BREEDING - THE BIG PICTURE!

By Dan Astibus sharplaninec.com (republished with permission from the author)

Many articles have been written about dog breeding, with the better ones usually covering some aspect of canine genetics as well. However, even those latter manuscripts merely revolve around Mendelian genetics. While this is undoubtedly valuable for the understanding of inheritance when breeding individual dogs, I have seldom encountered resources, where the authors tried to put dog breeding into a broader context. The question is, would our perception increase, if we took the focus away from single dogs or even individual breeding programs and started looking at breeds in their entirety? Is there any tangible benefit to interpreting our breeding efforts in the light of the impact on the complete breed?

Whenever we consider a dog breed as a whole, the term Population Genetics should come to mind right away. But what exactly is Population Genetics? Well, it essentially describes a discipline within genetics, where quantitative tools are applied to understand global genetic drift, gene migrations, allele frequencies of certain desired or undesired traits etc. This outlook - as I will try to illustrate here - has far reaching and I believe fascinating implications.

Let us dive into this matter with a little thought experiment at the beginning. Suppose you decided to recreate a breed of antiquity, which to all accounts has been extinct for centuries. To your own amazement, you were able to identify say 4 unrelated males that express this presumably ancient phenotype and another 7 females, all hidden away in various remote areas of the world. This basically becomes your foundation – or in genetics terms comprises the gene pool of your new breed. So far so good. But once you start breeding them methodically, you soon realize that your breed quickly becomes tightly related. After only two or three full generations you find yourself having to resort to inbreeding to further increase the numbers of specimens. So what exactly happened? And why could this development potentially be a bad thing? And what is inbreeding anyway?

Before we proceed, let us first briefly discuss the terms inbreeding and linebreeding. In the canine world, inbreeding is defined as breeding closely related dogs to each other, i.e. parent to offspring (vertically) or brother to sister or half-brother to half-sister (horizontally). Let me stress right away that inbreeding in itself can be a valuable tool to 'fix' certain desired genes and should not be quickly discarded as the works of unethical breeders.

This writing is really not supposed to become an argument for or against inbreeding, rather a plea that a full appreciation of its broader implications should be paramount before even considering such a breeding strategy. When we now look at the term linebreeding, it is traditionally referred to as a relaxed form of inbreeding, meaning the matching of distant cousins or aunts to nephews, grand-uncles to grand-nieces etc.

In reality, the distinction between those two forms of inbreeding is just arbitrary, as genetically speaking there isn't a fundamental difference between them. Emotional reservations aside, the actual genetic relationship of two individuals is scientifically determined by Sewall Wright's Coefficient of Relationship (RC), which basically computes a percentage of relatedness by derivation from the Coefficient of Inbreeding (COI).

Continued on Page 20

Continued from Page 19

BREEDING - THE BIG PICTURE! CONTINUED

I'll spare you the math. But it turns out that solely based on their four generation pedigrees, apparently unrelated or only remotely related dogs from the same breed can share a substantial amount of common genes, resulting in a notably high inbreeding coefficient, when mathematically verified over the past 10 generations. This is actually the case for the vast majority of today's purebred dogs.

Inheritance is not as straight forward as many believe. Oftentimes, people mention percentages of "blood" in their dogs as if these were absolute certainties, whereas in reality the percentages beyond the actual parents rather describe only probabilities. Believe it or not, this is an important distinction. There is no physical law that makes sure that a pup is 25% genetically identical with its grandfather. This is only the probabilistic mean, to be observed if one would fully genotype thousands of puppies and their respective grandparents, then calculate the average similarity; it's just a convenient simplification that works somewhat well in practical terms – nothing more. Please keep in mind that these numbers are only an abstraction of reality. Ok, now that I sufficiently clouded the neat and cozy Mendelian approach, let us get back to quantitative genetics, or at least a global viewpoint.

As various dog breeds evolved over time, people had primarily the same principal objective – to obtain sufficient consistency in the progeny of their dogs with regard to some defined labor task. They strived for a distinct conformation in phenotype as well as certain favored personality traits; in short, the optimal dog for a given task. When we really think about this from a genetic perspective, the underlying objective really was to limit the variability of a given gene pool in order to create a coherent type of dog, that performed well above average in the respective niche. In this procedure, an initial dog population of some intrinsic diversity would be progressively "pruned", until a new dog population of superior working quality had been obtained. Just as the consistency in phenotype improves, the variability in the offspring decreases over time, meaning that the range of available alleles in the gene pool narrows over time.

