

GRUNFELD GERMAN SHEPHERDS

INBREEDING AND DIVERSITY

By Fred Lanting

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Introduction

Jay Lush, father of modern animal breeding, stated that variation is the raw material with which breeder works. The focus of this article is on the use of variation and measures of variation, in making breeding decisions. It includes the related ideas of relationship and inbreeding, as well as systems of mating that make use of these ideas. The use of crossbreeding to introduce genetic variation into small populations will also be explained. Our goal is to provide some practical tools for genetic management and decision-making.

Most breeders keep records (pedigrees) of their animals and their animals' performance. Information such as litter size, milk production, and slaughter weight are collected when such information is of importance. The more information we have, the more informed and accurate our decisions become. This chapter will show us how to use the information at our disposal to make good decisions. As dog breeders, we are most concerned with breeding animals that typify breed standards for physical appearance, temperament, mental acuity, and similar traits. However, in most cases we only have pedigree information and a small number of recorded traits on which to base our decisions. While scientists now understand the genetic basis for moderately complex traits such as coat color and pattern, research in other species suggests that there is little or no significant genetic component to such indicators of performance as success in the show ring. The dog breeder, then, is often at a loss for accurate sources of information about performance traits he is interested in. We shall show how to make the most of what is available.

Relationship

When animals are related 'by blood', as the expression goes, they share a proportion of their genes in common. It is assumed that the genes shared in common between two related individuals have descended from the same ancestor. If that is true, the genes are termed *identical by descent* (IBD). That is, genes shared by two related individuals are identical because they have the same origin. Genes may also be what is termed *identical in state*, which means that the genes at a locus are identical in form, but did not descend from the same ancestor. The coefficient of relationship between two individuals X and Y, R_{XY} , is a measure of pedigree relationship, and may be thought of as either

- (1) the expected proportion of genes that are IBD between X and Y or
- (2) the correlation between the genotypes of X and Y based only on pedigree relationship.

The probability that genes are IBD for two individuals provides the basis for our numerical measure of relationship. We will develop the idea with an example that refers to the pedigree in Figure 1.

Figure 1. A Simple Pedigree

Bob	<i>Sire</i> Jack	<i>Sire</i> Tom
		<i>Dam</i> not applicable
	<i>Dam</i> Annie	<i>Sire</i> not applicable
		<i>Dam</i> not applicable

This pedigree says that Jack and Annie are the sire and dam of Bob. When Bob was conceived, half of his chromosomal complement was paternal in origin, and half was maternal. If you then sample one of Bob's genes at random, the probability that it is identical to one of Jack's genes is 50%, or 0.5. If we extend that sample to include the whole of Bob's genotype, we find that the relationship between Bob and Jack, denoted R_{BJ} , is 0.5. Similarly, the probability that a gene drawn at random from Bob is identical to a gene drawn at random from Tom is 0.25. This line of reasoning can be extended to find the definitions of some familiar degrees of relationship (Table 1).

Table 1. Some Common Coefficients of Relationship

<u>Relationship</u>	R_{XY}
Parent-offspring	0.5
Full sibs (siblings)	0.5
Half sibs	0.25
Grandparent-grandchild	0.25
Great grandparent-grandchild	0.125

(Full sibs share both parents; half sibs share only a single parent.)

Equations have been developed for determining the relationships between any two related individuals, and may be found in a text on basic animal breeding. In the simplest case, the relationship between two individuals that are only related through a single line of descent is $(\frac{1}{2})^n$, where n is the number of steps between the two in the pedigree. For example, there is a single step between parent and offspring, so $R_{XY} = (\frac{1}{2})^1 = \frac{1}{2}$. In the case of half-sibs, there are two steps in the pedigree: one from the first offspring to the common parent and one from the common parent to the second offspring. This gives us $R_{XY} = (\frac{1}{2})^2 = \frac{1}{4}$. This method was used to obtain the coefficients of relationship in Table 1. When inbreeding is involved, the resulting equations are very tedious to work with. A simple method that is suitable for small pedigrees will be presented later in the piece.

Inbreeding and Relationship

The idea of inbreeding is closely tied to that of relationship. Inbreeding may be simply defined as the mating of individuals more closely related than the population average. Another definition often used is that the parents of an inbred individual shared a common ancestor. In Figure 2, Horatio is the product of a sire-dam mating: his dam and paternal grand-dam are one and the same; Emma is the common ancestor. It is hoped that the lovely Emma is exceptional in some character that would warrant her use in this manner, rather than simply a victim of circumstance. The mating of close relatives such as seen here is sometimes called close inbreeding. Since more of an individual's genes come from the same source, in a sense the gene pool is getting shallower. More formally, homozygosity increases in a population that is inbreeding.

Figure 2. A pedigree demonstrating inbreeding

Horatio	Sire Vincent	Sire Edmund
		Dam Emma
	Dam Emma	Sire not applicable
		Dam n.a.

Inbreeding is a double-edged sword: it has both beneficial and detrimental effects. The most useful feature of inbreeding is an effect called *prepotency*, which is the ability of an individual to produce offspring whose performance is very much like their own. Inbred individuals are homozygous at more loci than the population average, and they produce fewer types of gametes, resulting in fewer types of zygote at fertilization. For example, inbred and non-inbred individuals may have the following genotypes:

Inbred AABbcc
 Non-inbred AaBcCc

The inbred individual can only produce two types of gamete: ABc or Abc. The non-inbred individual, on the other hand, can produce eight different gametes (ABC, ABc, AbC, Abc, aBC, aBc, abC and abc). Prepotency is particularly useful if a parent is homozygous for a dominant allele, which each offspring will receive with certainty. However, it is really only of great value if the trait is simply-inherited (under the control of a single pair of genes) or highly heritable. When a trait is complicated in its genetic control, or the environment is much more influential than genetics, any effects of prepotency are overwhelmed.

