Original article

Inheritance of color in Angora goats

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Abstract – Inheritance of color in Angora goats deviates from mechanisms previously
reported in other breeds and types of goats. Segregation data are most consistent
with the presence of a dominant white that is epistatic to the *Agouti* and *Extension*
loci. This newly documented locus, *White Angora* (*Wta*), has two alleles: *dominant
white* (Wta^D) and *wild* (Wta^+). Goats lacking *dominant white* are various colors as
determined by other loci. The segregation data support the existence of a dominant
black that is epistatic to the *Agouti* locus, an action consistent with *dominant black*
(E^D) at the *Extension* locus. Alleles at the *Agouti* locus segregate as well, and include
white or tan (A^{wt}), *badgerface* (A^b), *black and tan* (A^t) and *no pattern* (A^a). Two
other patterns, likely at the *Agouti* locus, were also segregating, and are called *peacock*
(A^{pck}) and *san clemente* (A^{sc}) after breeds in which each is widespread. Phenotype on
goats bearing *white or tan* varied from white to reddish, with a few goats being dark
tan-brown with darker tan shoulder and back stripes. One reddish tan kid segregated
from two black and tan parents, suggesting that a recessive pheomelanic genotype
might also be present in the breed. This is likely a recessive allele at the *Extension*
locus. The usual white Angora goat appears to have the *dominant white* allele in
conjunction with *white or tan* at *Agouti*. The allele *dominant black* at *Extension* is
also relatively frequent. © Inra/Elsevier, Paris

coat color / goat / Angora goat / genetics

Résumé – Hérédité de la coloration chez les chèvres Angora. L'hérédité de la
coloration chez les chèvres Angora diffère des mécanismes précédemment rapportés
dans les autres races et types de chèvres. Les analyses de ségrégation sont cohérentes
avec la présence de blanc dominant, épistatique sur les locus *Agouti* et *Extension*. Un
locus nouvellement répertorié, *White Angora* (*Wta*) a deux allèles : blanc dominant

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(Wta^D) et sauvage (Wta^+). Les chèvres dépourvues du blanc dominant expriment diverses couleurs déterminées par les autres locus. Les données de ségrégation suggèrent l'existence de noir dominant (E^D) au locus *Extension*. Il y a également ségrégation au locus *Agouti* avec les allèles blanc ou feu (A^{wt}), tête de blaireau (A^b), noir et feu (A^t) et indéfini (A^a). Deux autres motifs appelés paon (A^{pck}) et san clemente (A^{sc}) sont également en ségrégation. Le phénotype des chèvres blanc ou feu varie de blanc à rougeâtre avec quelques chèvres brun-feu foncées avec des épaules et des bandes dorsales de couleur plus prononcée. L'obtention d'un chevreau rouge et feu à partir de deux parents noir et feu suggère l'existence d'un génotype phéomélanique récessif, avec probablement un allèle récessif au locus *Extension*. La chèvre habituelle Angora blanc paraît posséder l'allèle blanc dominant associé à l'allèle blanc ou feu au locus *Agouti*. L'allèle noir dominant au locus *Extension* est relativement fréquent. © Inra/Elsevier, Paris

coloration du pelage / chèvre / chèvre Angora / génétique

1. INTRODUCTION

Relatively few studies have been accomplished concerning the inheritance of color in goats. These studies have been reviewed by Millar [12] and Millar and Lauvergne [13]. Early studies tended to be based on analysis of herd book data, which are usually incomplete [3–5, 11]. More recent contributions to understanding the inheritance of goat color have been based on segregation data [2, 7, 14, 19]. These studies have all been accomplished in a fairly narrow range of breeds, most of them European, and may not be applicable to all breeds and types of goats. These studies confirm that the final color of a goat is determined by the interaction of several different loci.

