

## Genetics of Goat Color

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### Introduction

Goat color variations have only recently been studied, in contrast to the very early work on sheep color variation. While homologies to sheep color are frequently present, goat color inheritance differs from sheep in a number of important regards. The study of goat color has usually been tied to the need for production of certain colors (usually white) in certain breeds of goats such as Angora or cashmere bearing goats, as well as many breeds which have breed-specific colors or patterns.

To best understand color genetics, it is helpful to focus first on the general biology of goat color, and then to delve into the genetic details. A clear understanding of the basic genetic phenomena is essential for those interested in the production of certain specific colors. A complete historic review of the world literature dealing with the loci and alleles affecting color in goats has recently been completed by the Committee on Genetic Nomenclature of Sheep and Goats (COGNOSAG). COGNOSAG recommendations on nomenclature are used in this chapter, which will focus on the action and interaction of the various loci that control pigmentation in goats and the biological processes that are involved.

### General Considerations of Goat Pigmentation

Color in mammals depends on the presence of melanins in skin and hair (Searle, 1968). Melanins reside in cellular organelles called melanosomes, which are produced in melanocytes. Melanosomes reside in the melanocyte cytoplasm, and are also deposited into epidermis and hair by a process of exocytosis which transfers the melanosomes from dendritic processes of the melanocytes into these other (generally epidermal) cells. Melanocytes are specialized cells that migrate from the neural crest during embryological development, and melanocytes have close embryological ties to cells of the neurologic system. Pigmentation of skin and hair depends on melanocytes being present, and on their relative level of melanogenic and exocytotic activity. The two main mechanisms by which pigmentation is reduced or absent are absence or relative inactivity of melanocytes. Decrease or elimination of pigment by either of these basic mechanisms can be regional, or can involve entire haircoat.

Melanins are large polymers that are formed of varying amounts of tyrosine and cysteine (Prota, 1992;

Jackson, 1994). Melanins occur as two types: eumelanin and phaeomelanin. Eumelanin is generally black or chocolate brown, and is predominantly made of tyrosine. Phaeomelanin is generally reddish brown or yellowish tan, and has varying amounts of cysteine in its polymers. The two types of melanin are important visually and genetically, and are usually considered as two discrete classes of pigment. Some overlap occurs between the two, but this overlap is usually trivial to an understanding of the genetic control of color in goats. Overlap can also occur visually, with very dark phaeomelanin being similar to lighter forms of eumelanin, but usually the two classes are distinct (Sponenberg *et al.* 1988, Sumner *et al.*, 1994). The differences between eumelanin and phaeomelanin have been demonstrated by electron magnetic resonance (Vsesolodov *et al.* 1981) as well as by analysis of chemical degradation products (Sponenberg *et al.*, 1988). Other techniques to demonstrate the difference between the two melanins include histologic evaluation of melanosomes (Alexieva *et al.*, 1985; Renieri *et al.*, 1995), and the use of color charts (Sumner *et al.*, 1994).

Melanins are formed from tyrosine and cysteine by a process of catalysis, and the main enzyme involved in this process is tyrosinase (Jackson, 1994). Tyrosinase activity is essential for melanin synthesis. Two other proteins, tyrosinase-related protein 1 (TRP-1) and tyrosinase-related protein 2 (TRP-2), are also important for melanogenesis. The exact function of TRP-1 is uncertain, although it is well documented to have an important role in the synthesis of eumelanin, and has little or no role in the synthesis of phaeomelanin. TRP-2 has dopachrome tautomerase activity.

Melanocytes are capable of forming both eumelanin and phaeomelanin, although they usually only produce one or the other at any one time. The dedication of melanocytes for eumelanin production depends on the presence of *alpha* melanocyte stimulating hormone ( $\alpha$ MSH) which is a pituitary hormone (Jackson, 1994). Melanocytes have surface receptors that bind this hormone. When  $\alpha$ MSH binds to the surface receptors the result is a cascade of events that activates adenylate cyclase. This activation in turn stimulates the melanocyte to produce eumelanin. In the absence of this signal, which is dependent on  $\alpha$ MSH as well as the surface receptors, melanocytes produce phaeomelanin. The switch between eumelanogenesis and phaeomelanogenesis depends on the function of the receptors to  $\alpha$ MSH.

The control of melanocyte function is intricate, and many loci have mutants which affect different components of the melanogenic control mechanisms (Jackson, 1994). Some loci affect cell differentiation or migration from the neural crest. Other loci affect the morphology of the melanocyte or its ability to deposit melanosomes in hair and epidermis. Other loci directly affect the enzymes and related proteins that are responsible for melanogenesis. A few loci have mutants that affect the interaction of  $\alpha$ MSH with the target melanocytes. All of these loci interact to give the final color phenotype of goats.

White has been an important color in many breeds of goats, especially those for fiber production. The expression of whiteness in mammalian hair can come about through a variety of different genetic mechanisms (Searle, 1968). Some of these mechanisms appear to be widespread throughout domesticated goat populations, but this is no guarantee that other mechanisms are not important to some specific populations.