Two types of problem generally arise when inbreeding is practiced in a population: an increase in the occurrence of deleterious recessive traits, and inbreeding depression. When inbred animals mate, the level of homozygosis in the population increases. This leads to a higher probability that deleterious alleles will appear in the same individual. In the German Shepherd Dog, somewhat common “simple”-recessive traits include long coat, progressive retinal atrophy and pituitary dwarfism. Other problem traits such as hip dysplasia (HD) are polygenic, and not as sensitive to homozygosis (homozygosity) at individual loci, but are also expected to increase with higher levels of inbreeding. Inbreeding depression is a decrease in quality or performance of inbred animals that is due to the expression of unfavorable genes affecting polygenic traits. The traits most affected are traits such as fertility and survivability, which have a negative effect on lifetime health and performance. Close inbreeding should be carefully avoided to prevent such problems. In livestock breeding, 6.25% is often used as an upper limit for an acceptable level of inbreeding in a population. This is not always the case, and should not automatically be assumed as a limit for dogs, but is a good starting point to consider.

There is a mathematical measure of inbreeding that is similar to that used for relationship. The *coefficient of inbreeding*, denoted F_X where “X” is the name of the individual in question, is the probability that two genes taken at random from an individual are identical by descent. F_{Horatio} in Figure 2 is 0.25 (25%), which implies that genes are identical by descent at 1 of every 4 of his loci. Such a high degree of inbreeding is almost certainly undesirable. Equations to predict the inbreeding coefficient of any individual (given a pedigree) have been derived, but we shall not discuss those here. Coefficients of inbreeding for some common matings are presented in Table 2, and you can see the similarity to Table 1. The method mentioned earlier for calculating relationships in small pedigrees also yields the coefficients of inbreeding for all animals in the pedigree.

Table 2. Coefficients of Inbreeding for Some Common Matings

<u>Mating</u>	F_X
Parent-offspring	0.25
Full sibs (siblings)	0.25
Half sibs	0.125
Grandparent-grandchild	0.125

You may now be anxious to point out that all members of a breed, and perhaps even a species, are related to one another. This potential problem has long been recognized, and to get around it, we define what is called a *genetic base*. This base is simply an arbitrary population that is assumed to be non-inbred. For example, the base might be assumed to be all dogs born in 1950. It must therefore be emphasized that F_X has meaning as a measure of inbreeding only relative to a base population. If we defined Vincent and Emma's generation as the base in Figure 2, then Horatio would have a coefficient of inbreeding of zero. The idea is not that inbreeding never occurred before that point, but that it occurred far enough back in time that it would not have a significant influence on the current population if inbreeding is avoided or carefully managed in the future. To illustrate the point, the *average* relationship between an individual and an ancestor eight generations back in their pedigree is only about 0.00391 (0.391%).

Comparing Relationship and Inbreeding

It is necessary to take a moment to stress carefully the differences between coefficients of relationship and coefficients of inbreeding.

R_{XY} measures the proportion of an animal's genes that are identical by descent to those of a second animal; relationships can exist in the absence of inbreeding.

F_X measures the proportion of an individual's genes that are identical by descent *to one another*; remember that inbreeding does not exist in the absence of relationship.

It may help to think of relationship as a characteristic of a pair of individuals, while inbreeding is a characteristic of an individual. As will be demonstrated in an example later, two unrelated, inbred individuals may be mated to produce an individual that is not inbred. It is simple to understand this if the differences between inbreeding and relationship are kept firmly in mind.

The Tabular Method for Calculating Relationship and Inbreeding

The advantage of the tabular method of calculating relationship and inbreeding is that it is much simpler to use than the so-called path method. It can become tedious to do by hand if there are a large number of animals in the pedigree you are interested in, but can easily be programmed into a spreadsheet for your computer to deal with. Since we do not know anything about a given offspring, we shall refer to him/her as "X".

Figure 3. A Mating Between Bob and Victoria

	Gen. 1. PARENTS	GRANDPARENTS	GR-GRANDPARENTS	
<i>Litter or Dog's name ("X") here.</i>	<i>Sire: Bob</i>	<i>Sire: Jack</i>	<i>Sire: Tom</i>	
			<i>Dam: n.a.</i>	
	<i>Dam: Victoria</i>	<i>Dam: Annie</i>		<i>Sire: n.a.</i>
				<i>Dam: n.a.</i>
		<i>Sire: Vincent</i>		<i>Sire: Edmund</i>
				<i>Dam: Emma</i>
<i>Dam: Emma</i>		<i>Sire: n.a.</i>		
		<i>Dam: n.a.</i>		

The first step is to set up the pedigree containing the individuals of interest. A common situation might be the examination of a mating between Victoria, a full sister of Horatio, and the Bob of the example in Figure 3 above. We shall refer to the offspring of this mating as "X". This pedigree will be used to demonstrate how to easily figure out coefficients of relationship and inbreeding.

