HOW TO GET WHAT YOU WANT FROM YOUR BREEDING PROGRAM

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"It is accomplished by understanding whose genes are most influential, and how to secure them!"

IT'S ALL IN THE GENES

As dog breeders, we all engage in genetic "experiments" each time we produce a litter of pups. To some breeders, determining which traits will appear in the offspring of a mating is like rolling the dice - a combination of luck and chance. For others, producing certain traits involves more skill than luck - the result of careful study and planning. In order to understand (1) how we manipulate genes within our breeding stock to produce the kinds of dogs we want and (2) why it's important for our breeding programs to do so, we have to first understand dogs as a species, then dogs as genetic individuals. The species, Canis Familiaris, includes all breeds of domestic dogs. Although we can argue that there is little similarity between a Chihuahua and a Saint Bernard, or that established breeds are separate entities among themselves, they all are genetically the same species. Therefore, while a mating within a breed may be considered an outcross, it still must be viewed as part of the whole genetic picture: a mating within an isolated, closely related interbred population. When evaluating your breeding program, remember that most traits you're seeking cannot be changed, fixed or created in a single generation. The more information you can obtain on how certain traits have been transmitted by your dog's ancestors, the better you can prioritize your breeding goals. Tens of thousands of genes interact to produce a single dog. All genes are inherited in pairs, one from the father and one from the mother. If the pair of inherited genes from both parents is identical, the pair is called homozygous. If the genes in the pair are not alike, the pair is called heterozygous. Fortunately, the gene pairs that make a dog a dog and not a cat are always homozygous. Similarly, the gene pairs that make a certain breed always breed true are also homozygous. Therefore, a large proportion of homozygous non-variable pairs - those that give a breed its specific standard - exist within each breed.

What genetic manipulations have occurred to create the different breeds? Each breed was developed by close breeding and inbreeding among a small group of founding canine ancestors, either through a long period of genetic selection or by intensely inbreeding a smaller number of generations. The process established the breed's characteristics and made the dogs in it breed true. Breeding closely related individuals increases the chance that identical genes from a common ancestor will be passed down both the sire's and the darn's sides of the pedigree.

BREEDING BY GENOTYPE

Such genetic manipulation is called inbreeding (and its less intense form, linebreeding). Inbreeding creates greater homozygosity in the offspring and fixes desirable traits. It also allows for greater expression of recessive genes that are not expressed in the heterozygous state. If a recessive gene (a) is rare in the population, it will almost always be masked by a dominant gene (A). Through inbreeding, a rare recessive gene (a) can be passed from a heterozygous (Aa) common ancestor through both the sire and dam, creating a homozygous recessive (aa) offspring. Unfortunately, undesirable recessive genes can also become fixed through inbreeding. However, inbreeding does not create undesirable genes, it simply increases the expression of those that are already present in a heterozygous state. A tendency toward disorders controlled by multiple genes, such as hip dysplasia and congenital heart anomalies, can be exacerbated by inbreeding.