One general mechanism for whiteness in mammals is due to white spotting. White spotting in mammals occurs in regions where skin or hair follicles lack melanocytes, since these regions are incapable for forming melanins. Absence of melanocytes can occur from a variety of mechanisms, including melanoblasts failing to differentiate from the neural crest, or failing to migrate to skin regions, or failing to survive once migration has taken place (Searle, 1968). The variety of mechanisms responsible for white spotting are affected by several different loci, each of which controls a different aspect of the process of populating skin and hair follicles with melanocytes.

A second general mechanism for whiteness is achieved through dilution of pigment, which is accomplished by decreased effectiveness of melanin production by melanocytes. Melanocytes are present, but are ineffective at forming melanins, placing them in the wool and hair fibres, or both. Their ineffectiveness at melanosome production or transfer results in unpigmented or weakly pigmented hair and skin even though melanocytes are present. The effects of both white spotting and dilution are important in goats, and separating these two concepts is important to understanding pigmentation in

goats.

The wild type color in goats must be considered as the standard type if the genetics of color is to make sense. The wild ancestor of the domesticated goats is most likely the bezoar of Anatolia and the Middle East. The color of the various species of wild goats has subtle differences one from the other, but similarities are striking (Novak, 1991). Wild goats are generally tan bodied (phaeomelanin) with pale bellies (dilute phaeomelanin, rather than nonpigmented white). Black areas (eumelanin) are present as a dorsal stripe and striping patterns on the heads and legs. Some sexual dimorphism is present, with bucks darker than does due to more extensive eumelanin patterns on the head and shoulders. The eumelanin areas, especially on males, become more extensive with age, and mature dominant bucks are therefore darker than are younger ones. The interplay of eumelanin areas with phaeomelanin areas is critical to the overall appearance of the color pattern, as is the presence of intense dark phaeomelanin areas along with dilute, pale phaeomelanin areas.

## Factors Affecting Color of Goats

### The *Agouti* Locus

One of the main determiners of goat color is the *Agouti* locus. This locus has many allelic variants, making it one of the more complex loci governing goat color. Variation at the *Agouti* locus is widespread among goat breeds, such that *Agouti* locus phenomena account for the majority of color variants in most goat breeds. The concept of multiple alleles is essential to understanding the *Agouti* locus, and was first documented in sheep for patterns closely related to those of goats. Roberts (1928) first noted that multiple patterns (his badgerface, reversed badgerface, black, and white) segregated as alleles at a single locus. Rendel (1957) first suggested the *Agouti* locus as the site for these patterns. The four patterns suggested by Roberts were confirmed as multiple alleles at a single locus by Brooker and Dolling (1969a). Alleles documented by these researchers, as well as several newly described ones, were ascribed by Adalsteinsson (1970) to the *Agouti* locus, and it is this work which put the entire study of sheep color on a sound comparative basis since this work was widely used as a base by other researchers. Demonstrating the character of the *Agouti* locus patterns in sheep was the breakthrough that finally provided for more rapid advances in the understanding of the genetic control of sheep color, because it put the science on a sound foundation of comparative genetics. Following this, sheep phenomena could be more readily coupled to homologous phenomena of other species including goats.

The manifestations of the *Agouti* locus in goats are relatively complex, although studies in mice indicate that the locus itself is relatively simple in its biology (Jackson, 1994). Many different alleles occur within the *Agouti* locus of goats, however all of the caprine *Agouti* locus patterns are characterized by symmetrical arrangements of eumelanin and phaeomelanin areas. In goats the eumelanin areas are usually black, although can be brown when the genotype at other loci modifies black to brown.

mechanism of action

The *Agouti* locus is responsible for the formation of a protein that acts to nullify the action of  $\alpha$ MSH on melanocytes (Jackson, 1994). In regions in which this protein is present the melanocytes fail to respond to  $\alpha$ MSH, and therefore form phaeomelanin and not eumelanin. Melanocytes in regions lacking this protein have full capability for stimulation by  $\alpha$ MSH, and therefore form eumelanin. (Jackson, 1994). In regions with a pulsatile formation of the agouti protein the result is banded hairs. These are important in mouse phenotypes, and while present in some goat patterns they are less important as a cause of color variation than they are in mice.

In mice the *Agouti* locus has been extensively studied, and implications of homology suggest that its biology is similar in other species including goats. The series of murine *Agouti* alleles is a consistent array as it progresses from the most recessive to the most dominant allele (Jackson, 1994). The most recessive murine *Agouti* allele allows for no agouti protein production in the skin, and therefore results in a completely eumelanin phenotype. The more recessive alleles, above the one coding for a completely eumelanin phenotype, allow for agouti protein in ventral body regions, resulting in these being

phaeomelanic. Successive alleles then add body regions to those of lower alleles, such that phaeomelanic areas of the coat are added successively as the series of alleles progresses from more recessive to more dominant. In a few of the intermediate alleles some regions have pulsatile agouti protein production, resulting in the banded hairs (on the dorsum) typical of the wild pattern in mice. These hairs have a eumelanic tip and base, and a phaeomelanic middle.