We are going to construct a table with as many rows and columns as there are unique animals in the pedigree. In Figure 3 there are ten animals, but Emma appears twice, so we will construct a 9-by-9 table. The animals in the pedigree should be ordered by generation from oldest to youngest. For example, we would order X's pedigree like this:

Edmund, Emma, Tom, Annie, Jack, Vincent, Bob, Victoria, X

The animals are alphabetized within generation, but this is not necessary. When an individual appears in successive generations, as Emma does, assign her to the group in which she first appears. A given entry in the table is the relationship between the individual at the top of that column and the individual at the far left of that row. Once the table is drawn out, the names should be filled in like this (and we will add more later, below Edmund, in subsequent steps):

Table 3 a.

					Tom/n.a.	Edm/Em	Jack/An.	Vin/Em	Bob/Vic
	Edm.	Emma	Tom	Annie	Jack	Vincent	Bob	Victoria	X
Edmund									

In some cells, such as Jack's, there are two or three names. The lower names, which I have highlighted in boldface, are the animals the columns correspond to. The upper animals are the parents of that animal.

We need this information close at hand to fill in the table. There will also be a row for each dog in the pedigree; the table has been abbreviated here in step 1 to save space. We will demonstrate how to fill in the table, one row at a time, in a series of four steps. I have used some abbreviations in the table to save space: Edm is Edmund; Em is Emma; Ann is Annie; etc.

The Row ‘Edmund’

The first cell in the table corresponds to Edmund’s relationship to himself, which will be 1 unless Edmund is inbred. Since we do not know who the parents of Edmund are, we assume he is not inbred and write in a ‘1’. The second cell is the relationship between Edmund and Emma. From the pedigree, we see they are unrelated, and write in a ‘0’; we do this for Tom and Annie as well. To find the *relationship* of Edmund to Jack, look in the cell for Tom in this row and *divide that value by two* (because Jack got half of his genes from Tom), which is ‘0’. The procedure for Edmund and Vincent is similar: look at the entry for each parent, divide the number by two, and add them up. For Vincent, we have $\frac{1}{2} + 0 = \frac{1}{2}$. For Bob, we get $0 + 0 = 0$, which you can confirm by looking at the pedigree. Victoria is the grand-daughter of Edmund, so they share a quarter of their genes in common. For X, we find $\frac{1}{8} + 0 = \frac{1}{8}$.

Table 3 b.

	Edm	Emma	Tom	Annie	Tom/n.a. Jack	Ed / Em Vincent	Jack /An Bob	Vin / Em Victoria	Bob / Vic X
Edmund	1	0	0	0	0	1/2	0	1/4	1/8

If you are confused or uncertain about the value you have calculated for an entry, look at the pedigree.

If you have a large number, but there are many steps between the two animals, you may have made an arithmetical error. The number in the cell should always make sense when compared to the pedigree.

The Row ‘Emma’

Now that we have added a second row to form a column, a comment is in order that will greatly reduce your labor. *Look ahead to the completed Table 3 e, for a moment.* If you draw a diagonal line down the matrix from the cell Edmund-Edmund to the cell X-X, the numbers above that line will be the same as the numbers below that line. The diagonal is darkly shaded in the completed table in Table 3 e (step 4 of this Bob-Victoria breeding exercise). The shaded upper-right “triangle” in the completed table can be flipped around the diagonal axis to fill in the lower part of the table. The *row* for Edmund contains exactly the same entries as the *column* for Edmund. So to get started, we copy the entry from Edmund-Emma into Emma-Edmund, which is ‘0’. The rest of the entries follow as in step (1):

$$\begin{array}{lll}
 \text{Emma} - \text{Tom} = 0; & \text{Emma} - \text{X} = 0/2 + 3/8; & \text{Emma} - \text{Bob} = 0/2 + 0/2 = 0; \\
 \text{Emma} - \text{Annie} = 0; & \text{Emma} - \text{Vin} = 0/2 + 1/2; & \\
 \text{Emma} - \text{Jack} = 0/2 = 0; & \text{Emma} - \text{Vic} = 1/2 + 1/4 &
 \end{array}$$

Since Emma is “related to herself” (“has the same genes” is another way of saying this) by a factor of one, look across her row and see who else she is related to. To Vincent, it is 1 (herself as one of the parents) divided by 2 (since she is only one of the two parents.) In the same way, relationship to Victoria is calculated by dividing 1.5 ($\frac{1}{2}$ for Vincent’s R value and 1 for her own as Victoria’s dam) by 2, to give the $\frac{3}{4}$ you see in the table. Emma has no relation to Bob because she has no relation to his parents Jack or Annie (therefore 0/2 in each case).

And now, back to where we were, in the early stages of constructing that coefficient of inbreeding Table 3:

Table 3 c.

					Tom	Edm / Em	Jack / An	Vin / Em	Bob /Vic
	Edm.	Emma	Tom	Annie	Jack	Vincent	Bob	Victoria	X
Edmund	1	0	0	0	0	1/2	0	1/4	1/8
Emma	0	1	0	0	0	1/2	0	3/4	3/8

We continue to build our table. Remember that for convenience more than anything else, we put the oldest ones on the left, and X, the Bob-Victoria pup, on the right:

Rows ‘Tom’ through ‘Victoria’

The next six rows were filled in as outlined in steps (1) and (2) above. Note that the values in the triangle below the diagonal are the same as in the upper triangle, flipped around the diagonal. When we look at Victoria’s pedigree, though, we see something that requires special attention. We said earlier that we can use the tabular method to find inbreeding coefficients, and Victoria is inbred (on Emma).

Table 3 d.