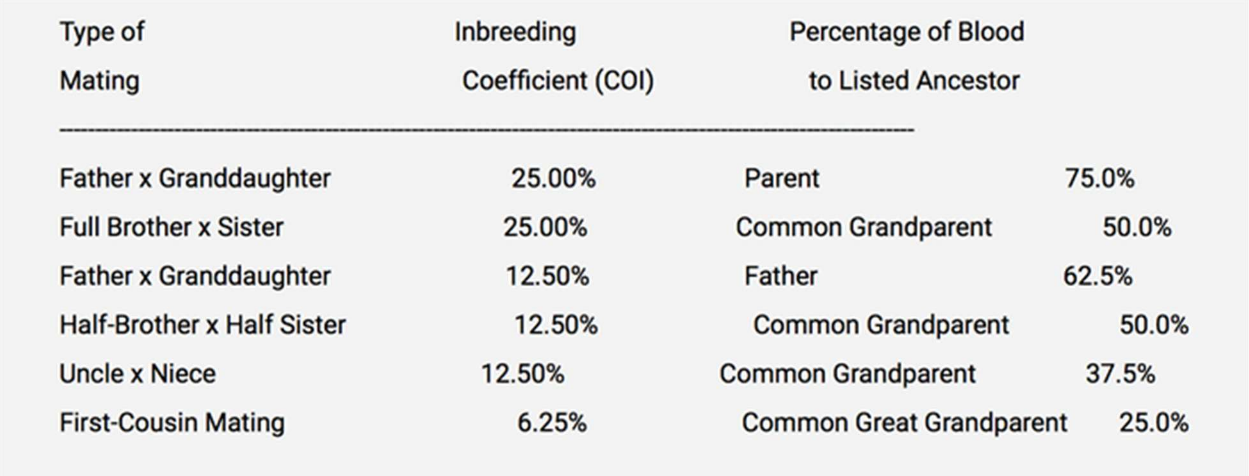
Geneticists' and breeders' definitions of inbreeding vary. A geneticist views inbreeding as a measurable number (called the "inbreeding coefficient" or Wright's coefficient) that goes up whenever there is a common ancestor between the sire's and dam's sides of the pedigree; a breeder considers inbreeding to be close inbreeding, such as father-to-daughter or brother-to-sister matings. A common ancestor, even in the eighth generation, will increase the measurable amount of inbreeding in the pedigree. (The process of calculating coefficients is too complex to present here. Lists of inbreeding coefficients based on different types of matings are indicated in Table 1 for general reference. Several books that include how to compute coefficients are indicated at the end of this article; some computerized canine pedigree programs also compute coefficients.)

[RCI Note: CompuPed v4.0 computes Wrights Inbreeding Coefficient faster and more accurately than any other PC program available.]

The inbreeding coefficient is an estimation of the percent of the variable gene pairs that are homozygous due to inheritance from common ancestors. It can also be viewed as the average chance that any one gene pair is homozygous due to inheritance from a common ancestor.

To visualize some of the concepts in this article, please refer to Pedigree 1, the pedigree of Gordon Setter "Laurel Hill Braxfield Bilye". Notice that the paternal grandsire, CH Loch Adair Foxfire, and the maternal granddam, CH Loch Adair Firefly, W.D, are full siblings, making this a first-cousin mating. As indicated in Table 1, this relationship contributes 6.25 percent to the pedigree's inbreeding coefficient.

TABLE 1: Coefficients for Sample Mating



Type of Mating	Inbreeding Coefficient (COI)	Percentage of Blood to Listed Ancestor	
Father x Granddaughter	25.00%	Parent	75.0%
Full Brother x Sister	25.00%	Common Grandparent	50.0%
Father x Granddaughter	12.50%	Father	62.5%
Half-Brother x Half Sister	12.50%	Common Grandparent	50.0%
Uncle x Niece	12.50%	Common Grandparent	37.5%
First-Cousin Mating	6.25%	Common Great Grandparent	25.0%

For the calculated inbreeding coefficient of a pedigree to be accurate, it must be tabulated from a number of generations. This is because inbreeding in the fifth and later generation (background breeding) often has a profound effect on the genetic makeup of the offspring represented by the pedigree.

In studies conducted on dog breeds, the difference in inbreeding coefficients based on four versus eight generation pedigrees varied immensely: a four generation pedigree containing 28 unique ancestors for 30 positions in the pedigree could generate a low inbreeding coefficient, while eight generations of the same pedigree, which contained 212 unique ancestors out of 510 possible positions, would have had a considerably higher inbreeding coefficient.

Knowledge of the depth of the pedigree may alter how you view it. What seemed like an outcrossed mix of genes in a couple of generations will appear as a linebred concentration of genes from influential ancestors in extended generations.

