

Baa, Baa, Black Sheep or How Inheritance Works

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Genetics is the science of heredity. It seeks to explain differences and similarities exhibited by related individuals. The application of genetics to livestock improvement is known as **animal breeding**. The objective of this article is to provide a refresher course on basic genetics and show how a knowledge of genetics can be used to improve sheep production now and in the future.

Basic Principles of Inheritance

Genes are the basic units of inheritance and, as such, form the link between generations. Genes are located on microscopic, threadlike structures called **chromosomes**. Chromosomes, and thus, genes, occur in pairs in the nucleus of all body cells. Each gene pair occupies a specific location on a particular chromosome pair. Each species has a characteristic number of chromosomes and all normal individuals of that species will have the same number of chromosomes. In sheep, every body cell contains 27 pairs for a total of 54 chromosomes. Each of the chromosomes carries many genes. Think of genes as beads on the various chromosome strings.

Chemically, chromosomes are made up of **DNA** (deoxyribose nucleic acid), and genes are specific portions of the DNA molecule. Each biochemical reaction that occurs within an animal's body is controlled by a particular gene or set of genes. Specifically, genes control the synthesis of proteins, which, in turn, operate as enzymes in controlling cell development and function.



Geneticists now have a 'virtual' DNA map of almost the entire sheep genome. This will enable them to pinpoint the genetic controls for economically important production traits. While most unique genes are not yet identified, the sequence of nucleotides (the building blocks of DNA), is known for a short distance at more than 50,000 places along the sheep genome. Identification of the variations in these sequences (called single nucleotide polymorphisms—SNPs and pronounced 'snips') is the next step toward identifying the actual genes and their roles in controlling specific sheep production traits. Using a genomic tool called the Ovine SNP₅₀ BeadChip (Illumina, Inc.), researchers are able to characterize the small genetic differences that produce a wide range of economically important traits in sheep, such as improved growth rate, fertility, parasite resistance, and healthier meat products. This has the potential to transform the way producers select and breed sheep in the future.

Although genes occur in pairs and both members of a pair act cooperatively to produce effects in an animal, genes are transmitted from parent to offspring not in pairs, but singularly. During the formation of the sex cells, the egg and sperm, the genes of a pair, separate or go apart. This is known as **segregation**. As a result, the sex cells each contain only one member of a gene pair.

Which gene of a pair goes to an egg or sperm is simply a matter of chance.

When the egg and sperm unite at fertilization, the genes of a pair recombine in the offspring. In this process, the sex cells are, in effect, paired in the body cells of the offspring. Thus, half of an individual's genes come at random from the sire and half come at random from the dam. It is this chance segregation of genes in the production of sex cells and their **recombination** at fertilization that is the main cause of genetic differences among related individuals.

Inheritance of Wool Color: An Example

A simple example involving color inheritance in sheep illustrates the segregation of a gene pair in sex cells and the subsequent recombination of the genes in the offspring. For illustrative purposes, we will assume this trait is determined by a single pair of genes.

The two genes involved are a gene for white wool, symbolized by W, and a gene for black wool, symbolized by w. Each sheep will have two genes for this trait. The two genes will be located on one of the 27 chromosome pairs, with one gene on one member of the chromosome pair and the other gene at the same location on the other member of the chromosome pair. There are three possible gene combinations (**genotypes**) for the two genes being considered. These are shown in Table 1 (pg 21).

Table 1. Possible Gene Combinations for Wool Color Example

Genotype	Phenotype
WW	White-wooled
Ww	White-wooled
ww	Black-wooled

However, only two *phenotypes*, white-wooled and black-wooled, are distinguishable. Phenotype refers to the appearance or measured performance of an individual for a trait.

Notice the phenotypes of sheep with genotypes WW and Ww are indistinguishable. The gene for white wool, W, is said to be a *dominant* gene because it masks or covers up the effect of the gene for black wool, w, which is called a *recessive* gene. Because the W gene is dominant over the w gene, black-wooled sheep must have the phenotype ww.