					Tom	Ed Em	Jack An	Vinc Em	Bob Vic
	Edm	Emma	Tom	Annie	Jack	Vincent	Bob	Vic	X
Edm	1	0	0	0	0	1/2	0	1/4	1/8
Emma	0	1	0	0	0	1/2	0	3/4	3/8
Tom	0	0	1	0	1/2	0	1/4	0	1/8
Annie	0	0	0	1	0	0	1/2	0	1/4
Jack	0	0	1/2	0	1	0	1/2	0	1/4
Vinc	1/2	1/2	0	0	0	1	0	3/4	3/8
Bob	0	0	1/4	1/2	1/2	0	1	0	1/2
Vict	1/4	3/4	0	0	0	3/4	0	1 + 1/4	5/8

In the entry Victoria-Victoria, we see that the entry is $1 + \frac{1}{4}$. Where did the $\frac{1}{4}$ come from and what does it mean? The 1 is Victoria’s relationship to herself in the absence of inbreeding. When an animal is inbred, or if you are not sure if an animal is inbred, you determine the coefficient of inbreeding from the table entry that corresponds to the relationship between its two parents. Victoria’s parents, Vincent and Emma, have a coefficient of relationship of $\frac{1}{2}$. If we divide by 2, we get the $\frac{1}{4}$ in the table entry. Victoria is the most linebreed/inbred dog in this chart.

We can write the formula out more formally as: $F_{\text{AnyDog}} = \frac{1}{2} (R_{\text{Sire-Dam}})$. To show that this works the way we assert it does, we’ll also find Bob’s coefficient of inbreeding: $F_{\text{Bob}} = \frac{1}{2} (R_{\text{Vincent-Emma}})$, and $\frac{1}{2}$ of (0) is 0. Examination of Bob’s pedigree confirms that his coefficient of inbreeding is 0.

Row 'X'

We are then left with only one row left to fill in, that belonging to X. If we fill out this last row as we have filled out all of the others, we will see that X is not inbred, despite the fact that his dam was. The fact that this is so may not come as much of a surprise because it is clear from the pedigree that Bob's line is unrelated to Victoria's.

Table 3 e.

	Edm	Emma	Tom	Annie	Tom Jack	Ed Em Vincent	Jack An Bob	Vin Em Vic	Bob Vic X
Edmund	1	0	0	0	0	1/2	0	1/4	1/8
Emma	0	1	0	0	0	1/2	0	3/4	3/8
Tom	0	0	1	0	1/2	0	1/4	0	1/8
Annie	0	0	0	1	0	0	1/2	0	1/4
Jack	0	0	1/2	0	1	0	1/2	0	1/4
Vin	1/2	1/2	0	0	0	1	0	3/4	3/8
Bob	0	0	1/4	1/2	1/2	0	1	0	1/2
Vic	1/4	3/4	0	0	0	3/4	0	1 + 1/4	5/8
X	1/8	3/8	1/8	1/4	1/4	3/8	1/2	5/8	1

We will now present a pair of brief examples to demonstrate two important ideas. The first point is that a table like the one above can be easily extended to answer "What-if...?" type questions about future matings. The second is that two inbred parents can produce offspring that are not inbred as long as the parents do not share a common ancestor. We will use the pedigree presented in Figure 4 for this example.

Figure 4. A Mating Between Bill and Victoria

dog's name ("Y") here	Sire: Bill	Sire: Jack	Sire: Tom	
			Dam: n.a.	
	Dam: Victoria	Dam: Lisa	Sire: Tom	
			Dam: n.a.	
		Dam: Emma	Sire: Vincent	Sire: Edmund
				Dam: Emma
		Sire: n.a.		
		Dam: n.a.		

The sire of Y, Bill, is the product of a half-sib mating, while the dam, Victoria, is the product of a dam-son mating. The completed table of relationships and inbreeding coefficients is:

Table 4

	Edm	Em	Tom	Tom Lisa	Tom Jack	Ed Em Vin	Jack Lisa Bill	Vin Em Victoria	Bill Vic Y
Edmund	1	0	0	0	0	1/2	0	1/4	1/8
Emma	0	1	0	0	0	1/2	0	3/4	3/8
Tom	0	0	1	1/2	1/2	0	1/2	0	1/4
Lisa	0	0	1/2	1	1/4	0	5/8	0	5/16
Jack	0	0	1/2	1/4	1	0	5/8	0	5/16
Vincent	1/2	1/2	0	0	0	1	0	3/4	3/8
Bill	0	0	1/2	5/8	5/8	0	1 + 1/8	0	9/16
Victoria	1/4	3/4	0	0	0	3/4	0	1 + 1/4	5/8
Y	1/8	3/8	1/4	5/16	5/16	3/8	9/16	5/8	1

Both parents of Y are inbred ($F_{\text{Bill}} = 1/8$ and $F_{\text{Victoria}} = 1/4$), but as they do not share a common ancestor, $F_Y = 0$. This example emphasizes a point made earlier: inbreeding is dependent on relationship. In small breeds, it often happens that there are a few very influential individuals to whom most of the population is related. These elevated levels of relationship can make it difficult to plan matings free of inbreeding.

Let us say, for the sake of argument, that we are thinking about mating Emma to Y because we are using her in a *linebreeding* program. The goal of linebreeding, usually connoting a “milder” form of inbreeding, is to maintain a high degree of relationship and similarity to a desirable individual, and is usually carried out by mating that individual recurrently. The pedigree in Figure 5 outlines a possible linebreeding scheme based on the repeated use of Emma as a dam. The paternal side of the pedigree is the same as shown in Figure 4.

