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Technical Note

Genetic Control of Color in Dorper Sheep and Their Crosses

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South African Dorper sheep were imported into the U.S. during the 1990's, and have generated considerable interest within the American sheep industry. The typical South African Dorper is a white animal with a black head, although both entirely white animals and white animals with red heads also occur. The Dorper breed was derived from crosses between the Dorset and the Blackhead Persian, beginning in the 1940's (Milne, 2000), and the Dorper color pattern is essentially the same as that of its Blackhead Persian parent. The typical Dorper coat is composed predominantly of hair fibers, although many animals possess a detectable proportion of wool fibers and some have a distinctively wooly coat (Cloete et al., 2000). Shedding of wool fibers, when they are present, is common, and shearing is not practiced in commercial flocks.

Many of the lambs produced by crossing blackheaded Dorper rams to ewes of American wool breeds are spotted or, in some cases, almost entirely black. In contrast, offspring of whiteheaded Dorper rams are normally white. As a result, some breeders have developed a preference for the white Dorper, while others prefer blackheaded animals. In all cases, the fleeces of crosses between Dorpers and wool breeds are a mixture of wool and hair fibers and have little, if any, value.

The inheritance of color in Dorpers and their crosses is complex, but relatively well understood (Sponenberg, 1997). The genes controlling color in Dorpers are distinct from those that control color in most American wool breeds, leading to novel combinations of genes influencing color in crossbred animals.

In American wool breeds, color is controlled predominantly by the Agouti (or A) gene. The predominant allele at this locus is A^{Wt} which is a dominant allele producing white fleeces in most wool breeds. The A^{Wt} allele is also associated with red or tan color in hair sheep and in a few wool breeds such as the Tunis. Several other alleles can be found at the Agouti locus (Adalsteinsson, 1970; Sponenberg, 1997), but most are rare in U.S. wool breeds. The most common alternative form of the gene is A^a, which is completely recessive and permits expression of colored wool. Animals of genotype A^aA^a are generally black, although the final expression of color can be influenced by other genes. The other, rarer Agouti alleles are intermediate to A^{Wt} and A^a in degree of dominance and produce various color patterns including badgerface (or blackbelly) and black-and-tan.

Most of the colored sheep that occasionally appear in U.S. wool breeds are homozygous for A^a at the *Agouti* locus. Most such animals are black or, occasionally, brown. Brown color is controlled the *Brown* (or *B*) gene. The dominant and most common allele at the *B* locus is B^+, which produces black wool. A rare alternative, recessive allele, B^b, produces a brown fleece which is sometimes known as a "moorit" fleece. Most black sheep that appear in U.S. wool breeds are of genotypes $A^aA^aB^+B^+$ or $A^aA^aB^+B^b$. The common observation that black coats in young lambs often fade to gray or that brown coats often fade to ivory results from the action of more poorly understood genetic modifiers.

In contrast, color in Dorpers is controlled predominantly by two different genes: the *Extension* gene and the *Pigmented head gene*. The dominant allele at the Extension locus (E^D) produces black fibers, whereas the alternative recessive allele (E^+) permits wool color to be defined by other genes. Most blackheaded Dorpers are E^DE^D or E^DE^+. These animals are not solid black because the effect of E^D is modified by the associated *Pigmented head* (or *Ph*) gene. In Dorpers, animals commonly carry the *Persian* allele (Ph^P) at the *E* locus. Two copies of Ph^P produce the classic Dorper color pattern. The typical blackheaded Dorper is thus $E^DE^DPh^PPh^P$. To fully understand Dorper color, especially in crosses, requires a change in viewpoint: the typical Dorper is not a white sheep with a black head. Instead, it is a black sheep whose body is covered with a large white spot resulting from the Ph^PPh^P genotype.