One of the most important loci controlling goat color is the *Agouti* locus, which controls the distribution of eumelanin and pheomelanin over the coat [2]. *Agouti* locus patterns are usually symmetrical, and include many individual patterns, each caused by a unique allele. Dominance relationships at the *Agouti* locus are such that pheomelanic areas are consistently expressed. As a result, the completely pheomelanic phenotype caused by the *white or tan* allele is dominant to all others, while the completely eumelanic phenotype caused by *nonagouti* is recessive to all. In between these extremes are several alleles that are codominant, each with a distinct symmetrical pattern of eumelanic and pheomelanic areas. Alleles assigned to this locus include: *white or tan* (A^{Wt}), *black mask* (A^{blm}), *bezoar* (A^{bz}), *badgerface* (A^b), *grey* (A^g), *lightbelly (black and tan)* (A^{lb}), *swiss markings* (A^{sm}), *lateral stripes* (A^{ls}), *mahogany* (A^{mh}), *red cheek* (A^{rc}) and *nonagouti* (A^a). Patterns assumed to be at this locus include *posterior mantle* and *anterior mantle* [10]. The *Agouti* locus patterns appear to be the main source of variation in goats so far studied, and in most goats one or another of the *Agouti* phenotypes is usually obvious in the color phenotype.

The expression of eumelanin as either black or brown is controlled by the *Brown* locus, to which four alleles are assigned [19]. These include *dark brown* and *light brown*, both of which are dominant to *wild type*, which allows for expression of black eumelanin. A recessive allele, *brown*, is responsible for a medium shade of brown that is frequently termed red by goat breeders, even though it is a eumelanic color rather than being pheomelanic as implied by the term 'red'.

White markings in goats include several different patterns, few of which have been carefully identified and studied. White spotting is variously called broken color, spotting or piebaldness. White spotting was regarded to be dominant to self color by Lush [11], Asdell and Buchanan Smith [3] and Eidregevic [5]. Lauvergne and Howell [9] postulated two alleles at the *Spotting* locus, S^+, for the wild type, and S^c for spotted phenotype (*cinta*), which is specifically a belt of white in the midregion of the body.

The genetic constitution of white goats has been poorly studied. Adalsteinsson et al. [2] determined that the white of crossbred cashmere goats was consistent with white being determined by the *white or tan* allele at the *Agouti* locus. Lauvergne and Howell [9] suggest that white Saanen goats result from homozygosity for a dominant gene, R, at the *Roan* locus.

The Angora goat is valued for its production of starkly white, lustrous mohair. It is a very specialized breed, and centuries of selection have made colors other than white very rare. Sponenberg [17], discussing homology between colors in sheep and goats, stated that it was not known whether the white color of the Angora goat was homologous to white in sheep, but pointed out that it was possible to select for redness in color in Angora goats, which is in keeping with the white of the Angora breed perhaps being caused by an *Agouti* locus allele, *white or tan*.

2. MATERIALS AND METHODS

Data from four goat breeders were available for study. These four breeders are working to develop colored Angora goats, and are using either colored goats that segregated from purebred Angoras, or high grade goats that resulted from several generations of Angora mates to nonangora goats. These goats were mated among themselves as well as to white Angoras, and the colors of the resulting kids were described. These results are outlined in *table I*.

Several colors and patterns appeared in these goats. The badgerface pattern is generally pheomelanic on the dorsum with an eumelanic belly and lower legs, with a dorsal eumelanic stripe and eumelanic areas on the head. Black goats are born black, although many of these later produce uniformly grey fibers in mohair producing regions while continuing to produce black fibers in the short haired portions of head and legs. The black and tan pattern consists of a black dorsum, with pheomelanic areas on the belly, lower legs and stripes on the head. Brown goats are born dark brown or tan, and then usually fade to a paler color. Brown and tan goats have the black and tan pattern, but with brown replacing black in the eumelanic areas. Grey goats were those born with intermixture of pale and dark eumelanic fibers, as distinct from the black goats many of which later produce uniformly grey mohair. Grey goats vary from relatively even mixtures of white and black fibers, to goats with predominantly white fibers and only occasional black fibers. Peacock goats have pheomelanic fronts and black rears, bellies, legs and facial stripes. Red goats are uniformly pheomelanic, and usually fade rapidly to off white or nearly so. The san clemente pattern is nearly an opposite to the peacock pattern, with black front, pheomelanic rear and belly, and pale facial stripes. White goats are starkly white. The patterns having both pheomelanic and eumelanic regions are illustrated in *figure I*.