Figure 5. A Linebreeding Scheme based on Emma

Z (offspring linebred Emma)	Sire: Y	Sire: Bill	Sire: Jack	Sire: Tom	
			Dam: Lisa	Dam: n.a.	
		Dam: Victoria	Sire: Vincent	Sire: Edmund	
			Dam: Emma	Dam: Emma	
				Sire: n.a.	
				Dam: n.a.	
Z's Dam: Emma (rest of Emma's pedigree not applicable)					

The first thing we do is add a column and a row to the table that we will fill in with coefficients of relationship between Z, the offspring of Emma and Y, and the rest of the dogs in the pedigree. We can also fill in the Z-Z cell because we already know the relationship between Y and Emma is

3/8, giving Z a coefficient of inbreeding of 3/16 (18.75%). The normal procedure is then followed to complete the table, which is presented below.

	Edm.	Emma	Tom	Tom Lisa	Tom Jack	Ed Em Vincent	Jack Lisa Bill	Vinc Em Victoria	Bill Vic Y	Y Em Z
Edmund	1	0	0	0	0	1/2	0	1/4	1/8	1/16
Emma	0	1	0	0	0	1/2	0	3/4	3/8	11/16
Tom	0	0	1	1/2	1/2	0	1/2	0	1/4	1/8
Lisa	0	0	1/2	1	1/4	0	5/8	0	5/16	5/32
Jack	0	0	1/2	1/4	1	0	5/8	0	5/16	5/32
Vincent	1/2	1/2	0	0	0	1	0	3/4	3/8	7/16
Bill	0	0	1/2	5/8	5/8	0	1 + 1/8	0	9/16	9/32
Victoria	1/4	3/4	0	0	0	3/4	0	1 + 1/4	5/8	11/16
Y	1/8	3/8	1/4	5/16	5/16	3/8	9/16	5/8	1	11/16
Z	1/16	11/16	1/8	5/32	5/32	7/16	9/32	11/16	11/16	1+3/16

The shaded row and column contain coefficients of relationship between Z and the other dogs in the pedigree. We can clearly see that relationships between these animals are rising quickly because of the ties back to Emma in three out of four generations. Many breed societies have rules that dictate how frequently the same animal may appear in a pedigree, perhaps four times in six generations, and those rules are based on this idea. However, you can now see that the influence of such an individual depends quite a lot on just where in the pedigree the repeat appearances are. A more sensible rule might be that animals with a coefficient of inbreeding beyond a certain threshold will not be issued papers. A second approach would be to restrict the average relationship to influential members of the breed. The American Jersey Cattle Club publishes what they call a coefficient of kinship (K) on their pedigrees. That number represents the average relationship between the pedigreed individual and a set of the most influential sires in the Jersey breed. A disadvantage of this approach, however, is that K cannot be computed using the tabular method or other simple technique, and can vary considerably depending on the definition of the “most influential” group.

Introducing Genetic Variation through Crossbreeding

Breeds small in numbers (such as the Shiloh, certainly the Chinook and Klee Kai) are sometimes faced with the need to introduce genetic variation from an outside source to keep their population viable. This is typically done using crosses between the breed's base (small gene pool) and another breed deemed to be suitable. The decision of what breed to outcross with can be based on anatomical conformation, behavior, or some other characteristic important to the base breed. A concern is often to limit the influence of the new breed to maintain an acceptable level of “purity”, or breed composition. An approach to calculating the outcome of matings between base and outcross animals will be presented and discussed.

Outcrossing may be used to take advantage of a phenomenon erroneously known as “hybrid vigor”, more properly heterosis. The idea is that a cross between two populations that have each become relatively homozygous will produce offspring that are heterozygous at many loci. Research has shown that such crosses are often much heartier, healthier and productive than either of the parental lines. Heterosis is an effect dog breeders have known about and taken advantage of for many years. [Note: technically, a hybrid is a cross between two species, such as horse X jackass, or bison X cattle; crossbred dogs or dog-wolf matings do not produce true hybrids. But we should recognize that the word is used, and consider the context, even though a wolf is just another breed of dog.]

A tabular approach can be used to determine levels of breed composition. By breed composition, we mean the percentage of base and outcross breeds in the improved population. For example, if you were to cross populations of German Shepherds and Labradors, the composition of the resulting breed would

be 50% GSD and 50% Labrador. Rules for acceptable matings are often based on distance between the outcross and current generation of individuals, and the tabular method to be presented can be used to determine if breed association rules are based on sound genetic ideas or breeder preferences.

We are going to use as the basis for this discussion a question posed to the author regarding breed composition and association rules. The situation is as follows: because of concerns about small population size, a breed association wishes to outcross for a single generation to bring in some new genetic variation. The outcross individuals will be used only for a single generation, and matings between composite (mixed) individuals will only be allowed if they are a certain distance apart in generations from the outcross. The rules as they currently stood stated that, (A): 2, 3 and 4 may only mate with 5 and 6, and (B): 5 and 6 may only mate with 2, 3, 4, 5, and 6.

Those numbers refer to distance, in generations, from the outcross event. A ‘1’ would be the offspring of the limited-numbers breed and the introduced “outcross” breed. We will use the pedigree in Figure 6 as the basis for our discussion.

Figure 6. Seven Generations From an Outcrossing Event

#s refer to							Outcross ¹
generations						1---	{
from the					2---	{	Pure ²
outcross				3---	{	Pure	
“event”.			4---	{	Pure		
		5---	{	Pure			
	6---	{	Pure		(these “Pure” dogs		
7---	{	Pure			are different		
	Pure				individuals)		

¹ “Outcross” represents the individual(s) of another breed

² “Pure” represents a purebred individual of the limited-numbers breed

(Read the above chart as: “Outcross” bred to the first “Pure” gave us #1; #1 bred to another “Pure” gave us # 2, etc.)