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Crosses between the Dorper and U.S. wool breeds may thus carry both dominant white (A^{Wt}) at the *Agouti* locus and dominant black (E^D) at the *Extension* locus. When this happens, the animal will be black because E^D takes precedence over A^{Wt}. Dominant black is also present in a few wool breeds. Black Welsh Mountain, Karakul, and Jacob sheep all express dominant black. Crosses between homozygous E^DE^D animals of these breeds and white wool breeds produce only black offspring.

The typical Dorper ram is $E^DE^DPh^PPh^P$ (black with a white body). The Agouti alleles that are present in Dorpers are not really known because E^D and Ph^P commonly mask their expression. The typical white ewe of a U.S. wool breed is $A^{Wt}A^{Wt}E^+E^+Ph^+Ph^+$ (a white ewe carrying recessive, and therefore unexpressed, alleles at the *Extension* and *Pigmented head* loci). *Brown* generally can be ignored because B^b is rare and in crossbreds will usually be masked by either A^{Wt} or E^D. A cross between these two types of animals (Figure 1) produces lambs that are $A^{Wt}A^?E^DE^+Ph^PPh^+$ where $A^?$ indicates that the Agouti allele obtained from the Dorper is usually not known. These lambs are commonly black with spots. Spotting occurs because animals that have only one copy of Ph^P exhibit spotting instead of a uniform white body color. The Ph^PPh^+ animal thus has an intermediate level of spotting between that of Ph^PPh^P and Ph^+Ph^+, and most crossbreds are black animals with spots.

Some exceptions to this classic pattern of color inheritance in Dorper crosses occur. All Dorpers do not have black heads, some Dorper crossbreds are solid black, and a few Dorper crossbreds out of blackheaded rams are solid white.

Whiteheaded Dorpers are homozygous for the recessive E^+ allele at the *Extension* locus and therefore do not express black color. In South Africa, these sheep arose from selection among foundation crosses between Dorset and Blackhead Persian or from use of other white South African hair breeds such as the Van Rooy (Campher et al., 1998) in development of the Dorper (Milne, 2000). Crossbred offspring of white Dorper rams should normally be of genotype $A^{Wt}A^?E^+E^+Ph^PPh^+$, and are expected to be white.

Many purebred Dorpers in the U.S. have been graded up by repeated matings of purebred Dorper rams to crossbred ewes. These animals carry residual amounts of genetic material from the ewe breeds used to make the initial crosses and may also occasionally carry color alleles from these animals. Production of solid white crossbred offspring from a blackheaded ram can occur if the Dorper ram carries only one copy of E^D. Such a ram ($E^DE^+Ph^PPh^P$) would have a typical Dorper color pattern, but one half of his crossbred offspring (Figure 2) are expected to receive the E^+ allele and, in crosses with wool breeds, would be white ($A^{Wt}A^?E^+E^+Ph^PPh^+$); the other half are expected to be spotted ($A^{Wt}A^?E^DE^+Ph^PPh^+$). Heterozygous E^DE^+ rams can result from grading up in U.S. flocks or from the presence of white Dorper ancestors in the animal's pedigree. Recent molecular characterization of the *Extension* gene (Vage et al., 1999) may allow development of a DNA test to identify carriers of E^+.

Solid black crossbred animals can occur if Dorper males carry only one copy of the *Persian* allele at the *Pigmented head* locus ($E^DE^DPh^PPh^+$). Such a ram would himself be spotted, a common occurrence in the early generations of a grading-up program. In matings with white wool ewes (Figure 3), half the progeny are expected to be $A^{Wt}A^?E^DE^+Ph^PPh^+$ (spotted) and half are expected to be $A^{Wt}A^?E^DE^+Ph^+Ph^+$ (black).

Finally, spotted Dorper animals may carry only one copy of both E^D and Ph^P (Figure 4). This situation would not be surprising in commercial Dorper rams produced in upgrading programs. Matings of such animals to white wool ewes would produce the full array of color patterns with expected frequencies of 50% white, 25% spotted, and 25% black.