The murine *Agouti* locus patterns exhibit no reversal of pigment type among the alleles, so that regions which have become phaeomelanic from the action of more recessive alleles retain this pigment type in all patterns determined by the more dominant alleles. In this regard the murine *Agouti* locus acts as though the various alleles were simply shifting melanin production in an orderly stepwise progression from one extreme to the other, adding phaeomelanic areas body region by body region. The more dominant alleles result in phenotypes that are entirely phaeomelanic, while the most recessive alleles have phenotypes that are entirely eumelanic. The stepwise progress of *Agouti* locus patterns gave rise to early hypotheses that the locus was a complex of small loci that each controlled pigment type in only a specific body region. Recent studies have shown that the complex hypotheses are mistaken, and that the locus is indeed single and simple rather than an array of miniloci (Jackson, 1994).

The most dominant murine *Agouti* allele is *lethal yellow* (Jackson, 1994). This allele is lethal to homozygotes, and the mechanism of lethality appears to be that the very high levels of expression of the agouti protein disrupt fetal differentiation and development. The heterozygotes for this allele also have somatic manifestations of it, such as obesity, reduced fertility, and increased incidences of certain neoplasms.

The action of *Agouti* locus alleles in goats is not as neat and orderly as is the murine series. It is fairly common for the intermediate agouti patterns in goats to have reversals of pigmentation type, so that areas that are eumelanic in one pattern are phaeomelanic in another, and *vice versa*. This reversal of pigmentation type results in some caprine patterns that appear to be opposites of one another, in contrast to the murine situation in which the *Agouti* locus patterns are characterized by a stepwise increase in phaeomelanic areas. The reversal of pigmentation patterns in caprine phenotypes is most remarkable in the "blackbelly" and "black and tan" patterns, which are nearly perfect opposites of one another in pigment distribution.

The action of caprine *Agouti* alleles is to consistently express phaeomelanic areas on a eumelanic background. The result of this is that the tan or pale areas are dominant to the dark areas. This is a key concept to understanding the function of the *Agouti* locus. Some mild degree of intermediate dominance is present in some animals of some breeds with certain combinations of *Agouti* alleles, but as a general rule it holds true that the phaeomelanic areas are consistently expressed, whether heterozygous or homozygous. Heterozygotes for intermediate alleles therefore express the phaeomelanic areas for each of the alleles, and this results in phenotypes with combinations of both phaeomelanic patterns. Some heterozygotes for intermediate alleles and the entirely eumelanic *nonagouti* allele are darker than homozygotes for the same intermediate alleles, although this is more thoroughly documented in sheep. This incomplete dominance has been noted for the *badgerface* allele, and it has also been found that overlapping phenotypes are more characteristic of females than of males (Brooker and Dolling, 1969a).

Goat *Agouti* locus patterns are numerous, and several have highly variable expression so that this locus is much more confusing in goats than in sheep. The patterns group themselves rather well, though, and considering them in groups can help to understand them. In this discussion the patterns will be discussed as occurring on a reasonably unmodified genetic background, so that the patterns take on a tan and black character. "Tan" (or gold or red) refers to phaeomelanic areas, and "black" refers to eumelanic areas. While this is not universally true depending on what variants are present at other loci, it does hold true for goats that are "wild type" at all other color loci and is therefore a useful point of departure for understanding this incredibly complex and variable locus.

Some of the distinctions between patterns are subtle, but are very repeatable and are indeed significant indicators of the presence of different *Agouti* alleles. Goats, in general contrast to sheep, have several *Agouti* patterns that are extremely variable. These can be confusing, as their dark and light extremes

resemble others of the patterns and it is only possible to be certain of the identity of the pattern by recognizing the range of effects over groups of individuals.

patterns capable of producing white

Several of the goat *Agouti* patterns produce white goats at the pale extreme of expression. These patterns are interesting, as nearly all of them have darker (more rufous or more eumelanin) expressions that are clearly not white, and also are distinct from one another. The convergence of these on a starkly white phenotype at the pale extreme can easily result in confusion as to which of the alleles is present.

A allele *white* may well occur as a distinct allele which consistently produces white goats and never darker colors. This is difficult to ascertain with no residual doubt. The overall level of intensity of the patterns varies with breed, and in some breeds that are long selected for white the modifiers that could provide for darker variants are lacking.

The allele *white or tan* yields unshaded, uniform colors that range from a fully intensely pheomelanin red, through yellow or gold, and to white. The genetic character of the modifiers is uncertain, although most manifestations of this allele cluster around deep red, medium yellow, or stark white and this suggests that the modifiers are few in number and may well be a single locus. This allele is a component of the Boer goat and other uniformly red breeds.