Table I. Results of crossing various colors of Angora goats.

Parents		bdgr	blk	blk/tn	brn	brn/tn	gry	gnt	pcck	red	sncl	wht
Bdgr	blk	2										1
	red		4						1	2		4
	wht	1	1									5
Blk	blk		3	1								2
	blk/tn	1	5	7		1	1			1	2	2
	brn		1	1								
	gry		1				1					1
	pcck			1						1		
	red		6		1	1				9		2
	wht		1				1			2		11
blk/tn	blk/tn		1	20	1	2				1		
	brn		1									1
	brn/tn			2						1		
	gry		3	1			7	2				2
	pcck		2						3			
	red		4	2	2	1				8		7
	sncl		1	1						5	2	
	wht		3	2								5
Brn	red				2							
Gry	red						1			3		2
	wht	1					2					1
Pcck	red									1		4
	wht											2
Red	red		3		1	1				54		
	sncl									3		1
	wht		3	1						4		10
Sncl	wht										1	
Wht	wht		1							2		2
Total		5	43	40	7	6	13	2	5	98	3	65

Bdgr refers to the badgerface pattern. Blk refers to black. Blk/tn refers to the black and tan pattern. Brn refers to any brown phenotype, and brn/tn to brown and tan phenotypes where the black of the black and tan pattern has been replaced by brown. Gry refers to any grey phenotype, gnt to grey and tan phenotypes. Pcck refers to the peacock pattern. Red refers to pheomelanic goats, which are usually reddish at birth and then fade to nearly white. Sncl refers to the san clemente pattern. Wht refers to uniformly white goats.

In addition, a limited number of results from the mating of Tennessee goats was examined to determine the genetic relationships of white and tan goats. These results are outlined in *table II*.

The results of the various crosses were examined to establish consistency with previously published details of the genetic control of goat color. Where deviations occurred, new hypotheses were generated and the results were compared to these.
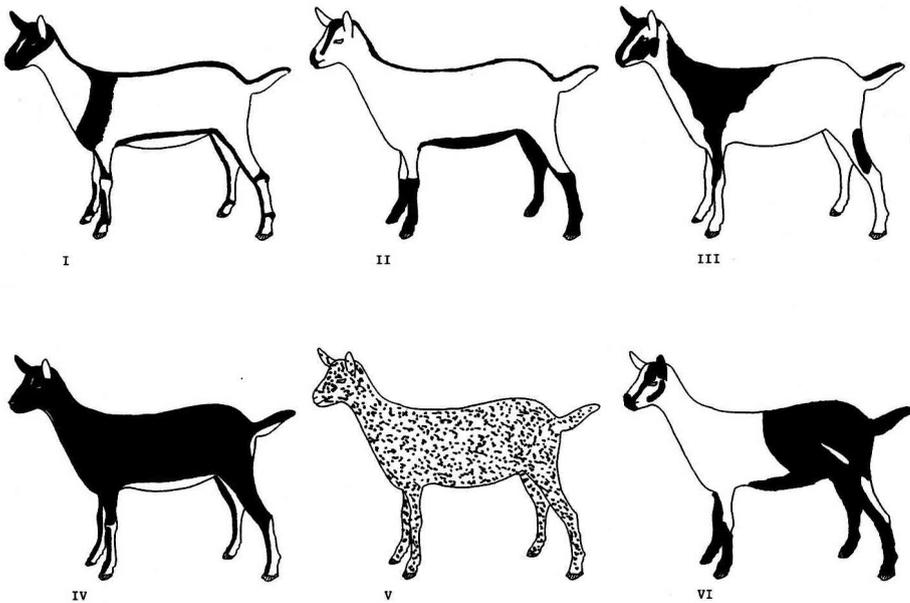
Figure 1. Patterns caused by intermediate *Agouti* locus alleles referred to in the text. These include bezoar (I), badgerface (II), san clemente (III), black and tan (or light belly) (IV), grey (V) and peacock (VI). The extreme patterns, white or tan, and no pattern, are, respectively, completely white (or tan), or completely black, and are not illustrated.

3. RESULTS

The results of the various crosses of Angora goats are presented in *table I*. These crosses yielded 287 kids. Of these, 65 were white and 222 were colored.