A while ago, I started a MolosserDogs thread with the title "What is a mutt?", only to illustrate how people would struggle to clearly define what the criteria for being a mutt would be. I believe that there is no clear cut definition. If anything in that regard can be said with confidence, then it is probably that purebred dogs display a tighter genetic variability than "mixed" dogs.

By the way, the consistent phenotypes due to limited gene pools with homozygosity for many alleles in pure breeds are of fundamentally different composition (and quality) than those of wild pariah dog populations. This has to do with masking of recessive genes, which unfortunately is beyond the scope of this topic. Only this much, in gene pools of pariah dogs, recessive genes can be carried along without being frequently expressed nor completely eliminated from the gene pool; only to pop up, if and when they prove advantageous. Anyway, as far as we are concerned for now, whenever we study the gene pool of a particular dog breed, it is safe to say that we are dealing with a more or less isolated subset of available gene alleles from the generic gene pool.

Continued on Page 24

Continued from Page 20

BREEDING - THE BIG PICTURE! CONTINUED

Now, narrow and isolated gene pools aren't an exclusive phenomenon of dog breeds created by man. Small wolf packs in nature for example aren't exactly fully transparent either, their sexually mature members are certainly not available to every potential mate out there but restricted to selected specimens even within their own family. While close incestuous pairings seem to be the rare exception in wolves, this arrangement still meets the criteria for loose inbreeding. If what we call "linebreeding" constantly occurs in nature itself, it can't be all that bad in breeding programs either, right? Yes, of course. But there's more to it. Let us come back to this issue a little bit later.

When linebreeding is performed in a meaningful manner of strategic breeding efforts, the objective is to emphasize desired features or to eliminate undesired genes. Inbreeding is used to 'fix' specific genes, essentially an attempt to concentrate the allele frequency of a targeted trait. This is a science in itself and the subject has been satisfactorily discussed in other threads already. I would only like to discuss the "side effects" here. Due to affects of gene linkage, we cannot pretend that we are solely tinkering with the targeted gene, when we try to modulate an allele frequency of a population to our advantage. When we fix one gene, we affect others in their relative occurrence as well. Without even realizing it, we are likely to increase the rate for infrequent recessive defects that just happen to be closely linked to our original gene of interest.

One might now hastily conclude that all inbreeding (whether incestuous or linebreeding) is "evil" and simply resort to selecting very distantly related specimens from the same breed. Let us investigate this potential strategy for a moment. I hope you still remember our initial thought experiment. Let us switch into the next gear. Suppose we are dealing with a rare breed of about 400 specimens total, which are unrelated. (I use 400 as this is the number that Gary Sicard came up with in a recent discussion. I will demonstrate shortly, how the exact amount of specimens in a breed is almost irrelevant.) For simplicity, we will assume that about 50% of these dogs are male, the other half obviously female; none of them spayed or neutered. How long do you think, will it take before all dogs are related to each other? If you guessed after eight generations, you are right. This seems so counterintuitive, doesn't it? The reason for this rapid decline in unrelatedness is that the genetic convergence follows a logarithmic function. For those who are interested, the equation to determine the first generation of inbreeding is $Gi= |(\ln(n)/\ln(2))+0.5|+1$, where n is the amount of dogs from the less represented gender. What this really means is that the possible number of available unrelated specimens is cut in half with each generation. So, if we had just 16 studs and equally as many females, we'd experience unintentional inbreeding within only 5 generations. And keep in mind that this would only hold true, if one employed every specimen equally in the breeding program. If any stud were to be favored as a show champion for example and all bitches were bred to that one stud, then complete relatedness would obviously be achieved much sooner; this could be considered as a founder's effect. The subsequent unintentional inbreeding would further amplify unwanted traits – or more precisely, genetic diseases. And in fact, this is precisely what happens in so many 'novel' breeds. The genetic base is so thin that it usually takes only 10 years or less in a breeding program, until more and more problems surface within the breeding stock. A perfect Pandora's box, as far as I am concerned.