These general rules should allow color to be predicted with reasonable accuracy in Dorpers and their crosses. Some exceptions may occur as a result of unanticipated interactions between the *Agouti* alleles of wool breeds and the *Extension* and *Pigmented Head* alleles of the Dorper, but should be few in number. Frequencies of the various *Agouti* alleles in Dorpers are not well known (because they are normally covered up by E^D) but may result in unexpected color patterns in some Dorper crosses. The extent of spotting in Ph^PPh^+ individuals is likewise variable, ranging from predominantly black to predominantly white.

There are a few other genes that may occasionally be expressed in crossbreds. A separate *Spotting* gene exists in some U.S. breeds (Sponenberg, 1997). A recessive allele at this locus (S^S) is responsible for spotting in Jacob sheep and is present in some wool breeds. In some cases, sheep that carry this gene have wool in the black areas that is longer and coarser than that in the surrounding white areas, producing a unique, sculpted fleece. A difference in rate of wool growth between black and white areas has been observed in a few Dorper crosses (D. R. Notter, *unpublished*). It is not known if this pattern of fiber growth occasionally accompanies spotting associated with Ph^PPh^+ or results from the action of other spotting genes.

Prediction of color is more difficult when Dorpers are mated to ewes of hair sheep breeds. In the U.S., crossing of Dorper rams on Katahdin ewes is widespread, and the Dorper is becoming popular in the Caribbean and Latin America as a terminal sire for use on local hair sheep breeds. The greater complexity in predicting color when Dorpers are crossed with other hair breeds has two sources. First, many hair sheep of genotype $A^{Wt}A^{Wt}$ or $A^{Wt}A^a$ are tan, red, or brown rather than white (Sponenberg, 1997). The A^{Wt} allele is thus expressed differently in hair breeds and can result in a range of colors from pure white to dark red or brown. The factors controlling expression of A^{Wt} in hair breeds are not well understood, but relate to the observation that color intensity is generally greater in coarser primary follicles and in hair than in finer secondary follicles. Differential expression of A^{Wt} accounts for the occasional redheaded Dorper. Crosses between Dorpers and Katahdins may express a range of colors including solid black, solid white, solid red or tan, and black-and-white spotting.

Caribbean and Latin American hair breeds are also more likely to carry alleles at the *A* locus that result in color patterns (such as blackbelly). Interactions of these alleles with alleles at the *E* and *Ph* loci of the Dorper can result in a wide range of color patterns. The *A* alleles that produce color patterns are generally recessive to A^{Wt}, resulting in unanticipated color patterns in crosses.

Development of a white Dorper flock should be relatively easy, once the E^{+} allele has been introduced through crossing with white wool sheep or use of white Dorpers. E^{D} is dominant, so whenever it is present, it will be expressed and can be removed by culling animals that show color. This cannot be done in the first generation after using a pure blackheaded Dorper ram ($E^{D}E^{D}$) because all offspring will be black, but white individuals will appear in future generations involving matings with white Dorpers or between crossbred rams and ewes.

Fixation of the typical Dorper color pattern in flocks developed by grading up from ewes of wool breeds will initially be challenging. Spotted animals will be common due to segregation of Ph^{P} alleles and white animals will occur when parents are $E^{D}E^{+}$. But with some attention to color, the frequency of occurrence of white individuals in a blackheaded flock eventually need not be meaningfully higher than the frequency of occurrence of colored animals in flocks of white wool breeds.

