



THE MATERNAL GRANDSIRE

by Cindy Vogels

Genetics work in horses and mice has produced revolutionary and exciting new insights that may influence your canine breeding decisions. For years, horsemen have acknowledged a phenomenon called the maternal-grandsire effect, when outstanding males do not immediately reproduce their greatness in the next generation. Instead, they produce daughters who are outstanding dams. An oft-cited example is Secretariat, perhaps the greatest thoroughbred of all time. Secretariat's achievement was not matched by his direct get, who by and large were unremarkable, but rather was passed on through his daughters, many of whom went on to produce great performers. Dog breeders, too, have noted that an extraordinary male, while not producing extraordinary offspring, will often produce daughters who are prolific and exceptional dams. For years, there was absolutely no scientific explanation of this phenomenon in which traits skip a generation and are passed along only by female offspring. Recently, however, an article documenting scientific evidence of the maternal-grandsire effect appeared in issue number 242 of *Equus*, an outstanding horse publication. I acknowledge that article for providing me with much of the information in this column.

Some Genetics Background

In each cell of a dog's body there are 39 pairs of chromosomes, one set from each parent. Each chromosome pairs off with a corresponding chromosome of the other parent, and in each chromosome there are thousands of genes, which contain the protein codes that determine every physical trait. Within a pair of chromosomes will be pairs of genes from each parent that determine various traits. When the genes are not in conflict with each other - both expressing brown eyes, for example - there is no problem.

However, if one chromosome contains the gene for brown eyes but another one contains the genes for green eyes, long-accepted Mendelian theory states that only the genetically dominant chromosome will be expressed. The theory also states that genetic dominance is unrelated to the sex of the gene donor. When both genes are expressed, they are considered to be co-dominant. Coat color, for example, is an area in which both genes can sometimes exert influence. Other times, both genes are recessive, but one is nonetheless more dominant than the other, thus allowing a recessive gene to be expressed. Recessive genes may also be expressed when both contain the same protein code for a trait.

A Startling Study

In 1969, Dr. W.R. Allen startled the world with a study that seemed to indicate certain genes might be gender-related in their expression. Allen bred horses and donkeys, and during pregnancy measured levels of the pregnancy hormone called equine chorionic gonadotrophin (ECG). Normally this level is high in horse-horse crosses and low in donkey-donkey crosses. According to Mendel, it should not have made any difference which species served as sire or dam. The levels should reflect a combination of the two species, and would either be a moderate level (indicating co-dominance), or if one species dominated, the level would be either high or low. Surprisingly, the mares (horse females) bred to donkeys exhibited low levels of ECG, much like a donkey-donkey cross, and the jennies (female donkeys) bred to horses registered high levels of ECG, as in a horse-horse cross. Although no definitive conclusions were reached, it appeared that the sires' genes were the only factor affecting the ECG levels in the females. The females' genes were silent.

It was not until 1986 that the topic reappeared in the literature. A research team headed by Dr. Azim Surani used mice to create embryos in which all the genetic material was received entirely from either one parent or the other. Since the material was transmitted in appropriately matched pairs, Mendelian theory would have predicted that the embryos would develop normally, since it was only the presence of two genes for each trait, and not the sex of the gene donors, that was considered relevant. Again, however, Mendelian expectations were confounded, as the all-female gene pairings resulted in large placentas with little embryonic material. The all-male gene pairings produced the opposite result: small placentas with large embryos. Surani's team concluded that some genes do not follow Mendel's laws. Some are "switched on" before fertilization and are always expressed, while others are "switched off" and never expressed. The sex of the gene donor is the factor that determines which mode a gene will fall into. A theory called "genome imprinting" was created to account for this previously unformulated phenomenon.

For example, say there is a canine gene that is paternally imprinted and, when expressed, produces three-eared dogs. When the gene is not expressed, the dog has two ears. A three-eared male inherits the gene from his mother, but because a gene that is paternally imprinted is switched off when passed on by a male to its offspring, he will have all two-eared offspring. His male two-eared offspring will not produce three-eared dogs, but his daughters will, because a gene that is paternally imprinted will be switched on in females.

Questions and Implications

Many questions still remain, and the literature is vague on why the phenomenon might occur. Researchers point to the significance of gender-related functions. For example, it appears that males strive to produce virulent, robust

get, while females, for their own well-being, control the size of their offspring. Imprinted genes are quite possibly involved in traits inherited polygenically. If only some of the genes are switched on, the work of the geneticist tracking inheritance becomes more complicated.

The implications of this finding go far beyond the world of Thoroughbred racers. Already, a number of imprinted human genes have been pinpointed. Ongoing mapping of the canine genome should increase the likelihood of detecting imprinted genes in dogs. The most important contribution would probably be in the realm of canine health, but eventually we might have the tools to track the inheritance of many canine characteristics that seem capricious in their skipping of generations.

Dog breeders should be aware of this possible maternal-grandsire effect. Keep in mind, however, that outstanding males tend to be bred to outstanding females, so even if some of the male's desirable genes are paternally imprinted, the offspring of such matings will probably inherit some excellent traits from their exceptional dams. For example, this year's Kentucky Derby and Preakness winner, Charismatic, was sired by 1990 Preakness winner Summer Squall, who is out of a Secretariat daughter. While Summer Squall's prowess on the track could be traced to the maternal-grandsire effect, he seemed to pass his greatness along directly to Charismatic. However, Secretariat's mother appears another time in Charismatic's pedigree and Secretariat's sire Bold Ruler appears twice. So, the talented colt's lineage points back to many outstanding individuals. A pedigree, whether for dogs or horses, always contains many influences and variables. We dog breeders tend to be impatient and are disappointed when an outstanding male does not immediately reproduce his excellence. Remember the maternal-grandsire effect, and wait a generation.