During reproduction, each parent transmits either a W or a w gene to the offspring. A sheep with genotype WW can only transmit a W gene to its offspring. Likewise, a sheep of genotype ww can only transmit a w gene to its offspring. Individuals with either of these two genotypes are said to be *homozygous* for this pair of genes because both genes of the pair are alike.

However, a sheep with genotype Ww can transmit either a W or a w gene to its offspring. Individuals with genotype Ww are said to be *heterozygous* for this pair of genes because the two genes of the pair are different. Heterozygous individuals are sometimes referred to as ‘carriers’ because their genotypes carry the recessive gene. On average, a sheep of genotype Ww will transmit the gene for white wool (W) to half its offspring and the gene for black wool (w) to the other half. As a result, the chance, or probability, an individual with genotype Ww will transmit the w gene to any one offspring is $\frac{1}{2}$.

Probabilities

Using this information, the next step is to illustrate how genes of a pair recombine in the offspring when the egg and sperm unite at fertilization. With the three genotypes possible for a trait controlled by a single pair of genes (Table 1), it is possible to have six different kinds of matings (Table 2). Because the reproductive process ensures one gene from each gene pair will be transmitted to each sex cell and because chance determines

Table 2. Possible Matings and Expected Genotypic and Phenotypic Ratios for Wool Color Example

Mating Type	Expected Ratios Among Offspring
WW (white-wooled) x WW (white-wooled)	All WW (white-wooled)
WW(white-wooled) x Ww (white-wooled)	1 WW to 1 Ww (all white-wooled)
WW (white-wooled) x ww (black-wooled)	All Ww (white-wooled)
Ww (white-wooled) x Ww (white-wooled)	1 WW (white-wooled) to 2 Ww (white-wooled) to 1 ww (black-wooled)
Ww (white-wooled) x ww (black-wooled)	1 Ww (white-wooled) to 1 ww (black-wooled)
ww (black-wooled) x ww (black-wooled)	All ww (black-wooled)

the union of egg and sperm at fertilization, the expected offspring genotypic ratios can be found using simple probabilities. For example, consider the mating of two heterozygous (Ww) white-wooled sheep. What is the chance, or probability, of getting offspring of the three possible genotypes, ‘WW, Ww, and ww’?

Two basic probability rules can be used to answer this question. First, the chance, or probability, two independent events will occur together is the product (multiplication) of the chance, or likelihood, of each separate event. Second, the chance of occurrence of one or the other of two mutually exclusive events is the sum (addition) of the chances of each event occurring separately.

Half of the sex cells produced by heterozygous white-wooled sheep (Ww) will contain the gene for white wool (W) and the other half will contain the gene for black wool (w). The chance of the sperm carrying the w gene is $\frac{1}{2}$ and the chance of the egg carrying the w gene is also $\frac{1}{2}$ in this mating. Thus, using the first probability rule, the chance of a lamb from this kind of mating being black-wooled (ww) is $\frac{1}{2} \times \frac{1}{2} = \frac{1}{4}$. Likewise, the chance of a lamb from this kind of mating being homozygous white-wooled (WW) is also $\frac{1}{4}$.

There are two ways of producing a lamb with the genotype Ww. A lamb will be heterozygous white-wooled if the sperm carries the W gene and the egg carries the w gene (which using the first probability rule will occur $\frac{1}{2} \times \frac{1}{2} = \frac{1}{4}$ of the time) or if the sperm carries the w gene and the egg carries the W gene (which will also occur $\frac{1}{4}$ of the time). Finally, using the second probability rule, the chance of a lamb being Ww from this type of mating is the sum of the chances of each event occurring separately, $\frac{1}{4} + \frac{1}{4} = \frac{1}{2}$.

On the average, the mating of two

heterozygous white-wooled sheep would be expected to produce one WW (white-wooled) to two Ww (white-wooled) to one ww (black-wooled) offspring when four lambs are produced. Although both parents are white-wooled phenotypically, there is a one-in-four chance a mating of this type will produce a black-wooled (ww) offspring. Thus, heterozygous individuals do not breed true. White-wooled sheep are known to carry the black wool gene if they have at least one black-wooled lamb or if one of their parents is black-wooled.