Look again at the sample pedigree (Pedigree 1). An inbreeding coefficient based on four generations computes to 7.81 percent. This is not significantly increased from the estimate of 6.25 percent based on the first-cousin mating alone. Inbreeding coefficients based on increasing numbers of generations are as follows: five generations, 9.86 percent; six generations, 16.64 percent; seven generations, 20.38 percent; and eight generations, 23.22 percent. Based on eight generations, there are only 106 unique ancestors for 510 possible positions in the pedigree. The inbreeding coefficient of 23.22 percent is close to what you would find in a parent-to-offspring mating. As you can see, the background inbreeding has far more influence on the total inbreeding coefficient than the first-cousin mating, which only appears to be its strongest influence.

In order to determine whether a particular mating is an outcross or inbreeding relative to your breed, you must determine the breed's average inbreeding coefficient. The average inbreeding coefficient of a breed will vary depending on the breed's popularity or the age of its breeding population.

Rare or recently introduced breeds usually have an inherently higher average inbreeding coefficient. (They have a limited number of potential breeding stock available to breed to, thus they share more common ancestors.) Popular, more established breeds usually have a lower average inbreeding coefficient because they have access to a wide availability of relatively non-related breeding stock.

A mating with an inbreeding coefficient of 10 percent, based on an eight-generation pedigree, would be considered moderate inbreeding for a Labrador Retriever (a popular breed with a low average inbreeding coefficient), but would be considered an outcross for an Irish Water Spaniel (a rare breed with a higher average inbreeding coefficient).
The average inbreeding coefficient for Gordon Setter pedigrees, based on an eight-generation pedigree, is 16.36 percent. Therefore, our sample pedigree (Pedigree 1) is relatively inbred compared to the average for the breed.

Knowledge of the degree of inbreeding in a pedigree does not necessarily help you unless you know whose genes are being concentrated. The relationship coefficient measures the relatedness between an ancestor and the individual represented by the pedigree. A relationship coefficient estimates the probable percentage of genes passed down from a common ancestor. We know that a parent passes on an average of 50 percent of its genes, while a grandparent passes on 25 percent, a great-grandparent 12.5 percent, and so on. For every time the ancestor appears in the pedigree, its percentage of passed-on genes can be added up and its "percentage of blood" estimated. The right-hand column in Table I shows the percentage of blood for ancestors of different types of matings.

The relationship coefficient will vary from the percentage of blood due to differences in the inbreeding coefficients between the ancestor and the pedigree as a whole. For example, if the ancestor has a higher inbreeding coefficient (and, therefore, greater homozygosity, then a single gene passed from a homozygous pair will always represent the ancestor.

Breeders have a greater chance of reproducing an ancestor through linebreeding, and the relationship coefficient will be higher than the percentage of blood. If the ancestor is relatively outcrossed (and, therefore, has a greater heterozygosity), then a single gene from a heterozygous pair of the ancestors will only represent 50 percent of the types of genes available to its offspring. Such a dog's descendants will have fewer total genes that will be the same as those of the ancestor. Its relationship coefficient will reflect this by being lower than its percentage of blood.

In the sample pedigree, the common great-grandparents, CH Sutherland Gallant and CH Sutherland Lass of Shambray, have a percentage of blood of 25 percent based on their being the parents of both CH Loch Adair Foxfire and CH Loch Adair Firefly, W.D. Referring to a pedigree analysis of the sample pedigree (Table 2), their relationship coefficients are higher than the percentage of blood. This is because both of their own inbreeding coefficients were higher than that of the sample pedigree. Through greater homozygosity, they are able to pass on a greater percentage of their total genes to their descendants.

Increasing an individual's homozygosity through linebreeding may not, however, reproduce an outcrossed ancestry. If an ancestor is outcrossed and generally heterozygous (Aa), increasing homozygosity will produce more AA and aa. The way to reproduce an outcrossed ancestor is to mate two individuals that mimic the appearance and pedigree of the ancestor's parents.

