The production of white fleeces in sheep and goats has come about through the use of very complicated combinations of genes. These combinations have been developed by animal breeders over centuries as they have sought to develop white fibres for manufacturing uses. The occurrence of a few coloured fibres in otherwise white fleeced animals can usually be related to the "leakiness" of the combinations used for the usual whiteness of the fleece. The occurrence of coloured animals in otherwise white populations is usually the result of segregation of recessive alleles at a variety of loci.

The inheritance of colour in sheep and in goats that are used for fibre production can either be taken from the goal of colour production or from the goal of the elimination of all coloured fibres from a white product. This discussion will center on the production of white fibres and the importance of colour inheritance to that end. The sheep is better known than the goat with regard to colour inheritance, and this discussion will first concern sheep and then deal with goats.

Selection for whiteness in sheep has been ongoing for centuries, and indeed is mentioned in Roman texts. Whiteness as a biologic phenomenon has two basic mechanisms. One of these is to remove melanocytes from the skin and hair follicles, which effectively removes any potential for pigment production. This is the mechanism at work in white spots of otherwise coloured animals, and does indeed result in very white fibres. The other mechanism is to make melanocytes ineffective even though they are still present. Albinism is the best example of this process. The processes that lead to ineffective melanocytes can result in very white fibres, but tend to be "leakier" than are the mechanisms for the outright removal of all melanocytes. The usual white fleeces in sheep and goats are achieved through the mechanism of ineffective melanocytes rather than by the removal of melanocytes outright. This mechanism has consequences in the various types of colour faults that are commonly encountered, as well as their inheritance.

Another basic factor in colour production is that there are two main types of melanins. Eumelanins are black to brown, and phaeomelanins are yellow to tan to red. The overlap between the brown eumelanins and the red phaeomelanins can be great in some instances. The importance of the two basic types is that they can each be modified in different independent ways. That is, factors which modify phaeomelanin production can leave eumelanin unchanged, and the converse can also be true.

The selection for whiteness in sheep has largely been through the mechanism of selecting concurrently for a wholly phaeomelanic wool and hair coat and at the same time diluting the paeomelanin to leave a pale cream or white color. These
processes are of varying effectiveness in different breeds. For example, the whiteness of most fine wool (merino) and long wool types is great, while in carpet wool types the production of red kelps and hairs is fairly common. Some breeds such as the American Tunis, are born tan to red and then the wool coat fades but the hair on the legs and head retains the characteristic red expected of phaemelanin areas. The importance of the fact that most sheep do have melanocytes at least potentially capable of phaeomelanin production is that selection constantly needs to be directed against the production of phaeomelanin fibres if the goal is totally white wool. Most white sheep (and especially most white sheep derived from European breeds) do have melanocytes capable of forming phaeomelanin and putting it in the wool. The tendency for the production of phaeomelanin fibres is heritable as a polygenic trait with a heritability of 0.46.

While the incursion of red pigmented fibres in otherwise white sheep is a constant problem, the opposite goal of selecting for a uniformly red sheep seems to also be a very difficult task. The selection for whiteness has been so extreme and has gone on for so long that the genetic variation needed for the production of a truly red wool may be lacking in most breeds. This concerns only the few instances in which a uniform red fleece may be desired. The genetic variation for the production of a few stray red fibres seems to be annoyingly present in a wide variety of breeds. If red fibres do appear they tend to be the fibres of wider diameter (kelps and hairy fibres), and so this problem is more prevalent in breeds that have an abundance of those fibres. Due to the heritability of this fault it is necessary for sheep breeders to constantly cull sheep with a tendency to produce red fibres.

The locus that is most important for the production of white sheep is the Agouti locus. This locus is also most important for the occasional occurrence of coloured sheep in otherwise white flocks. The Agouti locus governs the occurrence and distribution of eumelanin and phaeomelanin areas in the wool and hair coat. The areas are usually symmetrical, and the general pattern is that phaeomelanin areas are consistently expressed. This makes the several alleles at the locus codominant to one another with the exception of the top allele (white or tan) which is the cause of a wholly phaeomelanin coat and is therefore dominant to all the others, and the bottom allele (nonagouti) which is wholly eumelanin and therefore recessive to all the others. Intermediate alleles are numerous and include badgerface, black and tan, and a host of others with varying areas of phaemelanin production and distribution.

