a black calf suddenly appears in a herd of pristine White Park cattle, red or moorit lambs in a flock of uniformly black Hebrideans, or black flecks in the red coat of some Tamworth pigs? Such annoying aberrations, which may be most inconvenient and upset your breeding plans, are not the outcome of a witch's spell, and maybe not even the result of illicit introgression by a marauding male, but more probably the logical outcome of the genetic make-up of your animals.

The coat colour of the wild ancestors of our farm livestock was determined primarily by the importance of camouflage for survival, and necessarily in most cases was dull and unspectacular. Domestication largely removed the threat of predation, and thus permitted the expression of a wider range of colours. In some cases it is likely that unusual colours like palomino, blue heads and white belts may have been preferred by owners of livestock, and hence we see a wide variety of colours in modern breeds, especially in poultry, horses and sheep.

Pre-Mendel farmers (including Bakewell and the Colling brothers) bred their livestock without the benefit of a knowledge of genetics but even then could fix distinctive colour patterns such as the White Park's black points or the Hereford's white face. Now that the inheritance of colour is more clearly understood, breeding programmes can accommodate the desire to produce specific colours, and can explain black White Parks, white Hebrideans, spotted Tamworths, and even the case of two white sheep producing a lamb with Soay colour and markings.

Multicoloured North Ronaldsay sheep on Lihou (CI) 1977.

Research

The earliest significant work was probably done with poultry, and there is a long section on 'plumage colour' in 'poultry breeding', first published by MAFF in 1950. A more recent review is given by Scrivener (2005), who refers to the earlier

work of Carefoot (1985). A considerable amount of research has also been done on equines. There is a detailed chapter on 'Coat Colour and Texture' in 'Equine Genetics & Selection Procedures' (Wagoner, 1978), and Ann Bowling (who contributed a paper at the 1st RBI Congress) of Veterinary Genetics Laboratories in USA has also done much work. Less progress has been made with cattle but there is a useful website (Schmutz, 2005) with information on several breeds. There has been a surge of interest in pig colour genetics recently, particularly as part of the EU project PigBioDiv1 (Alderson and Plastow 2004) to such an extent that some breed-defining coat colour alleles have been patented.

However, apart from poultry, sheep have probably received the greatest attention. The great variety of colours and patterns found in the species stimulated interest, and the major authority is Stefan Adalsteinsson who produced an influential research paper on Icelandic sheep in 1970. He summarised the work in a keynote address at York in 1994, and several other authors (such as Ryder, 1994) have written on the subject. COGNOSAG (established at the 1st Coloured Sheep Congress in Adelaide in 1979 and currently administered by JJ Lauvergne in France) is the body responsible for identifying and classifying the loci/alleles controlling colour.

Cross-species

There are considerable between-species similarities in the inheritance of colour, and thus it is possible to cross-reference research work in different species. For example, in several species the E (Extension) locus is responsible for extending pigment in the coat, while alleles at the A (Agouti) locus determine colour patterns (ie, distribution of pigment over the body). At the same time, there are important differences, not only between species, but also between breeds within a species. For example, dun colour in cattle is caused by three different alleles in Highland, Dexter and Galloway.

This article will only skim the surface of the subject – a full description would take a volume – and will focus on sheep, but I would refer readers to the various authorities mentioned herein, and future articles can cover other aspects if readers would find that useful.

Basic genetics

Colour in sheep is controlled primarily at three loci (individual sites on a chromosome) – B, E and A. There are others, such as S (Spotting) and C (Albino), but they are of less importance except for one or two breeds. The B locus controls the production of eumelanin – a pigment which causes black or chocolate-brown colour. The E locus determines whether eumelanin can be expressed, or whether it will be partly replaced by phaeomelanin giving diluted colours (red or tan). The A locus determines the pattern of colours, and possesses many options through a variety of alleles (the coded units at each locus which determine development). The interaction between these loci can be complex, illustrated by breeds such as the Shetland which has a variety of colours combined in 30 different patterns, but the principles are relatively simple.