We are going to use a table of eight generations (“Outcross” through 7) to show the breed composition of a mating between any two individuals an arbitrary number of generations from the outcross event . Using the rules for computing a table of relationships presented earlier, we end up with the following table:

	Outcross	1	2	3	4	5	6	7
Outcross	1	½	¼	1/8	1/16	1/32	1/64	1/128
1	½	1	½	¼	1/8	1/16	1/32	1/64
2	¼	½	1	½	¼	1/8	1/16	1/32
3	1/8	¼	½	1	½	¼	1/8	1/16
4	1/16	1/8	¼	½	1	½	¼	1/8
5	1/32	1/16	1/8	¼	½	1	½	¼
6	1/64	1/32	1/16	1/8	¼	½	1	½
7	1/128	1/64	1/32	1/16	1/8	¼	½	1

The lower cells can be filled from the upper cells. The entries in this table are relationships between the individuals in the pedigree, as we have seen before.

We can construct from this table a second one that contains the breed composition, in terms of outcross percentage, between matings. In the following table, the entry 2-3, for example, is the percentage outcross in a mating between a second and a third generation animal. The value is computed as $\frac{1}{2} (R_{\text{Outcross-2}} + R_{\text{Outcross-3}})$, where the R_{XY} are taken from the above table.

	1	2	3	4	5	6	7
1	.5	.375	.3125	.2813	.2656	.2578	.2539
2	.375	.25	.1875	.1563	.1406	.1328	.1289
3	.3125	.1875	.125	.0938	.0781	.0703	.0664
4	.2813	.1563	.0938	.0625	.0469	.0391	.0352
5	.2656	.1406	.0781	.0469	.0313	.0234	.0195
6	.2578	.1328	.0703	.0391	.0234	.0156	.0117
7	.2539	.1289	.0664	.0352	.0195	.0117	.0078

The table entries are presented as decimals rather than fractions because it is easier to read off values that way. Our intuition tells us that as time passes, the influence of the outcross upon the breed will diminish, and this is confirmed by the table above. There is no column or row corresponding to the outcross because only one outcrossing event was permitted in the outlined breeding program. When reading this table it must be noted that these matings are based on the assumption that the outcross event occurs *only once* in each animal's pedigree. If there has been inbreeding in the population, the correct table may be computed from the appropriate table of relationships.

It is up to the individual breed associations to establish standards for breed composition, but we can provide a tool for studying possible rules. The following table is an excerpt from the second table above. The shaded portion of the table represents matings that are not permitted by the proposed breed association rules presented earlier. We are interested in answering the question: "Are these rules based on sound scientific principles?"

	2	3	4	5	6	7
2	.25	.1875	.1563	.1406	.1328	.1289
3	.1875	.125	.0938	.0781	.0703	.0664
4	.1563	.0938	.0625	.0469	.0391	.0352
5	.1406	.0781	.0469	.0313	.0234	.0195
6	.1328	.0703	.0391	.0234	.0156	.0117
7	.1289	.0664	.0352	.0195	.0117	.0078

Our answer is a firm "No." We can assume that the reasoning behind the mating rules was to limit the influence of the outcross and preserve distinct breed characteristics. One way to do this is to limit the number of times the outcross may appear in an individual's pedigree. The obvious problem here is that there are permitted matings with levels of outcross composition much higher than some of the forbidden matings. This is quite obvious when considering the 2-5, 2-6, and 2-7 combinations. A more reasonable approach would be to limit the percentage of outcross, and not issue papers if that limit was exceeded. Such a decision might have to wait until there are several matings of each combination to determine if there is a natural threshold between acceptable and unacceptable levels of composition. We would recommend the establishment of an arbitrary criterion at the beginning of an outcross program that would be reevaluated at set points in time. For example, it might be decided that the outcross percentage should initially be limited to 15% or less. After four generations including the outcross, that level might be changed to 10% or less based on observations of composite individuals.

Outcrossing can be used to great benefit when a population is having a hard time maintaining a healthy breeding population. There are procedures, outlined above, for determining the outcome of specific matings to outcrossed individuals that can be used to establish breed rules for purity. There are no hard and fast rules for what those breed regulations should be. What can be stated strongly is that breeders should not be afraid to use outcrossing as a management tool. A healthy, vigorous dog is much more desirable than a “pure” one.

Putting it all Together

We have discussed some important ideas and introduced some useful tools for the dog breeder in the preceding sections. We will now conclude with a discussion of how to design and manage an effective breeding program. It is not enough to simply mate good animals to one another and hope for the best, especially when such important traits as show-ring success are very strongly influenced by environmental factors.

Bourdon (1997) discusses what he called common sense animal breeding. He emphasizes traits common to effective and successful animal breeders that bear reiteration here. Qualities desirable in a breeder include knowledge of theory and technology, patience and deliberation. The most important tool used by the careful breeder is good information. Finally, a good breeding program is characterized by consistency and simplicity.

Technical knowledge is important for an animal breeder. To be most effective, he must understand not only the methods he uses, but also something of the theory behind them. One does not have to be a mathematician or statistician to effectively breed good dogs, but should have a command of certain fundamental knowledge. The breeder has to understand the idea of Mendelian inheritance, for example, before he can properly understand how methods of computing inbreeding and relationship work.

Another important concept to master is that genetic inheritance is a random mechanism that presents both opportunities and limitations. When the knowledge is available, the breeder should be aware of positive and negative genetic correlations among traits under consideration. If height is negatively correlated with litter size, and you are interested in fecundity, you should choose the short dog. Genetic mechanisms will not change for our wishing them to. Familiarity with the current publications and interaction with other animal breeders is very helpful in acquiring and maintaining technical knowledge.