The *shaded red* allele results in white goats at the pale extreme, and at darker extremes is red with slight eumelanin shading on the body. Darker goats also have pale facial stripes from above eyes to nose, frequently with a thin dark eumelanin border to the white facial stripe.

Likely as a variant of *white or tan* is a pattern that is tan with darker tan trim in a pattern resembling the blackbelly pattern. This pattern may indicate a separate allele, or may simply be a dark manifestation of *white or tan*. One reason for thinking that this is a separate allele is that many gold and red goats do not have the darker trim of this variant and the two types consistently occur in different families.

The *black mask* allele is another that produces white in the palest extreme, but darker extremes can be red or yellow. Most have dark eumelanin shading on the head, and in the darker extremes this can result in considerably blackish regions, although with the retention of pale stripes from above eyes to nose.

The *sable* allele produces goats vary from very dark with red pheomelanin and extensive black shading to stark white. This pattern is extremely variable, and the extent of eumelanin and the depth of pheomelanin vary separately so that this single allele can produce patterns that are very distinct from one another. Most sable goats have white legs, white belly, and then are shaded to be deeper tan as well as more black over the top. Some have a shaded black backstripe from poll to tail, as well as a black shoulder stripe from withers, along shoulder, to the point of the shoulder and then to the midline. Faces are usually shaded with black, save for pale facial stripes.

Tan patterns with black trim

The wild type color pattern is produced by the *bezoar* allele, which has only moderately variable expression. This, as with several other alleles, produces kids that are fairly light colored that then darken with age. The darkening is much more pronounced in males than in females, and is one of the dominance signals in the original species. The bezoar pattern is basically tan with a paler belly, perineum, and inside of the legs. Black trim includes facial shading which leaves pale facial stripes from above eyes to nose. The ears are rimmed in black, and a black stripe goes from poll to tail along the back. A black stripe is also common along the bottom edge of the neck. A black shoulder stripe is present. Black is present on the front aspect of the front legs as a stripe beginning beneath the carpus, and flaring out around the fetlock joint. A similar black stripe is present on the rear limb but is not discontinuous at the hock.

The *wild riedell* allele is named after the herd of origin, and is similar to the bezoar pattern but is overall much more eumelanic. It is minimally variable, and does not produce variants that could be easily confused with *bezoar*.

The “wild kolodzie” pattern occurs in a herd of Tennessee Myotonic goats. It is one of the extremely variable patterns, and this is evidence that it is not *bezoar* nor *wild riedell*. Light versions are white, while dark ones are nearly black. The most distinctive pattern resembles the bezoar pattern, although is generally darker than bezoar. The tops of the ears have distinctive mottled interplay of tan and black areas. Pale facial stripes are routine, sometimes only as dots above eyes as in the black and tan pattern described below. Striping on the legs resembles the bezoar pattern, as does the pale belly and perineum of this pattern.

The *badgerface* allele might more clearly be called *blackbelly*, and is similar to a homologous sheep pattern. These goats are tan, with specific black trim. The belly is black, as are the lower legs below tarsus and carpus. The inner aspects of the upper legs is also black, as is the perineum. A black backstripe is present from tail to poll. Black shoulder stripes are present, especially on males but generally on females as well. Dark facial stripes usually go from above eye, through the eye socket, and down toward or reaching the nose. The chin and throat are black, and this can continue down the bottom border of the neck as well. This is the common pattern of the Oberhasli goat breed.

The *serpentina* allele is named after a Portuguese goat breed. This breed is selected to have very pale pheomelanin, and whether this is due to the *Agouti* allele or to modifiers at other loci is uncertain. This pattern resembles blackbelly, but is somewhat paler in that the backstripe is discontinuous so that the neck usually lacks the stripe, and the shoulder stripe is minimal or missing. A pale region is present in the black area below the anterior aspect of the carpus.

Also in this group of patterns is the *caramel* of pygmy goats. This pattern retains the black belly and inner legs of the other others. The black lower leg is disrupted so that the anterior aspect is pale and the posterior remains black. This is most dramatic on the front limbs. The backstripe is incomplete, remaining on the tail and over the shoulders, which also have the black shoulder stripe. The neck lacks the stripe, and the head is extensively marked with black so that in older males the entire facial region can be black up to the ears. The bottom aspect of the ear is black, top is tan.

In addition to the paler variants of blackbelly is a pattern occurring in Alpine goats, *tan sides*, in which the black areas of the blackbelly pattern are much more extensive. The result is that the sides remain tan, but the black extends and merges on the neck and head so that these are nearly or entirely black.

Patterns with anterior/posterior divisions of black and tan.

A group of a few alleles produces dramatic divisions between the anterior and posterior portions of the goat. These patterns do not appear to have homologues in sheep.