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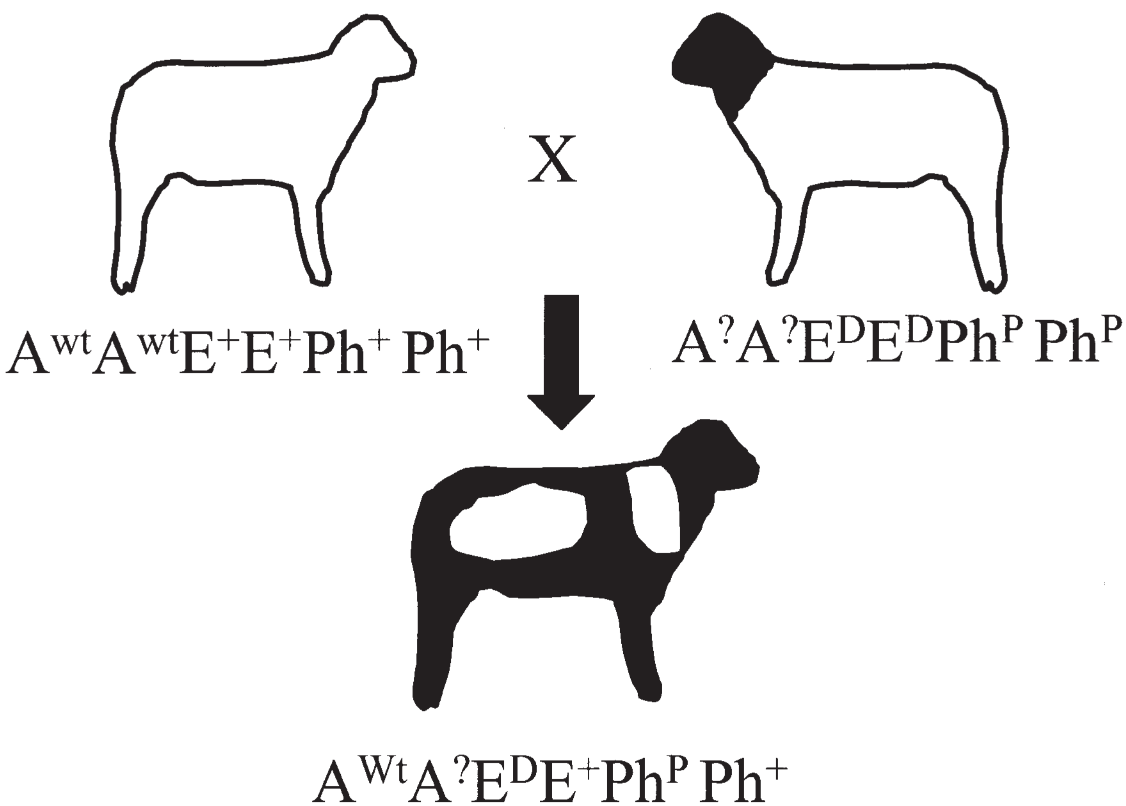

Fig. 1

Figure 1. Crosses between blackheaded Dorpers homozygous for both E^{D} and Ph^{P} and typical ewes of white wool breeds (genotype $A^{Wt}A^{Wt}E^{+}E^{+}Ph^{+}Ph^{+}$) produce spotted offspring that are heterozygous at the *E* and *Ph* genes. $A^{?}A^{?}$ indicates that the genotype of the Dorper at the *Agouti* locus is commonly not known.

