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Colour inheritance in livestock

Coat and skin colour inheritance in domesticated animals have always captured the interest of both the livestock breeder and the geneticist. While coat colour has limited economic importance in most livestock breeds, it plays a vital role in the adaptability of the animal, especially in the potent African sun.

Differences in coat colour and patterns form an important part of breed identification and breed standards of most livestock breeds. In companion animals, the coat colour and specific coat colour patterns are of higher importance compared to livestock in general. Over many years of research, basic patterns for coat colour have been described based on Mendelian inheritance, and several websites are available with examples for livestock and companion animals. The focus of this article is to briefly recap the physiological basis of expression of colour and simple inheritance of colour in livestock.

Skin and hair pigmentation

The skin and hair colour of mammals is determined by the presence of pigment granules that consist of melanin. The production of melanin occurs in melanocytes and is formed by a series of metabolic pathways that convert the amino acid tyrosine into either eumelanin or phaeomelanin.

Eumelanin is responsible for black and brown pigments, while phaeomelanin gives red or yellow pigments. White is the result of a lack of eumelanin and phaeomelanin in the skin. Eumelanin is found in the coat as well as other body parts that need pigment, such as the eyes and nose, while phaeomelanin is only found in the coat of the animal.

Dominant and recessive alleles

The amount and type of melanin produced as well as the distribution of the pigment granules differ, and are controlled by different genes. The different genes interact with each other in a mechanism called epistasis to cause the variation in colour distribution and intensity seen in domesticated animals.

These colour regulatory genes occur on different sites throughout the DNA of the animal, and at each site – or locus – the animal will have two versions of each gene. If these two versions of the gene are identical, the animal is said to be homozygous at that specific locus, while an animal with two different gene versions is heterozygous.

Many different versions – or alleles – of a gene are possible, but only two can be present at any one time, because the animal can inherit only one allele from each parent. Furthermore, alleles can be either dominant or recessive. This means that in a heterozygous animal (Kk), which has one dominant and one recessive allele, only the dominant colour will be expressed, but the animal will be a carrier of the recessive colour.

If mated to an animal with the recessive colour (kk), there is a 50% chance that the offspring will also have the recessive colour, as shown in the Punnet square (*Figure 1*). It can also happen that alleles are only partially dominant, and in such cases the colour would be intermediate to the dominant and recessive colours.

Figure 1: Punnet square showing inheritance of dominant and recessive alleles.

	K	k
k	Kk	kk
k	Kk	kk

Colour groups

The genes that influence colour can be organised into four different groups (see *Table 1*). In the first group is the genes that influence the distribution of colour over the body. The agouti gene (A) in the wild animal causes a light-coloured back and underline, as well as dark flanks and points. It also causes banded hair. The dominant A gene causes slightly different patterns between species, and will be elaborated on in the next sections.

The second group has genes that control the pigment colouration. The liver gene (B) dictates the colour of the eumelanin, with black (B) being dominant to brown (b). The extension gene (E) also affects the distribution of eumelanin – the dominant allele (E) causes no suppression of the eumelanin. The animal that is recessive at the locus (ee) will have the eumelanin completely suppressed, and will only have the phaeomelanin (red) pigments. The third group has genes that influence the intensity of the colours. These include various genes that dilute the colour either at birth, or cause a loss of pigment over time. In Group 4 are genes that control the distribution of pigmented and unpigmented areas over the body. These various genes not only have epistatic interactions with each other, but can also be expressed slightly differently in the different farm animal species.

Common colours in cattle

The most common colour in cattle is black (eumelanin) and red (phaeomelanin). In most breeds this occurs as either black or red, such as in the Angus. The three alleles (forms) of the gene that control black and red colour are black, wild type and red. Black is dominant to the wild type and red alleles, and animals with the black allele are a solid black colour or spotted (e.g. the Holstein).

The wild type allele produces cattle with a reddish brown to a brownish black colour. Two copies of the recessive red allele will result in a red coat colour. A white coat colour, characteristic of the Charolais, is due to two dominant D alleles, which dilute all black and red pigments in the skin to white, while heterozygous animals (Dd) will have a creamy to yellow coat.

Other coat colour genes act as modifiers of the basic colours (black, red and white), adding white spotting patterns or redistributing the basic pigments to cause brindle or roan coat colours. All spotting patterns are recessive to the solid colour,

and no spots will occur if the dominant allele (S) is present.