All possible crosses involving the three genotypes, with the expected lamb genotypes and phenotypes for each, are illustrated in Table 2. The expected offspring ratios can be obtained using the same procedure as was used to obtain the offspring ratios for the mating between heterozygous (Ww x Ww) white-wooled sheep.

Types of Traits

Qualitative Traits. Color inheritance (white versus black wool) has been used to illustrate basic genetic principles involved in the transmission of characteristics from parent to offspring because only a single pair of genes is involved. In addition to wool color, several other traits in sheep are determined by one or only a few pairs of genes. The presence or absence of horns and some genetic defects, such as parrot mouth, inverted eyelids (entropion), and cryptorchidism, are also examples of traits in which one pair of genes has the major influence. In these examples, non-genetic or environmental factors have very little influence on phenotypic expression. Also, sharp distinctions usually exist between phenotypes.

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Quantitative Traits. Most traits of economic importance in sheep production (growth rate, feed efficiency, fleece weights, carcass characteristics, etc.) are controlled by many pairs of genes, the exact number of which is still not known. In addition, there is often no sharp distinction between phenotypes. To complicate matters further, environmental factors, such as nutrition, climate, and disease, may have a large effect on the phenotypic expression of these traits. Birth weight, 60-d weaning weight, yearling weight, and grease fleece weight are all examples of quantitative traits in sheep.

Inheritance of a Quantitative Trait

Inheritance of a quantitative trait is more complex than that of a qualitative trait, such as wool color, because of the increased number of genes involved. Thousands of gene combinations are possible in any animal. In quantitative traits, genes may act *additively* and individual gene effects are often small. When genes act additively, their effects can be compared to adding block upon block in constructing a building. Although the principles of segregation and recombination still hold, it is currently still impossible to identify individual genes and determine specific genotypic ratios in quantitative traits.

Yearling Grease Fleece Weight:

An Example

The following simple, hypothetical example illustrates the concept of quantitative inheritance. Suppose yearling grease fleece weight in sheep is influenced by two pairs of genes (one pair at the A locus and the other pair at the B locus) with additive [$AaBb = \frac{1}{2} (AABB + aabb)$] and equal ($A = B$) gene effects. Also, environmental effects are assumed to be the same for all genotypes. Phenotypic values are assigned to genotypes to reflect these assumptions.

Suppose individuals with genotype *aabb* have yearling grease fleece weights of 8 lb and every A or B gene contributes 2 lb to an individual's yearling grease fleece weight. Thus, individuals with genotype *AABB* would have yearling grease fleece weights of 16 lb. If individuals with genotype *AaBb* (12 lb) are mated together, the expected genotypic and phenotypic ratios among the offspring produced are shown in Table 3.

Table 3. Expected Genotypic and Phenotypic Ratios for Yearling Grease Fleece Weight Example (AaBb x AaBb)

Genotypes	Yearling Grease Fleece Weight (lb)
1 AABB	16
2 AABb	14
2 AaBB	14
1 AAbb	12
4 AaBb	12
1 aaBB	12
2 Aabb	10
2 aaBb	10
1 aabb	8

Notice the individuals that were mated have yearling grease fleece weights of 12 lb and the average yearling grease fleece weight of the lambs produced is also 12 lb. However, considerable variation exists among the offspring (grease fleece weights range from 8 to 16 lb).

A Word of Caution

It is important to realize this illustration is oversimplified. Most quantitative traits, like yearling grease fleece weight, are influenced by other types of gene action, such as dominance and epistasis (genes at one locus influence the action of genes at another locus), in addition to the additive gene action illustrated here. Also, yearling grease fleece weight in sheep is influenced by many pairs of genes and the contribution of the different gene pairs may vary. Furthermore, yearling grease fleece weight is influenced by breed, as well as environmental factors, such as feeding level, season, and climate.

All of these factors tend to complicate the genotypic expression of the individual. In reality, the phenotype of a quantitative trait may not reflect the genotype directly because of environmental and non-additive genetic effects.

