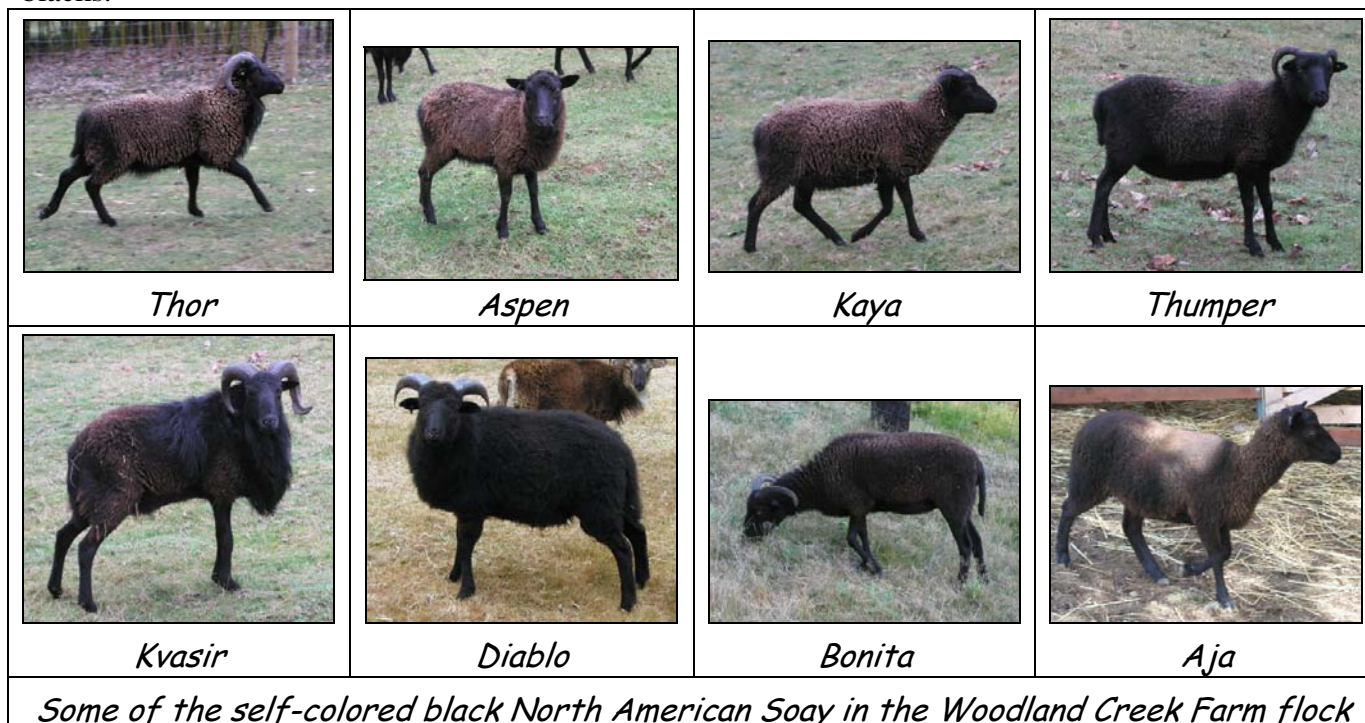


The Origins of Self-Colored Black Soay Sheep in the Pacific Northwest

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In my brief experience with Soay sheep in the Pacific Northwest (PNW) I have found that a number of breeders have self-colored black Soay sheep in their flock, and many mention pursuing the production of more. For example, Blue Mountain, skylonda ranch, Saltmarsh Ranch, Sound Soays, Greener Pastures, Teeds, and even our own Woodland Creek Farm produced self-colored black Soay lambs in 2005. I believe many or most of these farms still have, and are continuing to breed for, self-colored blacks.



As one relatively new to the Soay sheep world, I first assumed that, just like the flocks of Soay on Hirta (Jewell et. al. 1974), some proportion of the PNW Soay had always been self-colored blacks. Only after considerable study of area Soay flocks, flockbooks of cooperative breeders, pedigree charts, and internet photos did I come to realize that the number of self-colored black Soay sheep has (apparently) increased substantially in just the last few years. It would be very interesting to determine whether the *proportion* of self-colored blacks has actually changed measurably in the last 10 years, or whether it is just a perception. Recent discussions on internet groups suggests to me that breeders elsewhere have some interest in this topic as well.