Continued on Page 25

Continued from Page 24

BREEDING - THE BIG PICTURE! CONTINUED

I have previously mentioned that narrow gene pools are not bound to man-created dog breeds but also occur in wild populations of canidae. If these effects are as detrimental as I make it sound, why aren't wolf populations riddled with genetic diseases? Why do breeders and dog owners experience problems more frequently in recent decades and not as severely in the early days of breeding for type? The answer to that is that "linebreeding" is only one half of the story, only one part of a truly successful strategy. When we look at wild predator populations, one thing becomes immediately apparent. Let's assume an ecosystem of stable equilibrium between a population of some sort of prey and a pack of wolves. A female wolf comes in heat only once a year, and even then on average she produces around 25-30 young wolves throughout her life. However, in order to maintain that aforementioned perfect equilibrium (I will refrain from harmony, as the prey would probably beg to differ), statistically speaking, all she really needs to produce are two new wolves, one to replace herself and one to replace the sire. This progeny would maintain the wolf population stable, until the next generation eventually takes over. So the legitimate question is, what happens to the other wolves? It is well documented that the majority of the offspring will simply starve or die prematurely of other cause. Bluntly stated (and statistically of course), only the fittest survive. Nature "recalls" those that didn't make the cut – for whatever reason.

I was recently asked, if it was true that historically livestock guardian dogs such as the Sarplaninac truly had only very few puppies in a litter? The suggested 2 or 3 puppies per pregnancy would indeed be remarkably low, considering that those sheep guardians are pretty large dogs. My response was that I'm sure that in many cases only very few puppies officially made it to young adulthood, regardless of how many puppies the dam actually gave birth to. Well, these were different times and not all dogs in a litter were necessarily allowed to live long and prosper lives. Even at older ages, dogs that didn't perform as expected, were simply culled – no questions asked. Such a strict breeding regime ensured that only the toughest dogs survived; those with genetic impairments didn't make the cut. Almost like the unfit wolves.

Today, mentioning the word culling is almost a strict taboo. Yet, it is necessary to complement systematic breeding efforts, whether we like it or not. Now, before breeders rush off into the garage and get their big axe out, I would like to stress that I am IN NO WAY suggesting any killing of puppies. While people in the past supposedly did not know any better or didn't have the means, today we have the privilege to have modern tools at hand that would allow breeders to cull without actually harming the individual dog. Recall that the real objective here is only to eliminate unfit phenotypes from the gene pool, not to harm dogs. The overall goal of such an endeavor really should be to improve the health of the intact population as a whole. Modern tools could be comprised of spaying/neutering, limited registration, withholding pedigrees until breeding age, shared ownership etc. Responsible breeders should first and foremost keep the well-being of the breed in mind. Such an effort can only be a bottom-up approach and not dictated by breed registries.

In conclusion, linebreeding techniques are unquestionably useful in a breeder's aspirations to produce better dogs. Incestuous inbreeding, if applied correctly, can be very effective in fixing genes of interest. However, these techniques require very close monitoring of the offspring, in particular for undesired traits – and harsh culling.

Continued on Page 29

BREEDING - THE BIG PICTURE! CONTINUED

People are frequently unaware of how quickly a given dog population converges into a single cluster of interrelated specimens. This occurs at a much accelerated rate, when breeders all eagerly breed to the same show champion. This can cause problems rather sooner than later. It is therefore a myth that all puppies from reputable breeders will be of outstanding quality. This viewpoint may be lucrative for the individual breeder, but let's face it, not all puppies should be bred down the road. If culling is omitted for financial or emotional reasons, all that people are really doing is to support the increase of genetic problems for future dog generations.

I realize that I have only scratched the surface of many issues. I did not aspire to achieve even remotely thorough coverage of this complex matter. But I hope that I could at least provide some rationale, why breeders should start seeing the breed in a big picture, and especially the potentially detrimental effects that their own actions might have for the entirety of the breed. There will surely be those who will utterly refuse to accept the importance of culling as part of a comprehensive breeding strategy and I understand that this can be a controversial issue. Nevertheless, IMHO it is part of the equation.

Or just as the novelist and philosopher Ayn Rand put it, **"The way to kill greatness is to elevate mediocrity."**

By Dan Astibus sharplaninec.com (republished with permission from the author)