The *peacock* allele derives its name from a Swiss breed with this pattern. Generally, the posterior portion of the body is black and the anterior is tan. The posterior belly is black, as well as inner legs, and lower legs with a distinctive residual pale area distal and lateral on the anterior aspect of the front leg beneath the cannon bone. The top of the tail is usually tan, as well, although the rear half of the body is generally black. This varies from nearly entirely black to fairly pale with only the dorsal regions fully black and the other regions mixed tan and black. A triangular tan area usually remains on the lateral aspect of the thigh. The tops of the ears are tan, bottoms are black. The head is distinctively marked with black facial striped from above and through the eye to the nose, with a second lower stripe in an arc from the base of the ear, and down below the eye to the cheek. The least black of the expressions of this pattern could resemble black belly, although the leg markings, lack of complete backstripe, and facial pattern are unique to this pattern.

A near reverse of the peacock pattern is called *san clemente* after the feral goats from that island which commonly exhibit this pattern. This is one of the *Agouti* locus patterns that is highly variable in degree of

blackness. The result is that the blackest variants can be easily confused with the patterns produced by the *black and tan* or *eyebars* alleles, while the least black variants could be confused with a *shaded red*. The middle range of the pattern is very distinctive, with a tan belly, inner legs, and perineum. The lower legs have anterior black striping, which is discontinuous at the carpus (leaving it tan) and flares out around the fetlocks. The tops of the ears are black, undersides are tan. The head is black, with tan stripes from above the eye to the nose.

The *repartida* allele is one of a few that is typical of the Brazilian Repartida breed. This is similar to the middle expression of the the *san clemente* pattern, although the leg striping is very distinctive in that the anterior lower legs are tan, and the posteriors are pale. This is the reverse of most other *Agouti* locus patterns.

#### Grey or nearly grey patterns

Patterns within this group are not intuitively *Agouti* patterns, because they generally lack the distinctive symmetrical interplay of tan and black areas. However, they do reside at the *Agouti* locus in sheep, and segregation data suggest that this is true of goats as well.

The *grey* allele results in a relatively uniform mixture of black and white hairs over the entire goat, with no patterning. The shade varies depending on the relative proportion of black and white hairs. The palest ones are nearly white, while the darkest ones are still obviously grey. This pattern is uniform throughout the Azul Portuguese breed.

The *pygmy agouti grey* allele causes the “agouti” pattern of grey in the African Pygmy goat. The mixture of white and black hairs is usually uniform over the body, but the legs are distinctly dark.

The *grey striped* allele results in a pattern that resembles a combination of *toggenburg* and *grey* but as a single allele. This is evidenced by the production of solid black kids by such goats. This is one of few *Agouti* alleles in goats that has a phenotypic appearance of a combination of two other *Agouti* alleles. Such combination alleles are much more common in sheep.

#### Black patterns with tan trim.

A group of dark patterns resides at *Agouti*, and some of these are subtle enough to be confusing in some individuals. The differences between them are usually in the head and leg patterning.

The *toggenburg* allele results in a black goat with distinctive tan trim. The trim is generally quite pale, although it is possible to generate goats with darker trim by appropriate modifiers that darken pheomelanin. The pale areas include legs below carpus and tarsus, and facial stripes from above eyes to nose. The muzzle is also pale, as is the perineum but not the belly which is black. Scrotum/udder is tan. The top of the tail is black, bottom is tan. The top of the ear is generally pale, although the darkest manifestations have a distinctive shaded black bar down the middle of the ear. Usually there is a tan dot low on the cheek near the angle of the jaw, and possible one anterior to this as well. In the Toggenburg breed this pattern is further modified by having brown eumelanin, and also by having consistently pale pheomelanin.

The *black and tan* allele produces a pattern has a black body and head, with tan under the ear, small spots above the eyes, and usually ventrally on the throatlatch, belly, inside of legs, and perineum. The legs have black stripes on the fronts, with the foreleg stripe discontinuous just below the carpus, and an extension around the fetlock. The rear black stripe is continuous with the black of the body. Males darken somewhat with age, so that the tan “eyebrows” tend to be small or absent.

Very similar to black and tan is *eyebars* which is similar except in having more extensive tan. The facial tan is a complete stripe from above eyes to nose. Most *eyebars* animals have two small tan dots low on the cheek, one near the lips and one posterior to this. The throat region is tan.

The *angel* pattern is named after a goat by that name. This pattern is black with tan trim, including undersides of ears. A facial stripe runs from above eyes to nose, and is generally wider above the eyes and quite narrow near the nose. On some animals it is incomplete towards the nose. The chin is tan. A tan patch is present on the angle of the jaw. The perineum is tan, although the belly and scrotum/udder are black, which is one of the main distinctions of this pattern. The legs are pale with black stripes down the fronts. These are continuous from body to lower leg, and do not flare out over the fetlocks. They usually extend to fetlock or hoof, and end as a sharp point on the fetlock.

The *lateral stripe* allele results in a black goat with a tan stripe along the boundary of belly and body. The legs are pale, but with posterior (rather than anterior) black stripes.