Two alleles are found at each locus, one inherited from the sire and one from the dam. If they are the same, it is homozygous; if they are different it is heterozygous. There is a hierarchy of alleles whereby dominant alleles inhibit the expression of recessive alleles. Thus an animal may carry two different alleles at a particular locus (ie, it is heterozygous), but the effect of only one of them will be expressed. These are shown as the locus followed by the allele (eg, A^g – locus A and allele g for grey). If the main loci mentioned above are shown the genotype might be $A^aA^aB^BB^bE^+E^+$ which would be a black sheep because of the presence of B^B. Often these are set out in a matrix as shown in The Chance to Survive (Alderson, 1994a) although the symbols used in that example have now been superseded.

Currently, among the 21 different alleles found at the A locus, A^{Wh} (white) is the most dominant and A^a (non-agouti) the most recessive with the others ranked between them. In contrast, the B and E loci each have only two relevant alleles for sheep. At B there is B^B which is black, and B^b which is chocolate-brown. At E there is E^D (dominant black) and E^+ (recessive).

Soay ewe with extensive white markings. Photo by S Furness.

Coloured breeds of sheep

Native British breeds vary greatly in the variety of colour they possess. Some breeds, such as Manx Loaghtan, Hebridean and Black Welsh Mountain are a single solid colour (they are known as whole-coloured or self-coloured). Others are single-pattern breeds (ie, each shows only one colour pattern) and include the Soay, Castlemilk Moorit, Jacob, Torddu/Torwen and Balwen. Only the Shetland and North Ronaldsay possess a profusion of colour and patterns, although the Boreray patterns are also irregular and varied. Let us look briefly at some of these breeds to illustrate the inheritance of colour in sheep.

Other breeds might be considered, but are probably best left for the time being. Some breeds lose the colour of birth with maturity. The Herdwick is born black, and some Portlands are born red, but both are white-wooled as adults. Other white breeds carry coloured recessives; usually a black recessive in longwool breeds, and a Torddu-like pattern in Down breeds

Whole-coloured breeds

Moorit is recessive to other colours. Therefore moorit animals cannot carry other colours, otherwise they would mask the moorit. Thus the Manx Loaghtan genotype is $A^aA^aB^bB^bE^+E^+$ (B^b is chocolate-brown or moorit) whereas the Hebridean, varying from it only at the B locus, may be $A^aA^aB^BB^bE^+E^+$ (BB is black). However, black can be achieved by a different route. E^D is carried by the Black Welsh Mountain and produces dominant black which over-rides the effects of alleles at the A and B loci.

Dominant black has found its way into the Hebridean, probably from the Black Welsh Mountain and Jacob and, as the E^D allele does not allow the B^B allele to function, it prevents the ability to distinguish visually the source of black in any animal. E^D could be eliminated only by extensive test-mating, but that is a much wider subject. Nor does this simplistic description of whole-coloured breeds take into account complications such as epistasis, incomplete dominance, and variations such as white marks, sometimes seen in Manx Loaghtan and Hebridean sheep, which are caused by spotting alleles at the S locus.

The Manx Loaghtan genotype theoretically is the most straightforward for breeders to maintain. The genotype for moorit is recessive, and therefore should breed true. In contrast, black Hebridean sheep could carry moorit as a recessive and it might be expressed if an animal inherited B^b from both parents. In practice complications occur. There may have been introgression, legitimate or illicit. When Caesar Bacon was establishing his foundation flock of Manx Loaghtan a century ago, he introduced some Shetland breeding animals (Wade-Martins, 1990) and, although the influence was slight, some alleles may have persisted.

Single pattern breeds

Most Soay sheep carry a pattern of light-coloured rump patch, belly, and facial and leg markings (often known as moufflon) on a chocolate-brown background (67.5% on Hirta). The genotype is $A^WA^WB^bB^bE^+E^+$, where A^W produces the pattern, B^b is chocolate-brown, and E^+ permits the expression of A and B factors. Other variations include the moufflon pattern on a tan background where a higher level of phaeomelanin has been produced (22.5%), white markings (c.5%) as shown in the pictured ewe, and whole-coloured (c.5%) – either chocolate-brown (see Manx Loaghtan genotype) or tan. The latter, which is very rare, is associated with lower growth rate and higher mortality.

