Identification of the Coat Pattern in Soay Sheep

Gevan Marrs, Woodland Creek Farm April, 2006

There are three gene loci that largely determine all the main aspects of Soay sheep coat color and pattern. The **pattern** of colors is controlled by the alleles present at the Agouti locus (usually designated by *A*). There are two options for the agouti allele in Soay sheep: 'wild', (aka 'mouflon', *A+*) pattern, and solid colored, or 'self-colored', (aka 'non-agouti', *Aa*). The overall basic **color** in the parts of the coat that are pigmented with the black or brown pigment eumelanin (e.g., upper body of wild pattern sheep). There are two distinct forms that the eumelanin pigment granules can take, depending upon the alleles present at the Brown locus (designated *B*). The two choices are Black, (aka dark phase, *BB*) which is dominant, and Brown (aka light phase, or moorit, *Bb*), recessive. Lastly, there is a locus that determines whether or not there are distinct, often irregular, pure white patches of hair in areas that would otherwise be pigmented, based on the other two color genes above. This locus, **Spotting** (designated *S*) has two allele options: no white spotting is dominant (*SS*), white spotting is recessive (*Ss*).

There are a range of 'common' names used by enthusiasts, and unfortunately also varying 'technical' names for the gene loci and alleles used over the years by various authorities on mammalian coat color genetics, (not to mention the often somewhat less rigorous terms often used by internet enthusiasts for Soay and other colored-coat sheep breeds). There is as well as a range of shorthand symbols used for these loci and alleles, further adding to the potential confusion. I have assembled a one-page chart that lists a host of the terms and symbols used in the most widely cited Soay sheep reference works (Figure 1)[1]. This chart may help others who may read technical references to cross-reference where different terms are used for the same thing. White spotting is *not* shown in Figure 1, but it can be assumed to be completely independent of the other two loci (Agouti and Brown)—that is, imagine a second identical chart to Figure 1 but where each sheep *also* has some (usually asymmetric), very pure white markings.

Within these 4 pigmented coat color patterns, the **intensity** of the pigmentation can vary quite widely, so that in 'dark phase' there are very dark, almost black coats, on down to medium-dark 'chocolate brown' upper body Soay. Additionally, in 'light phase', they range from a medium brown to a very light tan or 'blonde'. Particularly in the North American Soay (NA Soay) population, the range of pigmentation is particularly large, and this population of Soay is especially notable for the range of *very dark* (heavily pigmented with eumelanin) Soay. These variations can add greatly to the difficulty of reliably identifying coat patterns.

Beyond the basic level of pigmentation intensity, there are varying degrees of susceptibility to fading of colors with exposure to sunlight. Thus, the same genotypes, with similar pigmentation levels and phenotypic appearance when the coat is newly formed may well, by the end of a long winter, appear quite different in overall color. When a breeder chooses to emphasis white spotting it can be carried to the point where white spots are so extensive that they conceal the basic underlying coat patterns (color is still *usually* detectable). The Hareknoll flock of Sue Furness in Wales is probably the best example of this effect.

The phenotype (appearance, or expression) of these coat patterns can be far better illustrated by photos than words. Figure 2 shows examples of a very heavily pigmented dark phase wild pattern NA Soay, and Figure 3 shows a Soay with such extensive white spotting that the underlying pattern is not detectable (at least to my eye, in this photograph).

---

[1] It should be acknowledged and noted that comparing absolute colors or intensities in photographs from different sources, lighting, origins, etc. can be notoriously misleading. The best comparisons will always occur when either the contrasting colored sheep are both in the same photo, but this was not always possible for this illustration.

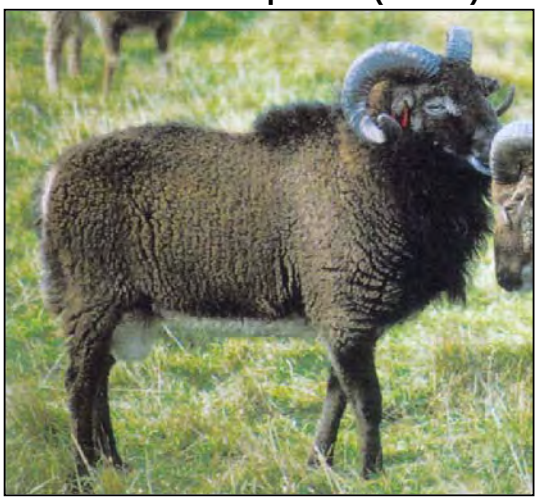
Figure 1. The four possible coat color patterns in Soay sheep with no white spotting being exhibited. Note that any of these four can also have white spotting, yielding 2^3=8 color morphs. *(Note that the sheep pictured have, of course, 2 alleles at each coat pattern locus, and I am only showing variations in terminology for a single allele.)*

Color Morphs of Soay Sheep from Hirta

Terms and notation used by 4 significant Soay sheep references.

