Colour Genetics

Dogs have probably been domesticated for at least 15 000 years. The first dogs likely had an appearance much like the wolf or coyote. However, over the time they have been domesticated, considerable selective breeding by humans has taken place to produce a wide array of sizes, colours and other characteristics that are the breeds we recognize today. All domestic dogs are the same species and theoretically can interbreed to produce a mutt (also known as a mixed breed dog). This is much like all humans are the same species and can reproduce regardless of skin colour, hair colour, size or shape. While all pets should be valued whether they are pure bred or mutts, we have a particular interest in protecting the breeds that have developed over hundreds to thousands of years of careful breeding.

Each dog breed has a specific set of characteristics that have been selected for and identify the breed, including coat colour and type, body size, shape, instincts such as herding and retrieving, and personality characteristics such as protectiveness, loyalty, etc. that are well-defined in the breed standards of the kennel clubs of the world. Each characteristic has a genetic basis to it. For some we understand well the genes and heritability, while for others we have years of breeding experience but little to no scientific understanding as to their basis.

The study of coat colour in dogs is one interesting, yet complex genetic undertaking. One need only look at the variability in the coat colour and texture among several breeds to understand that there must be interplay of many different genes to produce the unique breed-specific appearance. We do have considerable understanding of the coat type and colour genes in dogs, however there are many things we still have not fully uncovered. Many breeds have only one or a very few acceptable coat colours, for example the Rottweiler, Collie or Labrador Retriever. The Pomeranian is a unique breed in that there is a broad spectrum of coat colours that are accepted in the breed standard. This wide array of brilliant colours plays at least a part in the popularity of the breed. In order to understand the basics of Pomeranian coat colour, we must first digress into a brief lesson on basic genetics. By no means an exhaustive lesson in the intricacies of gene expression and heritability, we will simply introduce a few basic terms and concepts to help the reader understand a few fundamental concepts. We will start with a few definitions and then a description of basic Mendelian genetics, before we return to the complex example of coat colour in the Pomeranian.

Definitions:

1. DNA—the genetic material in the nucleus of the cell whose sequence encodes the genes.

2. Chromosome—discrete 'pieces' of DNA sequence that encode hundreds or thousands of genes. Humans have 23 pairs of chromosomes; 46 in total. That is 22 pairs of autosomal chromosomes and a pair of sex chromosomes: one X and a second X for a female or a Y for a male. Dogs have 78 chromosomes, or 38 autosomal pairs and 1 sex pair. One X chromosome and 22 autosomal chromosomes for the human, 38 for the dog, are inherited from the mother. One X (for a female) or one Y (for a male) and 22 autosomal chromosomes for the human or 38 for the dog are inherited from the father. Collectively the offspring inherits it full complement of 46 (human) or 78 (dog) chromosomes from both parents.

3. Gene—a sequence of DNA that encodes a particular protein. A 'mutation' or change in the sequence in the DNA of the gene can result in a change in the sequence of the protein and cause an altered structure or function in the protein product.

4. Protein—a sequence of amino acids encoded for by a gene. Proteins encoded in the genes of DNA include enzymes that carry out all biological reactions and processes in the cell, transporter proteins that move molecules around and in and out of the cell, structural molecules, signaling molecules and others.

5. Allele—a single distinct form of a gene, of which there may be 2 or more possibilities. Generally, all animals have 2 copies of each gene, or 2 alleles of each gene encoded in their DNA, one inherited from their mother and one from their father (an obvious exception is genes encoded on the X chromosome where in males there is only one chromosome and thus there is only one allele. The alleles inherited from the mother and father may have the same or a different sequence. There may be only one possible allele for a gene, there may be 2 or many more possible alleles.

6. Locus—the position of a gene (or other significant sequence) on a chromosome.

7. Genotype—the genetic make-up of an animal. This includes all genes received from the mother and father and includes recessive genes that aren't visible in the appearance of the animal. Not all animals that look alike necessarily have the same genotype.

8. Phenotype—the specific set of characteristics that are encoded by the genes that are expressed, i.e. the genetic characteristics that we can see by looking at the animal. All animals that look alike have the same phenotype, but not necessarily the same genotype.

9. Dominant—the form of the gene that is expressed as the phenotype when present in one or both alleles.

10. Recessive—the form of the gene that is expressed only in the absence of the dominant form, i.e. must be present in both alleles to be expressed.

11. Mutation—a genetic change in a region of a gene that may result in the change in the sequence of the protein for which it encodes.

12. Melanin—the pigmentation in hair and skin that gives it its colour. It is produced by enzymatic reactions carried out by protein enzymes encoded by genes.

13. Eumelanin—type of genetically encoded melanin that results in black/brown pigmentation in the hair.

14. Phaeomelanin—type of genetically encoded melanin that results in red/yellow/cream pigmentation in the hair.

15. Sable—colour variation in the individual strands of hair that results in both eumelanin and phaeomelanin being expressed. Typically a sable dog will express at least some hair that, as result of the ay agouti gene, undergoes pigment switching during its growth such that there is cream/yellow/red colour near the base with dark tips and there can also be solid black hairs intermingled with the redish hairs.