The results of mating the tan Tennessee buck to various does are presented in *table II*. These matings resulted in six black, three, intermediate *Agouti* pattern, six tan and seven white kids.

Table II. Results of mating a tan Tennessee buck to various colors of Tennessee does.

Dam color	Kid colors				
	Black	Intermediate	Tan	White	Total
Black	3			2	5
Intermediate	3	2	3	5	13
Tan		1	3		4
Total	6	3	6	7	22

Tan goats were distinctly yellowish or rufous tan, white goats were nearly stark white with occasional small patches of very pale tan color. Intermediate patterns are those of the *Agouti* locus, and included badgerface, bezoar, black and tan, peacock and grey.

4. DISCUSSION

Accuracy of color classification is essential for a study such as this. Most of the color classes of goats and kids were unmistakable, so that misclassification of kids was unlikely. Badgerface goats and black and tan goats, for example, are very distinctive throughout life and are unmistakable. Black goats, likewise, are easily identifiable throughout life.

A few color classes are more equivocal. Brown, for example, includes any kid born a reasonably brown shade. It is likely that brown therefore includes both eumelanic and pheomelanic types. A further difficulty with Angora goats is that both eumelanin and pheomelanin fade, although pheomelanin generally fades more than eumelanin. Regardless of this, it is likely that the brown classification represents more than one pigment type, and therefore it is of limited use in analysis. The only exceptions are goats that are of intermediate Agouti patterns, for which observers can be confident that the brown regions are eumelanic. Similar arguments hold for the grey goats, since this color class includes any goat born with a mixture of eumelanic and pale fiber. These goats may arise from the *grey* allele at the *Agouti* locus, or could also be roan and the result of various white spotting phenomena. As such, the grey category was of limited usefulness for analysis. Fortunately both brown and grey goats were rare in these data.

Peacock was chosen to designate a pattern that is pheomelanic on the front, and has a eumelanic rear, lower legs and distinct eumelanic facial pattern. Peacock is the name given a goat breed that is consistently this pattern, and this name therefore helps to avoid some of the confusion that arises from trying to remember on mantled, reverse mantled, posterior mantle or anterior mantle whether the mantle is eumelanic or pheomelanic. The san clemente pattern, which is nearly the reverse of the peacock pattern, is also a useful designation since it is nearly uniform for the San Clemente Island goat breed. The use of these names is an arbitrary decision, but those familiar with breed characteristics will find it a precise way to describe these two distinctive patterns.

Red goats varied from being richly pheomelanic to being very nearly white. Such goats are unmistakable with other color classes, with the exception that very dark ones can be confused with brown goats. Red goats are usually born a fairly rich color, and then fade to a pale color. In most goats a portion of the primary fibers remain pigmented with pheomelanin, so that it is possible to identify red goats throughout life, even after they have faded. Some pheomelanic Angora goats have a variable shade of red with annual seasons, and so fade and then darken the color repeatedly.

White goats are starkly white with no pigmented fibers. This is the usual phenotype for Angora goats. White can result from a variety of biological mechanisms, including removal of pigment by white spotting, or removal by dilution. As a result, white as a color class can include a variety of genetic mechanisms all leading to a single endpoint [16].

The color, and the whiteness, of sheep is relatively better studied than that of goats. Whiteness of sheep generally results from the *white or tan* allele [1]. In many breeds of sheep various spotting phenomena are also involved in producing starkly white sheep. Spotting combines with the *white or tan* allele to

result in sheep that are more extremely white than those with the *white or tan* allele but lacking spotting patterns. In addition, selection for extreme degrees of spotting can result in starkly white sheep that have Agouti phenotypes other than white or tan. Some spotting phenomena in sheep, specifically Akaraman type spotting, consistently result in fleeced regions that are white, with minor pigment remaining only in nonfleeced regions [6]. White spotting mechanisms are useful for producing starkly white fleece, since pigment cells and therefore pigments are entirely lacking. Spotting mechanisms on their own appear to have been used relatively rarely in white sheep breeding, which relies mainly on the *white or tan* allele at the *Agouti* locus for the production of white phenotypes.