The importance of the Agouti locus to the production of white wool is that the patterns are recessive to the usual white or tan allele that is present in most white woolled sheep. The phaeomelanin areas of the various patterns are generally white in sheep, due to the generalized inhibition of phaeomelanin production. The eumelanin areas are unaffected by this inhibition, and are usually fully black or grey. Most of the patterns that occur commonly are fairly dark, and would be easily and quickly selected out from white flocks. Some of the paler ones (especially paler greys) may survive in large flocks unless the flockmasters are careful observers and eliminate any sheep with a tendency for symmetrical pattern of light and dark, especially on the head. Some of these may have a fleece white enough to pass in a white flock, but the fact that they are not genetically the white or tan allele is a good reason for culling them.

The Brown locus is important in controlling the shade of eumelanin produced in
areas that are genetically capable of producing the eumelanin pigment. Areas that would have been black become chocolate brown of varying shades. The palest of these shades are beige to nearly off white. In most breeds that have pigmented areas (as in black faced breeds), or where pigment production is desired, the recessive brown allele is usually rare. In most white fleeced breeds that are selected for whiteness and then tested for the occurrence of the brown allele it seems to be more common. The reason for this is probably that white animals that carry brown at this locus, when they produce the odd pigmented fibre, are not culled as readily as are the white animals that are carrying the ability to form black pigment as governed by this locus. The genetically brown animals can also survive more readily than can the genetically black animals when the brown phenotype is combined with some of the Agouti locus alleles. These animals, while generally white enough in their own right, are a threat to the flock since once the specific Agouti-brown combination is disrupted to become Agouti-black the same Agouti allele may be unacceptable in the flock.

Other loci governing coat color are probably less important than are the Agouti and Brown loci. One such locus is the Spotting locus in which the recessive allele causes white spots on otherwise pigmented sheep. It usually causes at least a blaze on the face and white lower legs, and can be responsible for extensive spotting. This recessive allele is present in those white breeds that are selected for pink noses, and is absent from those that have pigmented noses. If the goal is the production of absolutely white wool, then every factor contributing to the whiteness should be used. The recessive spotted allele certainly contributes to this and should probably be used. There is also evidence that the combination of white or tan at the Agouti locus with spotted at the Spotting locus is more extensively spotted than are other Agouti patterns of the same breed. This phenomenon can greatly increase the overall whiteness of the animals.

The albino allele is also documented to occur in sheep, specifically in Icelandic sheep. This allele does result in very white fleece, and since it is recessive it would be easily made homozygous throughout a flock. This allele can be expected to have negative consequences in viability, especially in range conditions, and may therefore not be a wise choice for the production of white sheep.

One interesting locus of concern to breeders of white sheep is the Australian Piebald locus. A recessive, incompletely recessive allele at this locus is responsible for the production of random, usually single, eumelanic spots in areas that should be phaeomelanic as determined by the Agouti locus. The usual consequence in a white flock is the production of a random black spot in an otherwise white sheep. If small these can be overlooked, or one can succumb to the temptation to remove these by cutting them out at the time of shearing. Since this is a random effect and due to an incompletely penetrant allele it should be the target of strict culling in order to decrease its frequency in white flocks.

The other common colour fault in white sheep is the production of stray, individual black fibres in an otherwise white fleece. These tend to increase in incidence with the age of the sheep, or with the occurrence of injury to the skin. Overall selection for whiteness does act to decrease these (they are more common in blackfaced than whitefaced breeds), but their inheritance is not simple. Some selection based on age is warranted to decrease the incidence of
this fault.

A final locus commonly causing pigmented sheep is the Extension locus. The dominant black allele at this locus causes a wholly eumelanic fleece, masking any Agouti locus allele that may be present. The usual situation is a black dominant to white. As such it only survives in situations where pigmented sheep are desired. As a dominant pigmented type it quickly is eliminated in the face of culling pigmented sheep.

The occurrence of colour faults in goats is at least somewhat different than it is in sheep. In Angora goats the Agouti locus does seem to be active in producing recessive coloured goats. These usually have patterns similar to those seen in sheep, but occur with much more rarity in goats than in sheep. It is unknown whether the white of the Angora goat is conditioned by an Agouti locus allele as is the white of sheep. One fact that has recently come to light is the relative ease with which it is possible to select goats for redness. From a start of a few goats which were born with reddish birth coats it has been possible in a few generations to develop a uniformly red goat which fades very little to a dark honey colour. Exactly what this means for the biology of the whiteness of goats is uncertain, but it is certainly different than the situation in sheep. The ease with which it is possible to stabilize the red, phaeomelanic mohair covering on goats indicates that it is of even more importance in Angora goats to cull animals with a tendency for red fibres than it is to cull these in sheep.

REFERENCES