It is better for linebred ancestors to appear on both the sire's and the dam's sides of the pedigree. That way their genes have a better chance of pairing back up in the resultant pups. Genes from common have a greater chance of expression when paired with genes from other individuals, which may mask or alter their effects.

To reproduce or concentrate the genes of an ancestor, you should use a number of its offspring in the pedigree that share the ancestor's best traits. If an ancestor appears a number of times in a pedigree, but always behind the same offspring, you are only concentrating the approximately 50 percent of the genes passed from the ancestor to the single offspring. You are linebreeding on the offspring and not the ancestor. A common example of linebreeding is to have an ancestor as a triple or quadruple great-grandparent, with each appearance out of a different offspring. In many breeds, an influential individual may not appear until generations, but then will appear so many times that it necessarily contributes a large proportion of genes to the pedigree. In our sample pedigree, CH Afternod Drambuie has the highest relationship coefficient of all of the linebred ancestors. His genetic contribution to the pedigree is second only to the parents'.

He doesn't appear in the pedigree until the sixth generation, but then appears 33 times between the sixth and eighth generations. His dam CH Afternod Sue, appears 45 times between the seventh and eighth generations, and contributes almost as much of the genes to the pedigree as a grandparent. This again shows that the depth of the pedigree is very important in estimating the genetic makeup of an individual.

TABLE 2: Pedigree Analysis for LAUREL HILL BRAXFIELD BILYE

(Based on an eight-generation pedigree)

Coefficient of Inbreeding: 23.32%

1st Generation

Linebred Ancestors	Relationship Coefficient	Of appearance in pedigree	# times in pedigree
CH Afternod Drambuie	32.09%	6	32
CH Afternod Callant	26.54%	5	13
CH Sutherland Gallant	25.49%	3	2
CH Sutherland MacDuff	25.07%	3	3
CH Sutherland Lass of Shambray	25.05%	3	2
CH Afternod Sue	23.78%	7	45
Loch Adair Diana of Redchico	17.63%	5	12
CH Afternod Buchanon	17.34%	7	35
CH Afternod Hickory	14.67%	6	24
CH Afternod Woodbine	14.03%	6	15
Afternod Fidemac	13.01%	5	7
CH Afternod Amber	12.62%	5	5
CH Afternod Kate	9.37%	6	12
CH Wee Jock Adair, C.D.	9.33%	4	3
CH Hi-Laway's Calopin	8.53%	5	5
Afternod Ember of Gordon Hill	8.53%	8	23
Afternod Hedemac	8.07%	7	15
Afternod Hedera	7.79%	7	19
CH Wilson's Corrie C.D.	7.70%	7	16
CH Pages MacDonegal II	7.60%	7	19
CH Afternod Anagram	7.60%	5	4

BREEDING BY PHENOTYPE

Many breeders plan matings solely on the appearance (phenotype) of a dog and not on its pedigree or the relatedness of the prospective parents. Matings based on appearance are called “assortative matings". There are positive assortative matings (like-to-like) and negative assortative matings (like-to-unlike) for individual traits. Breeders use positive assortative matings when they wish to fix traits, and negative assortative matings when they wish to correct traits or bring in traits the breeding stock may lack.

Some individuals may share desirable characteristics, but they inherit them differently. This is especially true of polygenetic traits, such as ear set, bite or length of forearm. Breeding two phenotypically similar but genotypically unrelated dogs together would not necessarily reproduce these traits.
Conversely, each individual with the same pedigree will not necessarily look or breed alike. Therefore, breedings should not be planned solely on the basis of the pedigree or appearance alone. Matings should be based on a combination of appearance and ancestry. If you are trying

to fix a certain trait - like topline - and it is one you can observe in the parents and the linebred ancestors of two related dogs, then you can be more confident that you will attain your goal.