1. Doney et. al. ***Island Survivors***, (1974) Chapter 4, pp 88-125.
2. ***Mendellian Inheritance in Sheep***, (2003?), online document reader pages 2, 6, & 12
3. Clutton-Brock & Pemberton, ***Soay Sheep***, (2004), Cambridge Univ. Press, Figure 2.7 and Appendix 2, pp 321-327.
4. Lowder, Bethan (2005) ***The genetic basis of a coat colour polymorphism in Soay sheep***, on-line Masters Thesis. (Does not address nor use terms for pattern).

Dark Phase Wild pattern (DPWP)



Copyright 2004 Cambridge University Press

1.	'dark' B_1	'mouflon pattern' A_4
2.	'black' BB	'black and tan' At,
3.	'dark" BB	'wild' A+
4.	'dark' G	'wild' (NA)

Light Phase Wild pattern (LPWP)

Copyright 2004 Cambridge University Press

1.	'light' B_2	'mouflon pattern' A_4
2.	'brown' Bb	'black and tan' At,
3.	'light" Bb	'wild' A+
4.	'light' g	'wild' (NA)

Dark Phase Self pattern (DPSP)

Copyright 2004 Cambridge University Press

1.	'dark' B_1	'self-colour' A5
2.	'black' BB	'non-agouti' Aa
3.	'dark" BB	'self' Aa
4.	'dark' G	'self' (NA)

Light Phase Self pattern (LPSP)

So uncommon that no Soay photo could be found. This is a Shetland.
(Sheltering Pines)

1.	'light' B_2	'self-colour' A_5
2.	'brown' Bb	'non-agouti' Aa,
3.	'light" Bb	'self' Aa
4.	'light' g	'self' (NA)

Figure 2. A very heavily pigmented NA Soay, Blue Mountain **Atlas**.

Photo courtesy Kate Montgomery

Figure 3. Two very extensively white-spotted Soay, Hareknoll **Squib** and Hareknoll **Freckles**.

Photo courtesy Sue Furness

From Figure 1 it should be particularly noted that one considerable authority in the mammal coat color genetics field, Dr. Phil Sponenberg, feels that Soay on Hirta island have the 'black-and-tan' *At* agouti allele rather than 'wild' *A+*. Given his experience he is likely correct, but for practical purposes in North America the distinction between these two is difficult if not impossible to detect from the outward appearance (phenotype), and probably is irrelevant to most breeders. In fact it is quite possible that even if Soay on Hirta are all 'black-and-tan' *At*, that now *both* alleles exist in the NA Soay population (due to known interbreeding with other breeds, for example European Mouflon, which *by definition* has the *A+* wild or mouflon, coat pattern). It seems likely that NA Soay heterozygotes at the agouti locus (*A+/At*) would show intermediate colors due to co-dominance (speculation on my part—I have no evidence to back this). Since most enthusiasts rely heavily on Clutton-Brock and Pemberton's ***Soay Sheep*** (2004) as a reliable reference, I use terminology and symbols largely consistent with their practice[2]. Additionally, in this article I will focus entirely upon NA Soay, not NA RBST Soay, and in this population I am quite confident that the 'mouflon-like' pattern is *A+*, (wild, or mouflon).

This discussion will focus on the telltale visual hints to search for, (particularly in photographs instead of live examination) in order to reliably detect the Agouti pattern being expressed (wild or self) when the pattern is concealed either by heavy pigmentation, extensive white spotting, or the lighting and body parts shown in the particular photograph. I will assert that with *very few* exceptions, photographs will contain the evidence of the agouti pattern. Only with very poorly lit or exposed photos, or sheep with so much white that the few color areas are not sufficient to show the pattern, does the agouti allele remain a mystery.

The first item to become familiar with this the tell-tale patterns of the wild, or mouflon pattern. While most of us look at our Soay sheep every day, until one studies them very carefully with an intent to discern the consistent patterns, it can seem disorganized, or at least quite variable.