Genetic Improvement Through Selection

Genetic improvement results from selection and is possible because different genotypes tend to determine different phenotypes. Because genotypic expression is often limited or exaggerated by environmental effects in quantitative traits, their genetic improvement is more

complicated than genetic improvement of qualitative traits. Not all of the phenotypic differences exhibited by parents are transmitted to their offspring.

Heritability

The proportion of the phenotypic differences among animals for a specific trait that is transmitted to their offspring is known as *heritability*. The higher the heritability for a trait, the more rapid the rate of genetic improvement for that trait. Heritability values may range from 0 to 100%. Generally, reproductive traits are lowly heritable (0 to 20%), growth traits are low to moderately heritable (20 to 40%), and fleece and carcass traits are moderate to highly heritable (30 to 60%). Estimates of 30% for weaning weight and 40% for yearling weight indicate selection should be fairly effective for these traits. However, it is important to realize traits vary in heritability and, as a result, rates of genetic improvement will vary, depending on the specific trait involved.

Breeding Values

Heritability can be used to estimate an animal's *breeding value* (EBV). Every animal has a breeding value for each trait. Breeding values represent the total additive effect for all genes influencing the phenotype for a specific trait. In other words, breeding values are a measure of gene transmitting ability. Unfortunately, we cannot observe an animal's breeding value directly.

Breeding values can be estimated as the difference between the individual animal's performance and the average of its contemporary group (*selection differential*) multiplied by the proportion of the difference expected to be transmitted to the offspring (*heritability* for the trait). Because the breeding value is an estimate of what an individual is expected to transmit to its offspring for a particular trait, those animals with the highest breeding values should be expected to produce the most desirable progeny. As a result, they increase the frequency of desirable genes in the flock or breed.

Because an animal contributes only half its genes to its offspring, an individual transmits only half its breeding value. For example, if a ram has a breeding value of 12 lb for weaning weight, on the average he should transmit 6 lb of that to his progeny.

In other words, if this ram was mated to a random sample of ewes, the resulting progeny are expected to be 6 lb above average for weaning weight. This value (one half of the breeding value) is referred to as the **expected progeny difference (EPD)**.

Estimated breeding values are most useful for comparing genetic merit between individuals within the same breed. Suppose the ram in the previous example (weaning weight EBV = 12 lb; EPD = 6 lb) is compared to a ram having a weaning weight EBV of 4 lb (EPD = 2 lb). We would expect an average difference of 4 lb (6 - 2 lb) in the weaning weights of their offspring, with the advantage going to the first ram. The ram with the highest EBV (EPD) wins.

When available, performance of relatives (progeny, siblings, ancestors) can be used to estimate the genetic merit of an animal. For example, information from the individual, paternal half-sibs, maternal half-sibs, and progeny can be combined into a single estimate of the individual's EBV for a specific trait. Including information on relatives, in addition to the individual's own performance, will increase the accuracy

of EBV estimation, especially for lowly heritable traits. When the heritability of a trait is moderately high, the individual's own record is more important and the improvement in accuracy is less.

Presently, the National Sheep Improvement Program (NSIP), in conjunction with Australia's LambPlan, calculates EBV for maternal, growth, and wool traits using information on the individual, ancestors, collateral relatives, and progeny. These EBVs can be used to make genetic comparisons among the animals evaluated within a breed. Currently, breeds participating in NSIP/LambPlan include Border Leicester, Columbia, Dorper/White Dorper, Dorset, Hampshire, Katahdin, Lincoln, Oxford, Polypay, Rambouillet, Shropshire, and Sufflok.

Summary

Understanding the basic principles of inheritance is necessary if producers are to use genetic tools for sheep improvement. Although the basic principles hold for all traits, the inheritance and genetic improvement of a quantitative trait, such

as yearling grease fleece weight, weaning weight, yearling weight, etc., is more complex than that of a qualitative trait, such as wool color. Traditional selection, based on estimation of genetic merit using the individual's phenotype and information on relatives, has resulted in improved sheep production. This has been enhanced by breed-wide genetic evaluations conducted by the National Sheep Improvement Program and LambPlan. In the future, genetic improvement in economically important traits may be accelerated even further using genomic tools for direct selection of genetic differences underlying phenotypes.

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