In studying what is known about the genetics of coat colors and patterns in sheep, and in particular Northern short-tailed colored sheep (Icelandic, Shetland) and the primitive Soay sheep (believed to have been related in the distant past), I am struck by the seeming contradiction of a surprisingly simple genetic hypothesis for self-colored pattern in Soay sheep (straightforward Mendelian dominant / recessive pairs), yet the complexity and confusion about when and where and why self-colored Soays unexpectedly appear in flocks. The objective of this article is to reconcile the apparent contradiction between what should be simple genetics and apparently very complex (or at least seemingly unpredictable) expression of those genes.

Definition of a “black sheep” for this article

In order to stand any chance of sorting out self-colored black Soay genetics in one article, the coat color subject area covered here will be narrowed down to just one of the 3 commonly accepted primary coat color genes loci documented as occurring in Soay sheep—pattern (wild or self), black or brown (dark or light phase), and white spotting.¹ Without explaining these further here, I will assert that pattern gene for Soay sheep is as shown in Table 1. Because the terms and notation used for these 3 genes vary in different literature sources, it is important for comprehension to clarify exactly what terms will be used here and what they mean. I will strive to be largely consistent with the terminology already developed and widely used for other breeds of sheep, as well as with the vast collection of sheep genetic information assembled in the Mendelian Inheritance in Sheep website (ANGIS).

Table 1. Soay sheep coat pattern locus (location) and alleles (specific genes at that location)².

Gene Location Name (locus)	Controls	Symbol ³	Dominant	Recessive
Agouti	Coat color pattern	A	Wild (aka mouflon ⁴) A+	Self-colored (solid) Aa

Readers are encouraged to read in the ANGIS site page 4 (general effect of the agouti locus), page 7 (Wild, or mouflon), and page 6 (non-agouti, or self-colored). In order to have the best comprehension. For simplicity from here on I will simply use the term “black(s)” to mean self-colored (one solid color pattern) sheep that *also* have the dominant ‘Brown’ gene—which actually results in the black form of eumelanin, hence they are **self-colored blacks**. Not to confuse things much more, I must comment on white spotting. Blacks, as defined above, *still can have white spotting*—typically it shows up as a poll spot. It will be pure white (absence of any pigment) and is usually irregular and not symmetric. The key definition of a black, genetically, is that there are no symmetrical pattern delineated lighter colored areas on the belly, rump, under the chin, on the lips, or inside the ears (all places where even a very dark mouflon pattern can be differentiated from a black). It must also be noted that one should not be confused here with black sheep that turn a lighter shade due to exposure to sunlight. The black color of interest is that shown upon first emergence of the hair—and is usually still present at the base of the fibers if even a sun-bleached fleece is parted for examination.

Note that there are also self-colored ‘light phase’ (from the brown form of eumelanin) Soay sheep that occur on Soay and Hirta islands, but that color will not be addressed here. Limiting the discussion here to blacks (and not including self-colored ‘Brown’ (or tan, moorit, or light phase) does not affect this discussion of PNW Soay since no self-colored light phase Soay have been documented in North America, as far as I have been able to determine. Additionally, since no self-colored pattern (either

¹ Note that these 3 are consistent with those requested for the Saltmarsh Ranch Open Flockbook Project database at www.openflockbook.com.

² I do use the A+ ‘wild’ allele for the typical mouflon pattern in NA Soay, whereas ANGIS gives the typical Soay Island and Hirta pattern as At, or black-and-tan. Recent conversations with a leading expert in sheep coat color genetics—Dr. Phil Sponenberg—clarifies that he believes the ‘native’ coat pattern to be At, not A+. My observations of NA soay pattern—particularly the clear presence of reddish-brown (pheomelanin) in the body coat—makes me believe they are more like A+ ‘wild’. To be consistent with another recent work – Soay Sheep by Clutton-Brock and Pemberton—I choose to use the A+ here. In the end I am unclear how we would / will ever distinguish which is correct, nor even that it matters much. What is important is the very distinct difference from the self-colored pattern.

³ Conventions are those from Mendelian Inheritance in Sheep site – see references.