I came to be interested in the Soay wild pattern in a somewhat unusual way. I first owned American Blackbelly sheep. This was before I knew anything about coat color genetics or had even heard of Soay sheep. When I then discovered, and subsequently bought a NA Soay ram (dark phase, wild pattern), and brought him home to the same pasture as the blackbelly, I was absolutely astounded that

[2] I do occasionally substitute the term 'solid' for 'self', as I feel that 'self-colored' does not readily convey to many people the idea that the animal is one uniform color over the whole body, whereas 'solid-colored' is more readily visualized.

they were near ‘negative images’ of each other, as far as pattern. (One of my past hobbies was photography—developing and printing my own black and white—so I was used to trying to visualize a positive from a negative. I once even went so far as to electronically reverse a photo of blackbelly to see how closely it resembled a ‘wild’ pattern.)

These are best compared in real life, of course, but photos will have to suffice here. Figure 4 shows an American Blackbelly ewe, and an NA Soay ram. The agouti pattern shown by the blackbelly is technically called ‘badgerface’, although blackbelly is pretty darn descriptive. The pattern shown in the NA Soay, ‘wild’, is sometimes actually referred to technically as ‘reverse badgerface’ (talk about obtuse terminology. Most people would be less than clear about what a badger’s face looks like, much less a reversed one!).

Figure 4. Lucy, an American Blackbelly, is technically a ‘badgerface’ agouti pattern Ab. Massena’s **Max**, the NA Soay ram, is a wild agouti pattern, A+. This ‘wild’ pattern is often also called ‘mouflon’, an obvious reference to the similarity (and believed progenitor) of Soay, the feral (or semi-wild) European Mouflon.

The areas I have found to be reliable locations for a clue are, in the usual best order for spotting this pattern in photographs, are:

1. The belly, of course. There should be a clear, distinct color change along the belly.
2. The rump. Although not that apparent in either of these photos, it often shows. The underside of the tail will be the belly color, the upper part of the tail should be the upper body color.
3. The underside of the tail. This can be spotted readily in both photos above.
4. Under the chin. This often is visible in ‘heads-on’ shots of the *A+* wild pattern as a thin white ‘frosting’ on the lower lip.
5. Front leg patterns. In particular, the *A+* wild pattern shows dark areas just above the kneecaps, and this goes down the outside of the leg to the hoof. The kneecaps will be the belly color, and this color goes down the very front and inside of the lower front leg.
6. Rear leg patterns. There should be, in the *A+* wild pattern, a distinct upper-body color strip down the outside of the upper rear leg, shifting to a narrow stripe towards the front of the lower leg, continuing to the hoof.
7. Eye-stripe (or pre-orbital spot). The *A+* wild pattern should have a lighter area slightly above and to the front of the eye. Sometimes it’s an entire stripe, and often it ends up being a distinct ‘ring-around the eye’ of lightly contrasting color to the face color.
8. Ears. The inside of the ears will be the belly color, and the backs of the ears will be upper body color. There is usually a distinct rim around the outside of the ear that shows in front-on shots. The contrast between this rim and the inner ear is a very good hint for discerning between solid blacks and very dark wild pattern (see Atlas above in Figure 2).

White areas that show in Max above that are NOT *always* a part of a wild pattern are the white muzzle on around the nose, and the white 'saddle'. Some feel these are symptomatic of crossbreeding with European mouflon (they show both these traits). I'm not sure about this aspect. I do not have sufficient data on which to take a position.

The various points above are best demonstrated with some examples. Note that these have all been chosen precisely because there might be some question in some people's mind, or at first glance, they might be somewhat difficult to precisely identify the coat pattern.

Figure 5. Pages's **Bella** is a dark wild pattern, as is obvious here by her distinct belly color. Note however the clear markings under chin, the 'sugar lips', the pre-orbital eye spots, and the inner ear. One has to look hard to see the pattern in the legs, but it **is** there. (Not every photo shows every marking clearly.).

Figure 6. Blue Mountain **Basalt** is another dark wild pattern. While his belly and rump are clearly shown, his 'sugar lips', eye spots, and inner ears all would show him as clearly wild pattern. His legs also show the pattern. Basalt is from a group of related NA Soay that seem to have a very heavy load of dark phase eumelanin, but almost no pheomelanin, causing the belly to be nearly white, and virtually no hint of reddish in the upper body. His dam, Blue Mountain <Westwood> Boanna is very similar coloring. If any 'line' in the NA Soay were to be suspects for 'black-and-tan' genotype, this would be my candidate.

Figure 7. Pages's **Bonita**, a self-colored black. I find that the inner ears, and absolutely uniform color on legs and face to be the best consistently reliable indicators of self-coloring (solid pattern).