Nearly black patterns

A few patterns are very dark. One is *mahogany* which is black with tan regions (usually tan and black mixed) over the body and especially over the backs of the thighs.

The *tan cheek* pattern is black except for round patches of tan below the eyes. The backs of the thighs are also usually mixed tan and black.

The allele *no pattern* results in a completely (or nearly completely) black goat.

Patterns such as grey striped appear to be the result of combining two distinct *Agouti* locus patterns, and are the phenomenon that made attractive the hypothesis that the *Agouti* locus is a complex of miniloci each controlling some aspect of pattern or body region. The presence of certain repeatable components across several patterns (black stripes on legs, shoulder stripes, backstripes) also makes this hypothesis attractive. While the exact organization of the caprine *Agouti* locus is uncertain, it is unlikely to be much different than that of the murine locus, which has been shown to be simple rather than complex (Jackson, 1994). The caprine *Agouti* alleles do have differences from those of the murine locus, though, especially in the relatively high number of patterns that have reversals of pigment type distribution. Another major difference of the caprine alleles and those of other species is the tendency for some of them to have incredibly variable expression from blackest to least black, and from palest to most rufous.

pleiotrophic effects

Pleiotrophic effects for *Agouti* alleles have not been documented in goats, but similar alleles in sheep do have such effects. The  $A^{Wt}$  allele has pleiotrophic effects, in keeping with its status as the top dominant allele at the *Agouti* locus. Ewes with the  $A^{Wt}$  allele are on average less fecund than those without it. In Icelandic sheep, in which this has been best investigated, sheep bearing the  $A^{Wt}$  allele are on average 15% less fecund than those lacking this allele (Adalsteinsson, 1975b). In addition, sheep bearing the  $A^{Wt}$  allele are more strongly seasonal in reproduction than those lacking it (Dyrmundsson and Adalsteinsson, 1980). Obviously the breed genotype other than that at the *Agouti* locus is equally important in the overall fecundity and seasonality of any sheep, but the effects of this single allele are dramatic in breeds in which variants at the *Agouti* locus are segregating. However, it is worth a passing thought that the preference for red in Boer goats selected for size and meat conformation might be assisted by the pheomelanin *Agouti* allele that characterizes the breed.

Ryder *et al.* (1974) reported in Soay Sheep that the homozygous *nonagouti* genotype is less viable than others (usually *black and tan*). Soays are feral, and whether this trend holds true for sheep in less demanding environments is not known.

THE *EXTENSION* LOCUS

mechanism of action

The *Extension* locus encodes one member of a group of seven  $\alpha$ MSH receptor proteins (Jackson, 1994).

The  $\alpha$ MSH receptor, following activation by attachment of  $\alpha$ MSH, results in increased cAMP levels and increased protein kinase activity, which in turn activates eumelanin formation. In the inactive state phaeomelanin is produced. The wild type *Extension* locus allele in most species allows for control of eumelanin and phaeomelanin production to be governed by the *Agouti* locus as determined by the regional distribution of the agouti protein which inhibits eumelanin formation.

Many species have dominant alleles at the *Extension* locus which act to increase adenylate cyclase either spontaneously or in response to  $\alpha$ MSH. The specific mechanisms are different for different alleles in the mouse, and involve either responsiveness to  $\alpha$ MSH or autonomous adenylate cyclase production (Jackson, 1994). Either mechanism results in an entirely eumelanic phenotype, and these alleles are usually considered as "dominant black" regardless of the underlying mechanism used to achieve this phenotype.

Recessive alleles at the *Extension* locus consistently result in an inactive receptor that is unresponsive to stimulation by  $\alpha$ MSH. The inactive receptor results in a completely phaeomelanic phenotype. In this regard the *Extension* locus acts opposite to the *Agouti* locus since more dominant phenotypes are completely eumelanic, and more recessive ones are completely phaeomelanic. *Extension* locus alleles tend to affect the entire animal, so that this locus does not produce patterns as are typical of the *Agouti* alleles, with interplay of the two pigment types. The *Extension* locus is usually responsible for completely eumelanic or completely phaeomelanic phenotypes, although exceptions do occur in some other species (Searle, 1968).

alleles

The *Extension* locus has few variants in goats, and these occur in only a handful of breeds. In those few breeds this locus has important interactions with the *Agouti* locus in determining color. The *wild type* allele at the *Extension* locus allows the expression of the *Agouti* locus. It is by far the most common *Extension* allele in nearly all breeds of goats, most of which have obvious segregation at the *Agouti* locus to account for the majority of color variation.

The dominant allele at the *Extension* locus is called *dominant black* and is symbolized  $E^D$ . This allele causes a uniformly eumelanic coat, which is black on an otherwise unmodified background. Dominant black in goats has been documented in Angora goats, and anecdotal evidence suggests that it might also be present in some African breeds. In contrast to its rarity in goats, a similar allele is fairly frequent in sheep breeds of a wide variety of geographic origins.