While patience appears second in the list, it is perhaps the most important characteristic of the successful breeder. Genetic change occurs more slowly than many of us might like, but the trade off is that genetic gains are cumulative. The random nature of gene segregation makes much of inheritance unpredictable, so the wise breeder will play the averages. Adherence to a well-defined breeding program will produce successive generations that are better than their predecessors. Most offspring produced are considered average, but occasionally a truly outstanding individual will be produced. That individual should be patiently sought after, recognized and exploited.

No breeding program can succeed if it does not have clearly considered and realistic goals. The deliberate animal breeder will spend time thinking about his goals, his definition of the ideal animal, and the best way he can obtain animals with desirable characteristics. The temptation to jump on the bandwagon and follow the lead of other breeders should be resisted. A thoughtful manager will always know more about what is best for his program than anyone else.

The importance of good information cannot be stressed enough. Data about his animals is the single most important commodity any animal breeder possesses. Dog breeders do not have access to the kinds of information many livestock breeders do, typically genetic evaluations based on vast amounts of data and complex statistical analyses. Look for the most meaningful available. If pedigrees are the basis for most of your decision-making, do not accept incomplete or suspect pedigrees, and deal with “seedstock” producers (breeders) known to you to be of superior integrity and knowledge.

The nature of the information collected is also of interest. If it is not economically unfeasible, things like litter size, birth and mature weights and body dimensions should be collected, recorded, and contributed to breed databases. It is no disadvantage to breeders to share their hard-won information with others. When good quality data is available to everyone, the whole breed benefits. An example of the importance of collecting and sharing information might involve the discovery that a given line was a carrier for a deleterious recessive. The recognition of the problem would lead to breeders making more informed decisions about matings, particularly matings involving relatives. While the goal of a breeding program is the production of animals as close to ideal as possible, it does not relieve breeders of the responsibility of considering animal welfare.

The quality of information collected is of seminal importance. It really does not matter if there are thousands of records in breed books if they are not accurate records. You cannot make rapid genetic progress without sound information on which to base your breeding decisions. If you are faced with a tradeoff between the quality and the quantity of records you can record, always choose high quality.

The breeding program itself should be simple and consistent. By simplicity we mean that goals are carefully thought out and are reasonable in light of the information available and the genetics of the traits under consideration. Consistency implies that once goals are formulated, breeding strategies that lead to those goals are followed rigorously. That is not to say that there is no room for change in a breeding program; there is simply no room for hasty or ill-considered change. Frequent changes in breeding goals often result in contradictory efforts that lead nowhere fast. Clearly the patient animal breeder is better able to stick to goals once they have been established.

It can be difficult to formulate simple goals. There is often a temptation to try and improve several characteristics at once. Sometimes there will be positive correlations between traits of interest, and progress can be made in more than one area at once. However, you cannot change everything at once. There is a classic rule in animal breeding that states if you select for n traits, progress will only be $1/\sqrt{n}$ (one divided by the square root of n) as rapid as if you select for a single trait. If you select for two traits, you only make 71% as much progress as if you selected for a single trait, and 58% as much progress if you select for 3 traits. The old maxim of “keep it simple” should always be borne in mind.

While there exists no absolute set of rules to guarantee your breeding program is successful, there are general rules to play by. You should always thoroughly understand the goals you are trying to attain. You should understand as much as possible the genetic mechanisms underlying the traits you want to select for. And you should understand that there is, and there will always be, a lot of luck. You cannot change the rules, but you can stack the deck in your favor.

MORE ON INBREEDING

The dog world seems unwilling to learn from science in some respects, and inbreeding-linebreeding is one of those areas. I say “one” because there is no real difference or dividing line between the two terms; linebreeding is simply descriptive of inbreeding on animals a little further back in the pedigree than otherwise. Laboratory rats and mice have been consistently inbred to a great degree in order to be more predictive about the effects of medicines and other things that experimenters are working on. But such scientists keep several different families going at a time, because they know that restricting the gene pool also has adverse effects sooner or later, and when a line starts to die out because of inbred weaknesses, they can cross with another family or more, and start a new line again. In time, inbreeding results in “inbreeding depression”, with such signs as smaller size, less resistance to stress and disease, fewer offspring, and shorter lives. Doesn't that sound awfully familiar to those of us who've been watching the American GSD develop over the past

40 or so years? Except for the smaller size, perhaps, but those wouldn't reach the mainstream of the market anyway. We dog breeders do not have the ability as individuals or associations to maintain dozens of separate bloodlines as the lab mice breeders do.

The more research into inbreeding and genetic diversity is carried out, the more evidence mounts that artificial selection is deleterious and natural selection results in a much broader diversity and therefore greater health safety level. Even in Germany, where breeders formerly prided themselves on keeping "open" at least important sire lines that went back to dogs not found as often in modern pedigrees, it has become almost impossible to find GSD "show" dogs that are not linebred on Palme WildsteigerLand and the Q-litter Arminius. As a result of moderately strong linebreeding, we find such problems as the immune system deficiencies in Lasso Neuenberg and others' offspring, nagging high levels of HD in Zamb Wienerau descendants, low percentages of Körklasse-1 (or even Kkl-2 for that matter) in Tacko Wienerau and even Sieger Lasso offspring. These are not prejudicially singled out; they are too representative of many dogs in the same boat. When "everybody" breeds to the same small number of dogs or bloodlines, these types of weaknesses are what you'll get.