⁴ The term “mouflon” can be a lightning rod in Soay sheep discussions. Here it does not refer to the Mouflon breed, nor traits incorporated by cross-breeding with Mouflon, but instead to the **coat pattern type** typified by that breed, and referred to as mouflon (pattern).

black or light phase) Soay have ever been found in North America for the RBST Soay arising from the 1990 introduction—therefore they too have no data relevant to this article. Thus here I speak only of the subset from the ‘North American Soay’ group, and really only have any information for the further subset of those that are largely derived from the 1984 Dean Lewis (Oregon) introduction, those here are termed PNW Soay⁵. There is no intention here of ‘slighting’ the East Coast (or ‘Williams’) group of Soay nor the Canadian (or ‘Gardiner’)⁶ group—I simply don’t have the data at hand to comment on those sheep.

Sources of Information

Ideally, if we had full and complete breeding and offspring records for all Soay sheep in the Pacific Northwest, starting from the Winnipeg Zoo in 1970, Dean Lewis in 1985 down to the present (including crosses with other breeds, when they occurred), we would almost certainly be able to lay out a clear picture of where the current black Soay came from. Everyone in the Soay community owes a big debt of gratitude to Kathie Miller and her long and arduous detective work, assimilation, and documentation of Soay sheep history in North America—freely shared with all on her web site (www.soayfarms.com). Without this work most of us would still be in the dark about subjects like this one. Even with this fairly detailed Soay breeders history, alas, we are still seriously deficient in reliable records for those early sheep, and even today, sadly, not every breeder is keeping records and even some who have good information are unwilling to share it with others. Given the lack of credible specific breeding records, it seems unlikely we can ever develop a definitive case.

There is, however, what I think is a second-best alternative. One can study the sparse data available, and from that develop a hypothesis that *might* explain our observations, then seek data that would *contradict* that simple hypothesis. While this result will not be quite as compelling as the prior approach, it will likely teach us more than not studying the data at all. This approach will be used here. My data on existence of black Soay is the accumulation of those I have personally observed, those that have been reliably identified in publicly available sources (internet photos and descriptions), and the full detailed flockbook records for one particularly helpful and collaborative breeder—Kate Montgomery at Blue Mountain Soays (www.soaysheep.com). My thanks to her for her cooperation, without which this detective work would not be possible.

The simple hypothesis

Of course even the *possibility* that a simple explanation could help us understand many or most of the black NA Soay currently in the PNW only becomes apparent after considerable study of the data. I have studied it at length, and do believe there is a plausible, surprisingly simple hypothesis. I put that hypothesis forward here at the outset, before presenting the supporting data, simply to engage the reader to continue.

My hypothesis is that virtually all black Soay sheep in the PNW can plausibly be traced back to one key ram: Westwood⁷ **Zeus**. I solicit from readers any information they may have that would either support or refute this hypothesis.

⁵ I am not proposing that PNW Soay are anything like a ‘breeding line’, nor a breed, nor is anything inferred about ‘purity’ or crossbreeding. The term is one of convenience to describe the assemblage of sheep we have today that we call Soay and are largely or completely or most plausibly traced back to the earliest flocks and breeder set in the PNW.

⁶ The Gardiner sheep actually came from Dean Lewis so are really in the ‘PNW Soay’ group.

⁷ It is crucial for deductions about potential ancestors that the flock, and thus the flock-mates at the time of conception be as accurate as can be. In this article I will use the breeders name (or farm name) as the prefix, even if it differs from the prefix name shown on a registration, if any.

Genotype and Phenotype

It sometimes seems inconsistent that such a seemingly simple genetic trait like coat color pattern (mouflon or solid) could manifest itself in appearance in ways that make it very difficult to predict and understand. Table 2 shows the small set of coat color patterns genotypes and phenotypes (how they appear) that must be present in a population containing both solid and mouflon patterned Soays.

Table 2. Coat Pattern Genotypes and symbols used here; phenotypes and terms used here.

Agouti Genotype	Phenotype (appearance)
A+A+ (homozygous dominant)	Mouflon, (wild)
A+Aa (heterozygous)	Mouflon, (wild)
AaAa (homozygous recessive)	Self-colored, or solid (“blacks”, for this work)

The entire spectrum of possible crosses of these genotypes, and the resulting phenotypes, is shown in Table 3. Each parent contributes one allele to the offspring. Note that while ANGIS convention is to designate a gene with at least two characters (locus symbol and allele symbol), in this table I will only use two of the possible alleles at the Agouti locus since all have the “A” prefix, and for clarity (just in the table below) the A is dropped. In other contexts, and in particular for other breeds of colored coat sheep it is critical to retain the A prefix in designating a genotype.