The similarity of the phenotypes resulting from *dominant black* at the *Extension* locus and *nonagouti* at the *Agouti* locus can be confusing, as these two cannot be easily distinguished. Recent selection in favor of eumelanic phenotypes by some Angora goat breeders has resulted in the presence of both mechanisms for black in some populations. Visual inspection alone cannot distinguish between these two biological mechanisms that achieve similar phenotypes. The persistence of both mechanism can result in some strange segregations of color unless the observer is aware that both the *dominant black* of the *Extension* locus and the recessive *nonagouti* of the *Agouti* locus can be present.

A single occurrence of a red Angora kid from two obviously striped *Agouti* locus pattern parents points to the possibility of a recessive allele at *Extension* that codes for uniformly phaeomelanic color. No segregation data are available to substantiate this allele any further.

The *Albino* Locus

The *Albino* locus codes for the tyrosinase enzyme that is essential for melanogenesis. Recessive alleles at this locus are responsible for the production of abnormal forms of tyrosinase that either have reduced or nearly completely absent activity (Jackson, 1994). As a result, melanocytes are present but are incapable of melanogenesis. The *Albino* locus has never been documented to have variation in goats, although two different variants occur in sheep (Adalsteinsson, 1977, 1978a; Rowlett and Fleet, 1993).

## Expression and Modification of Pheomelanin

Phaeomelanin colors are subject to various modifications, some of which are well understood and many others of which are not. Many of these modifications do appear to have a genetic basis. Phaeomelanin colors are modified by independent loci controlling color directly, and are also modified by the physical structure of the hair coat. It is difficult to separate the results of these two phenomena.

Some evidence points to a fairly limited number of modifiers for phaeomelanin intensity in goats. In some families the expression of phaeomelanin clusters around deep red, medium gold, and cream to nearly white. The lack of all intermediates between these three classes supports the contention that control may be at a single or a few loci with incompletely dominant alleles. Proof of this hypothesis is lacking, though.

## Expression and Modification of Eumelanin

Eumelanin areas on goats are subject to modification by mechanisms distinct from those affecting phaeomelanin colors. One fairly common modification is the replacement of black eumelanin with brown eumelanin.

### The *Brown* locus

#### mechanism of action

Alleles assigned to the *Brown* locus are a common source of brown color in goats. This locus controls tyrosinase-related protein 1 (TRP-1), which has important but poorly documented action within melanocytes (Jackson, 1994). The recessive *brown* allele reduces activity of TRP-1, and the result is that all regions that are eumelanin have the black form replaced by a brown form. Brown melanosomes are structurally different than black ones (Alexieva *et al.*, 1985). In the brown phenotypes the catalase normally involved in melanogenesis fails to protect the eumelanin from the action of hydrogen peroxide which is produced during melanogenesis.

The murine *Brown* locus has a few dominant alleles in addition to the recessive ones. These usually have apical pigmentation and basal pallor on hair shafts, and similar effects have not been documented in goats. The banding on hairs that is caused by these murine alleles is due to the buildup of toxic metabolites within the melanocytes, which increase as the hair cycle progresses. The result is that the apical portions are pigmented since melanocytes are functional, but as the hair grows the melanocytes undergo toxicosis and pigmentation is therefore diminished as the base of the hair is produced.

#### alleles

At least three different alleles can result in brown eumelanin in goats. Whether these all reside at the *Brown* locus is undetermined, but they are all likely candidates for this locus. One allele is *brown*, and is recessive. This results in a medium brown color in areas where other loci allow eumelanin. Brown eumelanin can replace black eumelanin in any of the *Agouti* locus patterns, as well as in goats with the *dominant black* allele of the *Extension* locus. The brown pigmented version of the various *Agouti* locus patterns is usually more subtle than is the black one, because the contrast of the pale areas with the brown is less than that of pale areas with black.

More common among goats are dominant alleles leading to brown eumelanin. It is likely that two different alleles occur. *Dark brown* changes black eumelanin to dark brown. The kids are usually born barely "off black" and can easily be confused as having black eumelanin rather than brown. By the age of a few months, though, the difference is obvious and remains so throughout life.

*Light brown*, in contrast, results in a very obvious change from black to brown eumelanin. This is the allele that is responsible for the color of the Toggenburg breed.

At least in sheep, the  $B^b$  allele has pleiotrophic effects in addition to its action on color. Ryder *et al.* (1974) found that Soay sheep homozygous for  $B^b$  were less viable than sheep not homozygous for this allele. Homozygous sheep were also smaller bodied than those of other genotypes. This effect was most noticed in  $A^aA^aB^bB^b$  sheep. This work concerned the feral Soay sheep, in which the *brown* allele is relatively common. A similar effect on nonferal sheep has not been documented.