The loss of diversity of genes is directly responsible for much of the genetic problems we see in many species of domesticated animals, not only dogs. Some breeds of swine, for example, almost have to be slaughtered by the age of 5-7 months to take advantage of the best ratio of sale price to feed cost, but also to avoid the almost inevitable hip dysplasia in those breeds. Only a few of the better-hip pigs or those on a less accelerated diet are kept long enough to breed from. If the Germans don't start tightening up on GSD hip and elbow joint quality, and loosening up on the narrow focus of the bloodlines used (working lines are almost as bad in this respect as show lines), they will soon paint themselves into a corner the way the Americans have. Inbreeding depression walks hand-in-hand with loss of heterozygosity and the lower utilitarian beauty of the modern German Shepherd Dog.

The name "Border Collie" in the U.S. and a few other countries, was until recently in the same position the GSD was a hundred years ago, more a description of its occupation than its ancestry. Thanks to the self-serving and wrong-headed approach of the AKC, the Border Collie has become a "breed", with all the dubious rights and appurtenances thereto granted by the AKC, including severe restriction of genetic diversity. This true working breed is beginning to find itself in the same position the Akita has been in for all those years the AKC refused to open the stud book to imports from the country of origin. The Akita has a host of health and temperament problems as a result. New "rare" breed clubs have formed in the U.S., partly to satisfy the desire for novelty, partly as a haven for those fleeing the more established breeds after disappointments in genetic health. But that's jumping from the frying pan into the fire.

The "Shiloh Shepherd", a new breed (30+ years in the making so far) is basically a GSD family chosen for large size, old-fashioned level-back stance, and allowable profuse long coats. To bring in the desired qualities that the founder couldn't find enough of in the regular GSD, fanciers reportedly have brought in a couple other breeds in very small quantities. Still, the gene pool is extremely limited, and unless there is use of strict selection techniques for eliminating HD, dentition faults, and a few other problems, the breed will continue to have all the traditional inbred-GSD disorders plus a few more. The white GSD, recognized by some registries as a separate "breed", the White Shepherd, White Herder, and other names, likewise has a host of structural and other limitations and is at risk of genetic disease taking it over because of its lack of genetic diversity. The Chinook, based on a single big yellow dog of mixed Saint Bernard and other heritage, is being modeled into a more or less consistent Type by the "national" club via the use of "imported" genes from Siberians, Shepherds, and whatever results in the desired body style and personality characteristics. The English Shepherd is being pulled in two directions by those who want to breed for style and to show in conformation, and those who want to leave it as it is (a tremendous variation in appearance from an Australian Shepherd to Border Collie to almost a Leonberger look); the latter stress its farm and pet utility instead of pedigree. Whether "new" or not, breeds on the edges of what some consider "purebred" are faced

with the challenge to keep enough diversity to prevent problems from becoming so deeply imbedded in the gene pool that there is almost no correction possible.

Today, almost all black Poodles (and their genetic diseases) are bred on the Wycliffe line. Poodles are numerically among the worst afflicted with epilepsy. Dalmatians have a sack full of genetic disorders, and when the AKC and others proposed a scheme to rid the breed of hereditary deafness by judiciously blending a few Pointers into the breed, then culling to preserve Dal type while eliminating carriers, the Dalmatian club rebelled against logic and voted to stay on the course to self-destruction. Many feel that the Siberian Husky is a genetic mess because of the restriction to breeding only “pure” ancestry; they can’t work as well as sled dogs as can the mixed breeds which constitute the “Alaskan Husky”. Some 80% of Doberman Pinschers are either affected by or carriers of the genes for von Willebrand’s Disease (vWD), which means that those fanciers are in a real bind, as elimination of all those dogs would mean disaster for the breed. Copper toxicosis in the Bedlington; elbow dysplasia in the Rottie; PRA in the Irish Setter and Lab; PFK enzyme deficiency in American Cockers, English Springers, and Basenjis; dwarfism and hemophilias in the German Shepherd Dog, and many other examples of genetic disease are linked to the decrease in outcrossing over time. Germans for the most part still echo the official (but untrue) line that Canto was not a Type-A hemophiliac, and for a long time many of his GSD descendants suffered from that disorder; fortunately it is sex-linked so that only daughters are carriers of the recessive and sons tend to die early, and it has not been seen in recent years to be a major problem.

Whenever possible, outcross! And encourage the national breed club to use genetic diversity in recognizing the value of the dogs and lines. To quote an Internet/e-mail message on the subject, we all should take a closer look at “the dark side of inbreeding — what happens when everyone breeds to Mr. Wonderful, and what to do when everyone discovers they have the same problem.” (Genetic Diversity Project, Dr. Catherine Marley and Dr. John Armstrong). University of California-Berkeley canine genome researcher Jasper Rine sums it up: “There are just crazy levels of inbreeding in many breeds of dogs”.

One common route to inbreeding is the widespread use of a single popular “Grand Victor” or “Sieger” (national top winners), or a handful of top Award-of-Merit/Select animals to the exclusion of other good but less-highly placed competition dogs. While you may be increasing the chances of getting a dog that has some of the same obvious (probably dominant or homozygous) desirable qualities, you are at the same time increasing the concentration of so far hidden recessives, many or most of which are bad for the breed. When most people flock to the leaders for stud service, these bad genes are concentrated as well, and the good genes that an unused dog could have contributed may be lost forever. The undesirable recessives previously hidden in the lines will soon become glaring problems, impossible to ignore and difficult to get rid of.

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