Examples of association of colour with other characteristics occur in many species. The negative aspect seen in whole-coloured tan Soays, is also seen in the white heifer disease in Shorthorn cattle, and in lethal effect of homozygous yellow in mice and homozygous roan in horses. Adalsteinsson's research in the 1950s and 1960s shows a more positive aspect whereby coloured Icelandic sheep had better fertility/prolificacy than white sheep (Adalsteinsson, 1970).

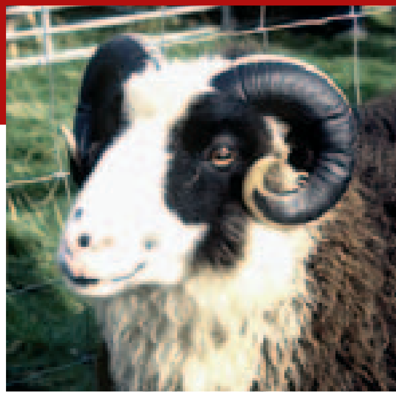
The Castlemilk Moorit, Torddu ('black belly', also known as Badgerface) and Torwen ('white belly') have a similar pattern to the Soay, and it may be carried as a recessive by white sheep. A Soay-marked lamb resulted from mating a white Welsh Halfbred ewe to a white Down ram (Alderson, 1994b). Both carried the B^b allele (chocolate-brown), and the A^W allele alongside the AWh allele. By chance the lamb received a double dose of both B^b and A^W making it homozygous for Soay colour and pattern. The colour of the Balwen and Jacob is an expression of the spotting gene with white marks of varying extent on black, limited to the points in the Balwen but extensive in the Jacob. The Jacob is interesting because it carries dominant black (E^D) which is inhibited through epistasis by the spotting gene, but which appears in crossbred Jacob progeny except when the other parent is a pink-nosed breed such as the Dorset Horn.

Multicoloured breeds

Two breeds show an arresting display of colour and patterns. A survey of North Ronaldsay sheep on Linga Holm by Pilkington in 1979 showed that white and grey were the most common colours. This would be expected because of their dominance over other colours, but the latter (black, moorit, tan, roan, etc.) were present in small numbers together with various patterns (Alderson, 1994c). Based on the number of coloured animals, it can be calculated that perhaps as many as 40% of the flock might have been expected to carry the recessive alleles for minor colours.

The Shetland has an even greater array of colours and patterns, which have been codified but may still perplex the layman! Is the ram pictured a Smirslet? A website (Baker, 2005) identifies the colours of Shetland sheep and 30 different patterns, many known by words derived from Old Norse. Some correspond to patterns seen in other breeds. For example, Katmoget (A^b) and Gulmoget (A^t) have the same genotype as Torddu and Torwen respectively (and A^t is very similar to the Soay A^W), but the great majority are evidence of the presence of spotting alleles. Krunet, Bleset and Sokket have similarities to the Balwen pattern. However, the overall hierarchy of dominance at the A locus is White (A^{Wh}), Grey (A^g), Katmoget (A^b) and Gulmoget (A^t), and finally Non-agouti (A^a), as for other breeds.

No matter whether you are breeding sheep such as Manx Loaghtan with a solid recessive colour, or Shetlands with unusual colours in multiple patterns, the rules governing their selection are the same. We have come a long way since Gregor Mendel experimented with sweet peas, but we can now use the principles of genetics evolved by him to our advantage in breeding sheep. The variety of colour that we see in both field and showring is part of their attraction and each breeder now has the ability to understand best how to achieve their chosen objective. The reward may be realised in the higher productivity conferred by coloured genes, or in a championship sash on the back of a sheep whose colour caught the judge's eye.



Shetland ram at Walls Show 2000. Photo: Countrywide Livestock Ltd.

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