However, several different recessive alleles are possible at this locus, and homozygous animals may have the random spotting seen in Holsteins, or specific spotting patterns, such as Dutch belting, the white rump seen in the Pinzgauer or the white face of the Hereford. The P locus also interferes with the spotting gene, and animals with the dominant P allele will have pigment on the legs while retaining the brockle-face pattern.

The roan and white genes interact to produce roan animals, which is an intermingled colour with the base colour usually being red mixed with white hairs. Animals with recessive alleles at the W locus have a white belly or underline – this is usually seen in the Simmentaler. Two

dominant alleles at the W locus result in white animals, while coloured animals have two dominant alleles at the R locus. The heterozygote animal expresses the roan phenotype.

Sheep and goats

In sheep and goats white is a very common colour, but its genetic background is still not clearly defined. In Merino white colour results in a phaeomelanic background by the segregation of the most dominant allele at the agouti locus, A^{wt}, that produces a completely tan (phaeomelanic) covering. In most breeds this was changed to a white animal by the modifying actions of genes at the other loci.

In sheep the spotted gene at the spotting locus is known to have a modifying effect. The dominant allele at the spotting locus causes no spotting, while the spotting of the recessive allele usually involves the distal legs and top of head before other areas, and tends to result in reasonably recognisable patterns of spotting. In goats, the most recognisable spotting patterns are those seen in the Boer goat, as well as the Swiss markings seen in breeds such as the British Alpine and the Toggenburg.

Colour in horses

The base colours in horses consist of bay, chestnut and black. A pure black horse will have two recessive alleles at the agouti locus, and any other combination of alleles at the extension locus, except two recessive alleles that will cause red pigment. In contrast, the chestnut horse will have the two recessive alleles at the extension locus, and any other combination of alleles at the agouti locus. The bay horse can have any combination of alleles at these two loci, as long as the alleles at each locus are not the same.

These base colours can be further modified by interactions with other loci. The chestnut horse becomes a palomino if one dominant cream allele is present at the cream locus. The single allele only affects the red pigment and not the black. If both alleles at the cream locus are recessive cream alleles, both the red and black pigments will be affected, and will be completely diluted to give a cremello coat. These horses are characterised by a pink skin and blue eyes. Other loci that can dilute the base colours include dun, champagne and silver dapple. A dominant allele at the roan locus will cause white hair in the base colour.

The dominant grey allele will cause pigment intensity to be lost over time, and horses born dark will eventually turn white, while still retaining the dark pigment in the skin. True white horses will have no skin pigments.

The spotting patterns seen in Appaloosas, Paints and Pinto's are controlled by several spotting loci, such as tobiano, sabino, frame, leopard and splashed white, and the differing combinations and interactions between these loci result in the unique patterns seen in these horses. However, the inheritance mode of white markings on the face and legs are unknown at this point.

Table 1: Summary of genes responsible for coat colour in mammals, not exhaustive (Minick Borman, 2015).

Group	Gene		Effect
1	Agouti	A	Distribution of pigments.
2	Liver	B	Colour of eumelanin.
	Extension	E	Suppression of eumelanin.
3	Dilution	D	Reduces colour intensity.
	Cream	Cr	Reduces colour intensity.
	Dun	Dn	Reduces colour intensity.
	Champagne	Ch	Reduces colour intensity.
	Silver dapple	Z	Reduces colour intensity.
	Grey	G	Reduces colour intensity over time.
4	Pattern	P	Pigmentation of the legs.
	Roan	R	White hair intermingled though coat.
	Spotting	S	Various spotting patterns possible.
	White	W	Loss of pigment in skin.

Conclusion

Colour inheritance in domesticated livestock is by no means a simple process and with recent molecular research available, much more complex as previously known. Our understanding of the modes of inheritance and interactions is still incomplete.

The advances in genomic technologies have identified several additional genes that influence the expression of colour. Most notable is the KIT gene, which is responsible for loss of pigmentation. This gene may also be responsible for certain spotting patterns, as well as the complete loss of pigmentation in die animal.

As more livestock species are being studied at a genetic level, we are sure to learn more about the genetic interactions at different loci and our understanding of colour inheritance and mutants will improve.

References are available from the author at email Lydia.Bosman@up.ac za. SB