Of critical importance to this study is documentation that a single allele, *white or tan* at the *Agouti* locus, can be responsible for phenotypes that range from dark tan to white. The results from the Tennessee goat crosses demonstrate that the *white or tan* allele can indeed cause these variable phenotypes. The tan buck is heterozygous for *white or tan* and *nonagouti*, as demonstrated by producing black kids from mates with intermediate *Agouti* alleles, as well as kids with maternal *Agouti* intermediate patterns which are obligate heterozygotes for his *nonagouti* allele.

All but two does to which he was mated had previously been proven by production or pedigree to be heterozygous (or in some cases homozygous) for *nonagouti*. The data include two tan does, one of which was heterozygous for *black and tan*, and the other of which is heterozygous for *badgerface*. The kids from these two must be removed from the data since it is uncertain if they have received the *white or tan* allele from sire or dam. By removing the kids from these two tan does it is assured that all kids that are black or some intermediate *Agouti* locus pattern have received the nonagouti allele from the sire, while all tan or white kids (if these are due to a single allele) have obtained the *white or tan* allele from this buck. When the kids are so grouped, the result is that he passed to the kids eight *nonagouti* alleles, and ten *white* or *tan* alleles ($P = 0.167$ by binomial expansion).

If the white kids are not the result of the same *Agouti* allele as the tan kids, then these should be due to a locus other than *Agouti* and can be removed from the analysis. The result should still be that half of the nonwhite kids are tan and half are nontan. By doing this, the results are eight kids bearing the buck's *nonagouti* allele, and only three bearing his *white or tan* allele ($P = 0.08$ by binomial expansion). This result is therefore unlikely, although not significant. It does remain most likely that the *white or tan* allele accounts for both the tan and the white phenotypes in this kid group, perhaps as determined by modifiers at other loci. The importance of this result lies in the fact that the *white or tan* allele can account for white as well as intensely pigmented pheomelanic goats. White can, therefore, segregate (with tan) as if at the *Agouti* locus, as determined by a previous study [2]. This previous studies did not directly document the range of phenotypes arising from a single allele originating in a single animal.

Some of the results in *table I* vary from those expected if previous theories of color genetics are applied to Angora goats. Badgerface × black matings produced one white kid. Black × black matings produced one black and tan kid and two white kids. Black × black and tan matings produced two red and two white, along with one badgerface, one grey and one peacock kid.

Black and tan × black and tan matings produced one red kid. One black and tan × brown and tan mating produced a red kid. All other results are consistent with previous theories in the literature. Most of the deviations from previously reported mechanisms take the form of black goats and white goats not producing as if these were at the *Agouti* locus.

Black goats mated to intermediate *Agouti* locus patterns produced three red and four white kids, which cannot occur if this sort of black is at the *Agouti* locus. A likely candidate for such a black is dominant black at the *Extension* locus. Unfortunately no individual goat had a sufficient record of production that would unequivocally prove this hypothesis. In favor of this hypothesis are various characteristics of the color segregations in these data. One is that black × black and tan matings produced a peacock individual, as well as both red and white individuals. This is only possible if the black animal has *Agouti* alleles other than *nonagouti*. One black doe was repeatedly mated to a red buck and produced five red and three black kids. This same red buck was mated to three badgerface does and produced only red kids ($P = 0.125$ if this is nonagouti black and he is heterozygous for it). He also produced 31 red kids from red does, and no other colors. It could have been that these does were all homozygous for *white or tan*, but this is unlikely. This red buck, then, is most likely homozygous for *white or tan*, and the black kids he produced with the black doe are therefore black by a mechanism not at the *Agouti* locus. In addition, one black × black mating produced a black and tan kid, which is impossible if these color patterns are at the *Agouti* locus. These results are consistent with *dominant black* at the *Extension* locus, which is well documented in sheep but for which these are the first data in goats [15].

The white phenotype in the Angora goat is at a very high frequency, such that colored goats only segregate very rarely from purebred herds. Accurate estimates of this phenomenon are impossible since breeders of registered goats tend to deny the existence of any colored goats segregating from white goat herds. The general impression, though, is that this occurs much more rarely in the Angora goat breed than it does in most white sheep breeds. The segregation data from matings with white goats deviate from this being strictly an *Agouti* locus phenomenon.