Figure 8. Blue Mountain **Adagio** and **Allegro**. At first glance, particularly from the lack of pattern on the legs, one might wonder if these twins are self-colored. But there are clear markings both around the eyes, and in particular inside the ears that definitively show that these two are wild pattern. I has been my (limited) experience that the markings in the short-haired regions (face, legs) are far less distinct in lambs and 'resolve' as the lambs approach 6 months of age. *Photo courtesy Kate Montgomery, Blue Mountain Soays.*

Figure 9. Greener Pastures <Half Mile Mica>[3] Caravaggio and (very rare!) Soay triplets. The reader should be able to readily discern that the dam is a solid black, as are two of the triplets, but one triplet is wild pattern. *Photo courtesy Kate Montgomery, Blue Mountain Soays.*

[3] Some Soay are incorrectly registered under the flock name of the birth farm, rather than the conception farm. I include the proper conception farm in < >.

Figure 10. Blackhorse **Dagmar** Winzig. In this backlit photo it is particularly difficult to see Dagmar's belly, rump, legs, or inside her ears. But the chin and upper lip 'frosting' are still a clear giveaway - Wild pattern. *Photo courtesy Kate Montgomery, Blue Mountain.*

Figure 11. Blue Mountain Astoria. In some cases of a light phase wild pattern, the pigmentation is so light, and/or the fleece is so long, and/or so sun-faded, that it can be difficult to spot the pattern. But here the eye-rings, inner ears, and leg patterns show clearly that this sheep is wild pattern. (No light phase solid color Soay has yet been identified in North America).

The other end of the spectrum for difficulty in identifying the underlying pattern can be when there is so much white spotting that the brown pattern leaves little evidence to examine. Such is the case with many of the Soay sheep in the Hareknoll flock of Sue Furness in Wales.

In her flock, so many sheep have so much white that many individual photographs simply do not have the key markings to examine. Additionally, her flock carries all combinations of dark and light phase, wild and self pattern, and white spotting and not, so it can be a challenge to deduce the genotype with certainty. One particularly interesting case for our discussion here is **Annabel**, shown below.

Figure 12. Hareknoll Annabel. Even with the extensive white, the non-white areas still are fortuitously left in just the right locations to show patterns in the legs that clearly identify her pattern as wild. This is also affirmed by her pre-orbital spot and partial eye-ring. In other photos the wild pattern in both the insides of her ears and rump spot are distinct as well.

Figure 13. Hareknoll **Jimmy**. Despite very little brown to examine, the uniformity of color around his eyes, and inside his ears **strongly** suggests that he is self-colored. Other photos of his legs and rump affirm that indeed he is self-colored, and furthermore light phase, obviously with heavy white spotting. This genotype—where all 3 coat color genes are homozygous recessive (*Aa/Aa Bb/Bb Ss/Ss*), is the rarest of all Soay coat patterns. There may have only been a few, ever, in captivity or in the wild[4]. The Hareknoll flock has several.

It should be noted here that in the NA Soay population there has been inter-breeding with various other breeds in recent times, so coat patterns are likely to still appear that have never occurred in the original Soay Island (or Hirta Island) Soay sheep (by definition the type of the Soay breed). Whether this makes them more or less valued (and valuable) depends entirely on the owner or potential buyer.

Astute readers may note that there are virtually no NA RBST Soay photos used to illustrate this article (except for Figure 1). I have far less access to, and experience with, the range of colors present in NA RBST, although I have not seen any photos of any as dark (and therefore as challenging to identify) as the examples given. Additionally, there has never been a self-colored (solid) NA RBST Soay produced in North America, so by definition *they are all wild pattern* (or 'black-and-tan agouti', if you ascribe to Sponenberg's thinking on this).

In future works I plan to present more information and discuss some ideas about identifying light and dark phase as well as the phenotypic evidence of cross-breeding (always a hot-button topic with NA Soay!).

---

[4] ***Soay Sheep*** lists, in Appendix 2, the frequency of color morphs on Hirta for about 1,200 Soays surveyed sometime in the mid-60's, when it is presumed that an equilibrium frequency had been established. There were only 1.5% in the self-colored, light phase morph, irrespective of white spotting. Separately they describe that about 4% of all Soay on Hirta exhibited white spotting. Assuming complete independence, and that only homozygous recessives for white spotting exhibit it, then the presumed percentage of 'triple homozygous recessive coat color' Soay (*Aa/Aa Bb/Bb Ss/Ss*) would be 0.060%. Yes, that's only 6 sheep in 10,000, or roughly 1 every 1,700 Soay on Hirta. Typical numbers in the last 50 years are average about 400 new lambs each year, so one might only be expected to appear on Hirta every 4 or 5 years.