Table 3. All possible crosses for coat **pattern** in Soay sheep. Blue cells will be sheep that are mouflon pattern and homozygous, yellow cells are mouflon pattern but heterozygous, green cells are solid black sheep.

			Ram 1		Ram 2		Ram 3	
			+/+		+/a		a/a	
			+	+	+	a	a	a
Ewe 1	+/+	+	+/+	+/+	+/+	+/a	+/a	+/a
		+	+/+	+/+	+/+	+/a	+/a	+/a
Ewe 2	+/a	+	+/+	+/+	+/+	+/a	+/a	+/a
		a	+/a	+/a	+/a	a/a	a/a	a/a
Ewe 3	a/a	a	+/a	+/a	+/a	a/a	a/a	a/a
		a	+/a	+/a	+/a	a/a	a/a	a/a

The two important points that one should take away from studying the possibilities in the table above. First—a black Soay sheep will only appear when *both* parents contributed the **Aa** allele (so each parent must have had at least one **Aa** allele at the agouti gene locus). Second—a black sheep *must* pass along an **Aa** allele to it’s offspring since that is all it carries on the Agouti locus. Thus in tracking down the likely origins of black sheep, using the two factors above is crucial. By studying pedigree charts with this in mind, one can deduce the genotype of many sheep that *must* be carrying the **Aa** recessive allele, but not showing any external evidence. While technically these should be called heterozygous, it seems far more comprehensible in this forum to call it “hidden black” (sometimes enthusiasts call them “carriers”—which often captures the same idea⁸). Such genotypes are shown in Table 3 colored yellow.

⁸ I have heard the term ‘carrier’ applied when the only evidence was some blacks in distant relation—half-siblings, grandparents, etc. The only *positive* evidence of heterozygous black is when either a parent or a direct offspring is black.

An example of black genetics

The theoretical treatment above is rather difficult to translate into probabilities that are comprehensible. It may be far easier to take an example from our current NA Soay population and see if the presumed relationships above help explain and identify sources of black Soays in the PNW.

A good candidate for this examination is the 2003 ram **BM⁹ Atlas** (Figure 1). He is a very dark mouflon ram, and at a first casual glance (particularly in this photograph) might appear to be a black. However, even in the backlit photo below, the telltale mouflon pattern marks can be observed—the lighter areas inside his ears, white under the chin, light spot in front of the eye, and even the lighter area on the backs of his front legs.

Figure 1. Blue Mountain Atlas
(photo by Kate Montgomery.
Used with permission.)



Atlas had little evidence of black in his ancestors. In his first lamb crop of 5 lambs (2004) there were no blacks. Yet, to the surprise of some, in 2005 he produced at least six blacks (out of 14 lambs). It was as if magically something had caused blacks to appear. How could blacks seem to suddenly arise when only one of the 4 ewes producing the blacks was black herself? Diagramming the relevant relationships, even with the help of modern pedigree software, is tedious. Figure 2 shows a mapping of the 6 blacks sired by Atlas in 2005, the ancestors of those dams as well as Atlas. In this chart, in addition to direct ancestors of the 2005 Atlas blacks, those sheep that are black and related to those ancestors, (demonstrating that the ancestor was carrying, but not showing black) are included.