One family of goats helps to fully illustrate that the transmission of white and black are different in Angoras than their transmission in other breeds. This family is presented in *table III*. The black doe which produced the black kids to the red buck (and was most likely dominant black) was also mated to a registered white buck. The result was a white doe. This doe was in turn mated to a red buck to produce three black and three white kids (reappearance of a black phenotype recessive to a white phenotype). One of these black kids was mated to two red does, producing a red and two black kids. Mated to a black and tan doe he produced a white kid (which is only consistent with a dominant black epistatic to *Agouti*), and to a registered white doe produced two white kids. These results are most consistent with *dominant black* being masked by a white that is dominant and epistatic to the *Extension* locus as well as to the *Agouti* locus. This locus is suggested as *White Angora (Wta)*, with two alleles: *dominant white* (Wta^D) and *wild* (Wta^+).

One additional kid is perplexing. This is the red kid produced from the mating of two black and tan parents. This kid was phenotypically identical

Table III. Transmission of white, red and black in a single multigenerational family of Angora goats, with genotypes consistent with hypothesis of this study.

Sire color and identification	Sire genotype	Dam color and identification	Dam genotype	Kid colors and identification	Kid genotypes
Red A	Wta^+Wta^+, $A^{wt}-$, E^+E^+	black B	Wta^+Wta^+, $A^{wt}-$, E^D-	5 red	Wta^+Wta^+, Awt^-, E^+E^+
				3 black	Wta^+Wta^+, $A^{wt}-$, E^D-
Registered white C	Wta^D-, $-,-$	black B	Wta^+Wta^+, $A^{wt}-$, E^D-	1 white doe D	Wta^DWta^+, $A^{wt}-$, E^DE^+
Red E	Wta^+Wta^+, $A^{wt}-$, E^+E^+	white doe D	Wta^DWta^+, $A^{wt}-$, E^DE^+	3 black (F and 2 others)	Wta^+Wta^+, $A^{wt}-$, E^D-
				3 white	Wta^D-, $-,-$, $-$
Black F	Wta^+Wta^+, $A^{wt}-$, E^D-	red G	Wta^+Wta^+, $A^{wt}-$, E^+E^+	1 red	Wta^+Wta^+, $A^{wt}-$, E^+E^+
		red H	Wta^+Wta^+, $A^{wt}-$, E^+E^+	2 black	Wta^+Wta^+, $A^{wt}-$, E^D-
		black and tan I	Wta^+Wta^+, A^t-, E^+E^+	1 white	Wta^+Wta^+, $A^{wt}-$, E^+E^+
		registered white J	Wta^D-, $-,-$, $-$	2 white	Wta^D-, $-,-$, $-$

to all other red kids, in that no Agouti pattern was evident, but rather a uniformly pheomelanic phenotype that faded from the birth coat. This kid unfortunately died while young, so no breeding results are available. This kid could have been a recessive brown nonagouti phenotype, although it did not appear phenotypically to be so. Alternatively, a recessive pheomelanic red phenotype could be segregating rarely, as would be consistent with a recessive *Extension* locus allele. Such an allele has never been documented for sheep or goats, although it is common in other species such as the horse [18]. It could be argued that such a recessive red explains the majority of the results of red to black matings in these data, but the results of red mated to intermediate *Agouti* alleles are only consistent with the red being due to the *white or tan* allele at the *Agouti* locus.

The Angora goat has long been selected for whiteness, and other colors, or even individual colored fibers, occur very rarely in the breed. The selection history of this goat breed implies that they might have several different genetic mechanisms that lead to whiteness. One of these is the *dominant white* at the *White Angora* locus. The allele *white or tan* at the *Agouti* locus is also common in this breed, and it may well be that most goats are homozygous for both of these alleles and that the combination routinely produces starkly white goats. The result of using two dominant genes, each of which can result in white, would assure that few colored kids were ever produced. The presence of dominant *black* in the breed is somewhat perplexing, since obviously it is difficult to modify the resulting phenotype into a white goat in the absence of an allele epistatic to the *Extension* locus.

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