16. Wolf sable—Wildtype form of the Agouti gene (aw) in wolves and coyotes but more rare in dogs. Seen in the Eskimo dog as well as the wolf sable Pomeranian among a few other examples. A wolf sable has banded hairs that are black-reddish-black. In most cases the reddish region is very light to silver in colour. Therefore the coat generally has a black and silver appearance with little orange colour.

'Simple' Mendelian genetics

Gregor Mendel was a 19th century Austrian monk who studied the genetic characteristics of garden pea plants (Pisum sativum) and from these studies developed the clearest understanding of heritability of traits of his time. For many genes his general concepts still hold true today. In the mid 1800s, Mendel crossed tens of thousands of pea plants and studied their discrete characteristics. Mendel studied yellow and green seed skin, wrinkled or smooth seed skin, large and small plant size, white and purple flowers and many other characteristics. By crossing pea plants exhibiting these characteristics he developed the Principles of Mendelian Inheritance which were published in 1866. The work was dismissed as it was largely considered to be only applicable in very rare instances. Later, however, as our understanding of genetics improved, it became clear that Mendelian genetic principles are widely applicable across species for a broad array of genetic traits.

Mendel had no understanding that DNA was the genetic material or that offspring inherited one set of chromosomes and allele for each gene from the mother and a second set of chromosomes containing a second allele for each gene allele from the father. He deduced correctly, however, from his crosses that each parent transmitted one factor for a given trait from the mother and a second factor for the same trait from the father. There were two types of traits, one considered dominant and one considered recessive. The dominant trait is visible whenever it is present, whereas for a recessive trait to show (be seen as the phenotype) it must be present in 2 copies, that is it must be inherited from both the mother and the father.

Mendel's first law is the law of segregation. It essentially states that when an individual produces offspring, each offspring will randomly inherit one set of traits from it. The other set comes from the other parent. Mendel's second law is the law of independent assortment. This law states that individual genetic traits segregate independently of one another when they are passed to the offspring. In general these two laws hold true, though there are some exceptions to these laws in certain specific circumstances. In general we can assume for our purposes here describing Pomeranian coat colour that these rules hold true unless I otherwise specify for specific examples.

A reasonable example of dominant and recessive traits can be found in the garden pea that Mendel studied, where the flower can be white or purple. Mendel took a line of pea plants producing white flowers for many generations and it was crossed with plants producing purple flowers for many generations. See figure below. If the concept of dominance didn't exist, we might expect that all of the flowers on the first generation progeny would be a light purple, which is a blend of the white and purple traits from the parents. This of course was not the case. In fact, in the first generation all of the plants produced purple flowers of the same intensity as the purple-flowered parent. Mendel then went on to cross these plants and examined the flowers of their offspring. In what may have been quite a surprise at the time, he consistently found a ratio in the second generation offspring of 3:1 purple: white, with no mixed colour flowers. We now know that the purple flower colour is dominant and the white is recessive. Therefore we can understand the results if we draw out the experiment as shown below: Each plant in the first generation inherits one white copy of the flower colour gene and one allele for the purple colour. Therefore in this generation, all plants show the dominant colour, purple. But they still have one copy of the recessive white allele. When these plants are crossed, as we see from the figure, ¼ of their offspring inherit two copies of the purple allele and produce purple flowers. ½ of the plants inherit one of each allele and produce purple flowers, and ¼ inherit 2 copies of the white allele and produce white flowers. This gives the 3:1 ratio. It is important to realize that not all of the plants with purple flowers are genetically identical as 2 of the 3 could produce white offspring if crossed with other plants carrying a white allele. The plant with 2 purple alleles can't produce white offspring. It is only when the plants are bred can we determine what the genetics of the purple flowers truly are.