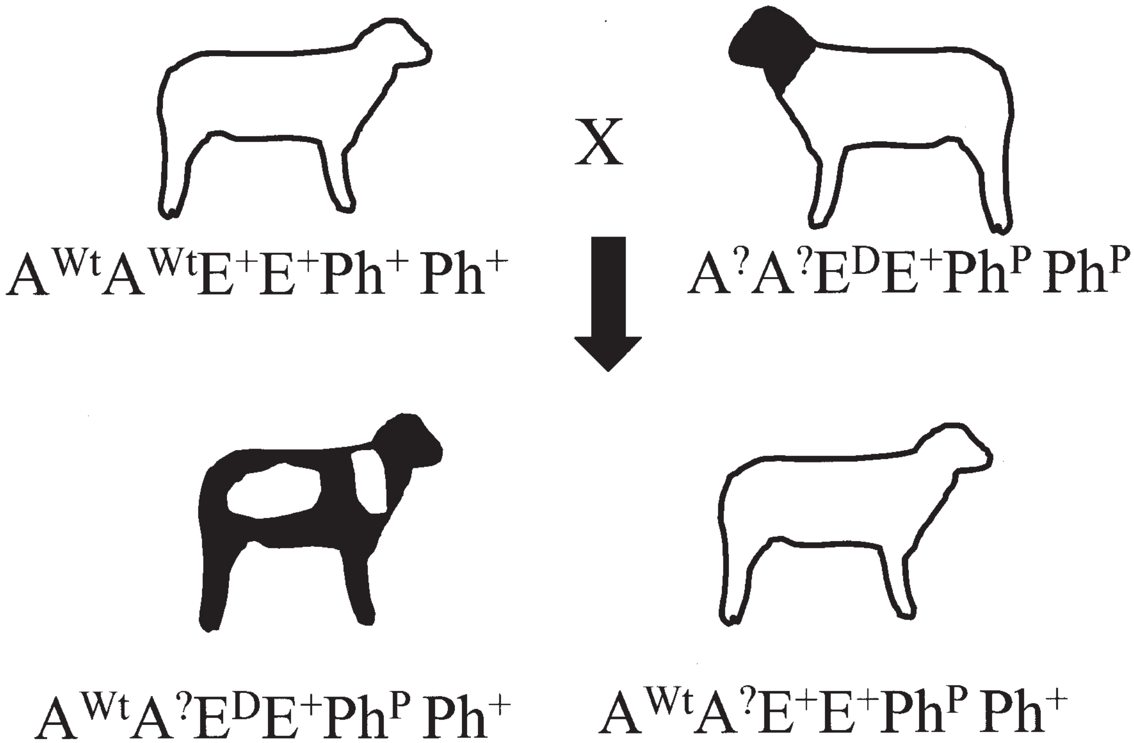

Fig. 2

Figure 2. When ewes of white wool breeds are mated to blackheaded Dorper rams that are heterozygous at the *E* locus, 50% of the resulting lambs are expected to be white and 50% are expected to be spotted.