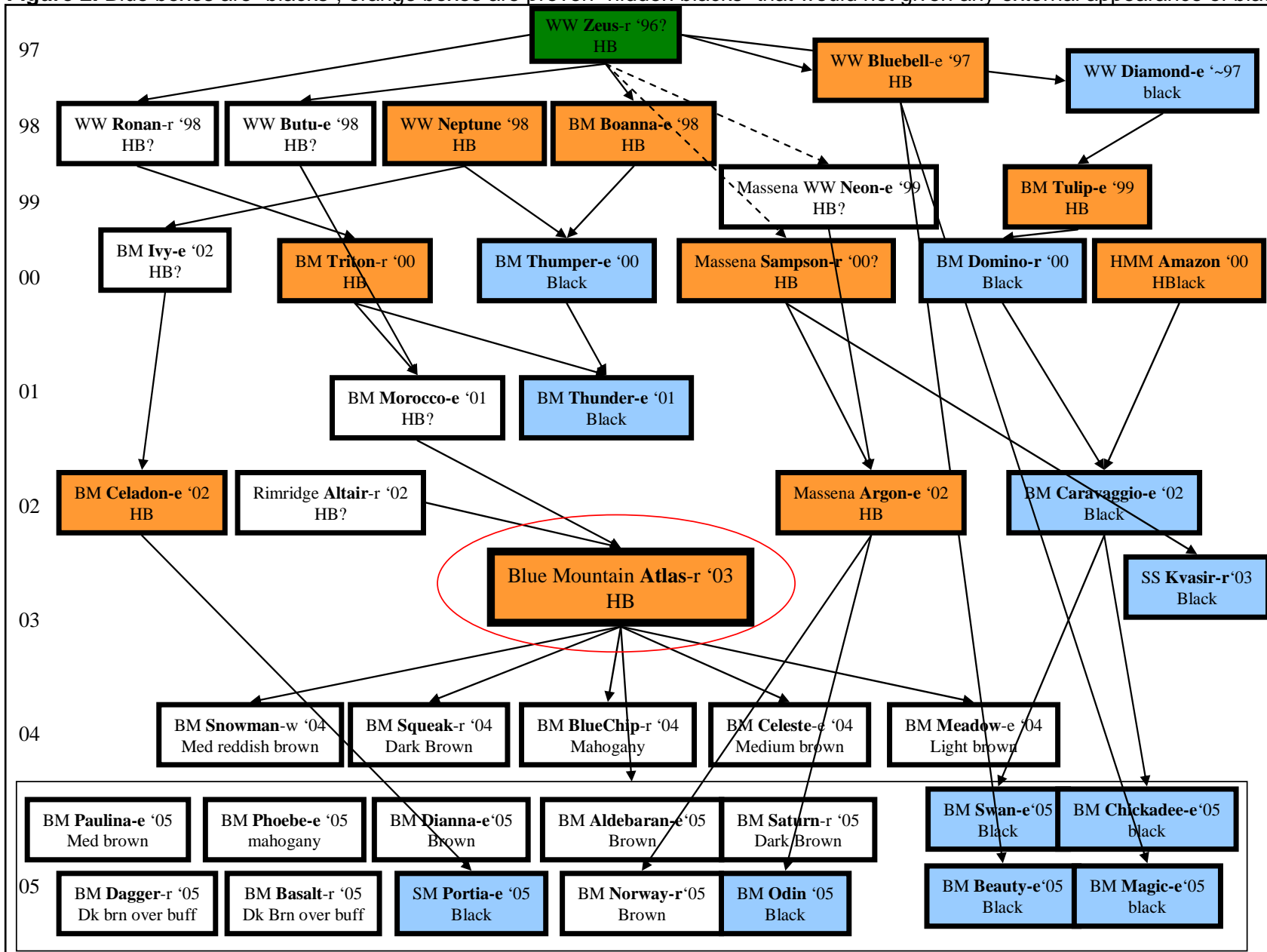
It should be noted that this diagram does not show many more sheep that are related back to **WW Zeus** in some way, and even when pared down to only the Atlas connection, without both a

clear grasp of the genetics and good records of the ancestors, it is very difficult to sort out the relationships. It is little wonder that over 9 generations over 9 years with multiple exchanges of sheep with other breeders that no one breeder can readily detect the underlying genetic patterns.

It seems to many only logical that black offspring should *only* appear if there were some solid black sheep in the lineage somewhere. If there was not a solid black Soay, then perhaps some other breed that is typically solid black must have been the source. In fact it is equally likely that the black was hidden for many generations in the Soay lineage (as a heterozygous *Aa* self-colored agouti allele), and it came from the original Soays imported into Canada. It is likely that we can never prove one way or another whether the solid blacks came from Soays or some other breed. In the end, I doubt that it matters much. The solid black *is* a genetic type present in Soay sheep as we know them on Hirta and Soay islands, and the *Aa* self-colored agouti allele is present in quite a number of current breeds (Soay, Black Welsh Mountain, Jacobs, Barbados and American Blackbelly, Hebrideans, Shetlands, Icelandics, Navajo-Churro, and even European Mouflon) and we now have that trait (*Aa* allele) in the NA Soay group. In my opinion how it got there is of relatively little importance, and in fact we likely can never know.

⁹ For brevity the names of frequently used flock names will be abbreviated. BM is Blue Mountain, WW is Westwood, GP is Greener Pastures, SM is Saltmarsh Ranch, SS is Sound Soays.

Figure 2. Blue boxes are “blacks”, orange boxes are proven “hidden blacks” that would not given any external appearance of black.



References

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