### Moonspots

Moonspots are a conspicuous if unusual phenomenon in goat color. These are round to oval spots of varying size, and are superimposed over any background color. They are not white, but are usually very pale. They tend to be more intensely pigmented in kids than they are in adults, and can easily be confused with white spots in adults. The exact genetic control of these is uncertain, although it is likely that they have at least some dominant characteristics. The number and size of moonspots is highly variable, and they can easily be overlooked in some goats. They are most common and dramatic in AngloNubians as well as in other African and Indian breeds, although they do occur as a rare variant in a wide range of goat breeds.

### Loci Controlling White Spotting

Patterns of white spotting are added independently to any colored background of goats. Multiple spotting patterns occur. Very few of these have any importance to goat breeds worldwide, but several occur in a wide range of breeds.

### The Angora White Locus

The *Angora White* locus derives its name from the Angora breed, in which it is a common cause of white coat. It may not be the only genetic mechanism for the highly desired white mohair fiber of this breed, but it is one of the more common and is therefore important. A dominant allele, *angora white*, results in a completely white phenotype. Some evidence for slight incompleteness of dominance has been found, such that some heterozygotes have colored (usually black) stripes in horns and hooves. The allele is epistatic to *Agouti* and *Extension*, which makes breeding for color in Angora goats especially challenging.

### Piebald Spotting

In mice the *Piebald (S)* locus has been documented to act on the differentiation of melanocytes at the neural crest, as well as on their migration from the neural crest to the rest of the body (Jackson, 1994). The result is an array of white regions on otherwise pigmented mice. The specific color of the pigmented regions is governed by the other coat color loci, so that white spotting can be superimposed over any color or pattern.

Mice with extremely white manifestations of spotting are afflicted with aganglionic megacolon, which is a lethal condition that occurs relatively early in life. This condition results from failure of neurons to migrate from the neural crest to the colon, much as the white spotting results from failure of the migration of melanocytes from neural crest to skin. The alleles for spotting at the *S* locus are recessive in most species, and result in unpigmented regions of skin and hair.

No definitive research in goats has documented alleles at the *S* locus. Patterns resembling the spotting of other species (including the taxonomically close sheep) suggest that this locus does indeed have variants in goats. Especially likely as candidates are minor white marks on head, tail, and distal legs. In addition, some obviously spotted goats have round patches of color over ears and eyes, and on the body. These are especially likely to betray *S* locus patterns. The dominance or recessiveness of these is undetermined. Spotting from alleles at this locus may be important in yielding the final color of the Boer goat.

### Belt

A fairly repeatable marking in goats is a white belt over the midsection of the body. The belt can vary from narrow and incomplete, to very large and including one or more legs and the rump or shoulder and neck. This segregates as a dominant gene, and is likely to be one of the components of the Boer pattern. The belted pattern is among the most common white spotting patterns in goats.

### Roan

Roan goats result from a mixture of white hairs into any background color. The amount of roaning varies tremendously, and in minimal grades might not be readily noticed. In more pronounced manifestations the intermixture occurs over the body and neck, but generally spares the head and legs which remain the background color. No segregation studies have been done, but results from some families suggest that this is a dominant allele. A dominant mode of inheritance is consistent with its action in most other species.

### Flowery

The flowery pattern is a breed characteristic of the "Florida Sevillana" breed, and derives its name from that breed. This pattern consists of small (up to about 1 cm) spots of white scattered over any background color. The pattern varies, and maximal grades are very pale while minimal grades are very dark. The white speckling tends to be most intense on the ventral midline, and on many flowery goats the result is a nearly white ventral midline that feathers out into speckled roan sides, and then to a nearly solid colored topline. Segregation in a few families suggest that a dominant gene is responsible for this pattern.

### Goulet

Goulet spotting derives its name from the herd of Tennessee Fainting Goats in which the pattern was first documented. Minimal grades of spotting include white ears with a few residual small spots of color, and facial white that usually does leave the nose, lips, and eyes with pigment. A few white spots, usually about 1 cm, are scattered over the rear flanks and hips, and the tail is generally white. Medium grades of spotting include white ears, facial white sparing the eyes and nose, and then a ragged interplay of white and colored areas over the body. Maximal grades are nearly white, with residual ragged colored spots over the body.

### Algarve

The Algarve breed sports a ragged and irregular spotting pattern that resembles the spotting of the Goulet pattern except that it consistently has colored ears even in very white individuals.

### Barbari

The pattern of the Barbari goat is somewhat elusive, and consists of small colored spots in areas that are white in patterns consistent with the belting or spotting patterns. These dark spots are present at birth, in contrast to the ticking pattern in which they grow in later. This appears to be a modification of any spotting pattern, and the genetics of this have not been documented although early results are consistent with a dominant gene.

### Ticking

Small spots of pigment grow into the fleece or haircoat of some goats that are spotted by virtue of any of the spotting patterns. This is called ticking, and the small spots are not present at birth but grow into the white areas later. Ticking is dominant to its absence, and varies considerably in extent. The mechanism that allows melanocytes to populate regions that are embryologically devoid of them has yet to be elucidated. This gene is analogous to ticking in dogs, on which species it is extremely variable in extent and in size of the tick marks (Little, 1957).