If a linebreeding produces a puppy with magnificent qualities, but those qualities are not present in any of the ancestors the pup has been linebred on, then the dog may have a wonderful show career, but it may not breed true. Therefore, careful selection of mates is important, but careful selection of puppies from the resultant lifter is also important to fulfill your genetic goals.

OUTCROSSING

Outcrossing (matings with a lower inbreeding coefficient than the average for the breed) tends to increase heterozygosity, matching pairs of unrelated genes from different ancestors. Most outcrossing tends to produce non-uniform litters. The exception would be if the parents are so dissimilar that they create a uniformity of heterozygosity. This is what usually occurs in a mis-mating of two breeds. The resultant litter tends to be uniform, but demonstrates "half-way points" between the dissimilar traits of the parents. Such litters may be phenotypically uniform, but will rarely breed true due to the mix of dissimilar genes.

Outcrossing can be a useful tool to bring in traits that you do not have in your breeding stock. While the parents may be genotypically dissimilar, you should choose a mate that corrects your dog's faults but phenotypically complements your dog's good traits.

It is not unusual to produce an excellent quality dog from an outcrossed litter. The abundance of genetic variability can place all the right pieces in one individual. Many top-winning show dogs are outcrosses. Consequently, however, they may have low inbreeding coefficients and may lack the ability to uniformly pass on their good traits to their offspring. After breeding an outcross, breeders should breed back to their original stock to increase homozygosity and attempt to fix newly acquired traits.

PUTTING IT ALL TOGETHER

Decisions to line-breed, inbreed or outcross should be made based on the knowledge of an individual dog's traits and those of its ancestors.

Inbreeding will quickly identify the good and bad recessive genes the parents share in the offspring. Unless you have prior knowledge of what the pups of milder line-breedings on the common ancestors were like, you may be exposing your puppies (and puppy buyers) to extraordinary risk of genetic defects.

As a geneticist, I am a proponent of linebreeding and occasional, prudent inbreeding. To breed dogs for more than one or two generations, type has to be established. In your matings, the inbreeding coefficient should only increase because you are specifically linebreeding (increasing the relationship coefficient) to selected ancestors.

If your breeding program is stagnating after several outcrosses, there is really no concrete direction you can go with it. You will have an abundance of heterozygosity, little uniformity and a diminished response to selection. Conversely, if you run into trouble with a linebreeding program, you can always outcross in one generation, which will bring in new genes and allow you to immediately change direction toward more specific goals.

Don't set too many goals in each generation, or your selective pressure for each goal will necessarily become weaker. Genetically complex or dominant traits should be addressed early in a long-range breeding plan, as they may take several generations to fix. Traits with major dominant genes become fixed more slowly, as the heterozygous (Aa) individuals in a breed will not be readily differentiated from the homozygous-dominant (AA) individuals. Desirable recessive traits can be fixed in one generation because individuals that show such characteristics are homozygous for the recessive genes. Dogs that breed true for numerous matings and generations should be preferentially selected for breeding stock. This prepotency is due to homozygosity of dominant (AA) and recessive (aa) genes.

Trying to develop your breeding program scientifically can be an arduous, but rewarding, endeavor. By taking the time to understand why you wish to linebreed on selected ancestors, you can then concentrate on those particular traits and produce a better dog.

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Further Reading

If you are interested in learning more about these subjects, consult the following books:

- Abnormalities of Companion Animals: Analysis of Heritability C.W. Foley, J.F. Lasloy, and G.D. Osweiler, Iowa State University Press, Ames, Iowa. 1979.
- Genetics for Dog Breeders F.B. Huft, W.H. Freeman Co, San Francisco, California. 1979. • Veterinary Genetics F. W. Nicholas, Clarendon Press, Oxford England. 1987.
- Genetics for Dog Breeders R. Robinson, Pergamon Press, Oxford England. 1990.
- Genetics of the Dog (equally applicable to cats & other animals) M.B. Willis, Howell Book House, Now York, New York. 1989.

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