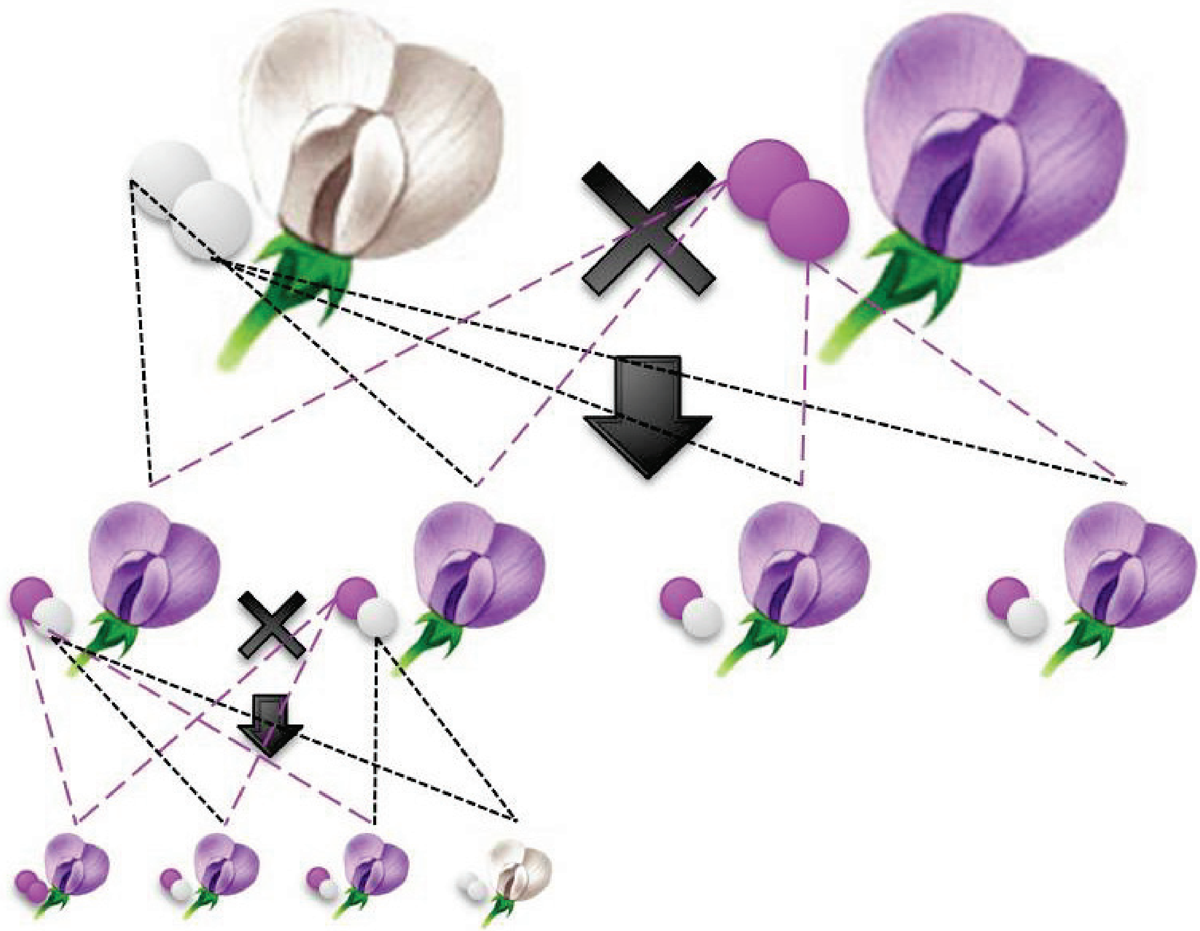

Figure 1. Mendel's pea flower crossings. The top row represents the cross between a true breeding white flower pea plant and a true breeding purple flower pea plant. Circles represent the colour produced by the alleles of each plant. The first generation cross results 100% purple flowers that carry one of each alleles. However, when two first generation progeny are crossed, we find the second generation progeny occur in a ratio of 3:1 purple: white. We see that the white and ¼ of the purple are homozygous, meaning that they carry only alleles for one colour. ½ of the second generation are heterozygous, meaning they carry two different alleles, but they still appear as purple. The only way to distinguish the genotypes of the two different types of the purple progeny is by future breedings. The phenotypes of the purple flowered plants are identical. But how do we explain why white is recessive to purple? Imagine that there is an enzyme that is produced by one particular allele of the purple flower colour gene. When normal, this enzyme produces a pigment that has a purple colour and this colour gets distributed in the petals of the flower making it purple. Now, if another allele, say the white allele, had a different gene sequence where there is a mutation that renders the enzyme defective, it would not be able to produce any purple coloured pigment and thus the flowers would remain white. When the functional purple allele is present in both alleles inherited from the parents, or even when just inherited from one parent, purple pigment will be produced from that functional enzyme. Only when both alleles encode the defective enzyme would the flowers be white, and thus we see purple as being dominant over white.

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Incomplete dominance and co-dominance.

Many traits follow the simple dominant-recessive scheme that Mendel described. However not all do in all species.

Sticking with flower colour, a suitable example is the Mirabilis jalapa (Four O'clock) flower. In this case, we see co-dominance. Take the case of white and red flowers. When we cross true breeding white with true breeding red, rather than getting all red as in the pea plant example, we see both genes expressed and we see pink flowers. In the second generation, we see ¼ red, ¼ white and ½ pink flowers. The red gene is incomplete dominant because the phenotype is intermediate between the two. Very similar is the concept of incomplete dominance is co-dominance where the offspring expresses a phenotype that has traits of both alleles. For our purposes there is little difference between incomplete dominance and co-dominance. A good example of co-dominance is the human ABO blood groupings, where a person can be AB if they receive the A type from one parent and the B type from the other. **Armed with an understanding of these basic concepts, we can begin to examine the genetics of coat colour in the Pomeranian…to be continued shortly...**

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