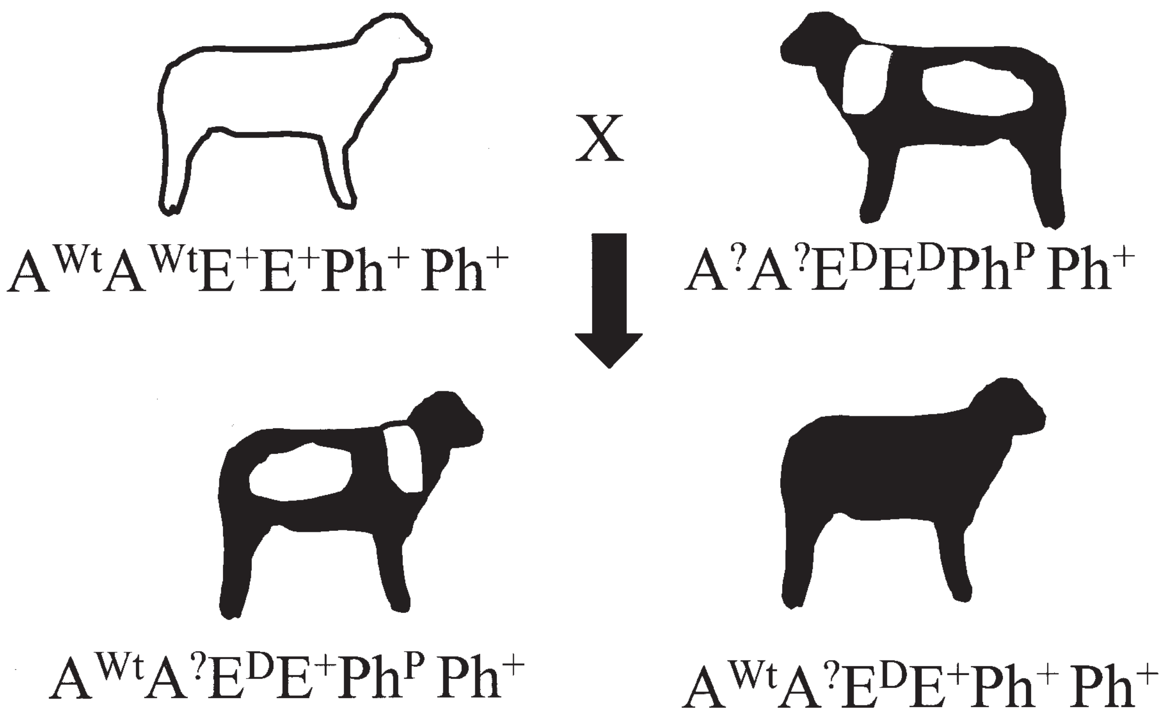

Fig. 3

Figure 3. When ewes of white wool breeds are mated to spotted Dorper rams ($Ph^{P}Ph^{+}$) that are also homozygous for E^{D}, 50% of the resulting lambs are expected to be black and 50% are expected to be spotted.

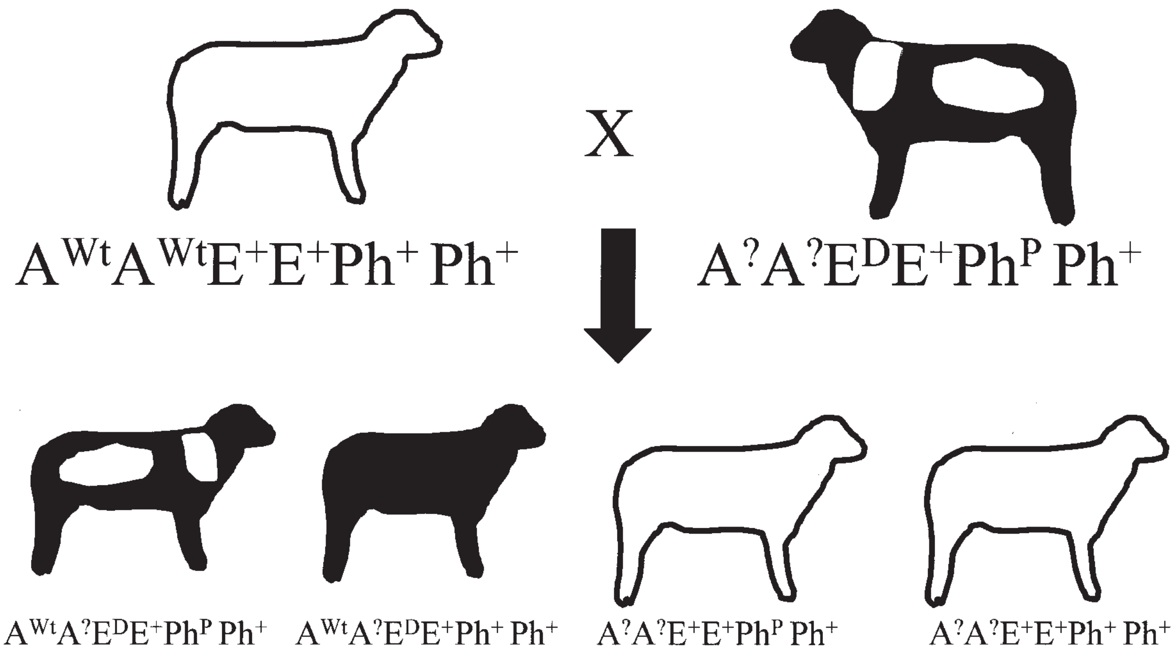

Fig. 4

Figure 4. When ewes of white wool breeds are mated to spotted Dorper rams that are heterozygous at both the *E* and *Ph* loci, the resulting lambs are expected to be 50% white, 25% black, and 25% spotted.