

THE RELEVANCE OF BREED IN SELECTING A COMPANION DOG

By Janis Bradley

National Canine Research Council



The Relevance of Breed in Selecting a Companion Dog

An NCRC Vision Series Publication

Janis Bradley

The National Canine Research Council is committed to preserving the human-canine bond. We publish, underwrite and reprint accurate, documented, reliable research to promote a better understanding of our relationship with dogs. We make grants to universities, independent research organizations and independent scholars. We also conduct our own research on contemporary issues that impact the human-canine bond, including the dynamics of popular attitudes towards dogs and canine aggression; public health reporting on dog bites; public policy concerning companion animals; and media reporting on dogs.

Copyright © 2011 by National Canine Research Council, LLC

All rights reserved.

Printed in the United States of America

ISBN 978-0-9835085-0-2

Published by National Canine Research Council, LLC

www.nationalcanineresearchcouncil.com

Acknowledgements

Janis Bradley would like to thank Jane Berkey, Donald Cleary and Kara Gilmore for their vision in supporting this effort to shine the light of science on one of the most mythologized aspects of the human-canine relationship.

The National Canine Research Council would like to thank Amy Marder, V.M.D., CAAB, and Alice Moon-Fanelli, Ph.D., CAAB, for lending their expertise in reviewing this NCRC Vision Series Publication.

The Relevance of Breed in Selecting a Companion Dog

Executive summary

Prospective pet owners and policy makers would like to be able to predict the probable future behavior of dogs in order to choose appropriate companion dogs and to anticipate problematic behaviors such as aggression toward humans. Such predictions are commonly made based on presumed breed characteristics, both in the case of purebred and mixed-breed dogs. These predictions rest on three main assumptions: that dogs are readily identifiable as members of a particular breed; that behavior can be reliably predicted according to breed; and that the behaviors associated with specific breeds are relevant to the contemporary function of most domestic dogs as companions for human families. The purpose of this paper is to examine these assumptions in order to determine whether a breed label is a useful indicator of the suitability of a companion dog.

Identifying the breed of individual dogs presents many difficulties. A majority of dogs in the United States, including many of those awaiting rehoming in shelters or with rescue organizations, are of mixed-breed ancestry. Visual breed identification of these dogs has been shown to be extremely unreliable when compared to DNA analysis. When adoption agency personnel were asked to list the various breeds they thought comprised a dog's background, they were only able to include the actual predominant breed for one dog in four. What's more, these observers often did not agree with one another's identifications.

Although the influence of genetics on behavior can certainly be demonstrated, the primacy of appearance over behavior as the selection criteria for modern purebreds often makes the variability of behavior within breeds similar to that of the species as a whole. For example, while studies differ in the extent to which aggression varies between breeds, all agree that aggression varies most dramatically from individual to individual. It is possible that members of completely closed gene pools gradually become more and more alike in characteristics other than those actively selected for, in a phenomenon called genetic drift. But there is no clear evidence as yet that this has happened with specific dog breeds. Even in a breed such as racing Greyhounds, which are still selected for the specific simple behavior of chasing a small prey-like object, the target behavior is expressed in only 70-80% of individual dogs, a rate that may not be much higher than that found among the species as a whole. Of course, dogs have been selectively bred and continue to be selectively bred for specific kinds of work, and those with a genetic predisposition to express certain behaviors will excel when they are put in a training environment that rewards and perfects those behaviors. This is particularly true with very specific specialized behaviors such as pointing game and “eyeing” livestock.

Nevertheless, there is strong evidence that some earlier types of dogs, such as flock guardians and the hunting dogs sometimes called “walking hounds,” which appeared long before the advent of modern purebreds in the late nineteenth century, acquired their specialties for such behaviors as guarding livestock and hunting more through socialization and simple training than selective breeding. Moreover, many behaviors initially selected for among various types of dogs are fragmented aspects of predation such as stalking,

chasing, and grabbing, which have little relevance to desirable companion-dog traits, beyond, in some cases, indicating general energy level.

Therefore, since a majority of dogs in the U.S. are of mixed-breed ancestry that cannot be reliably identified even by professionals, since, even among purebreds, breed is an unreliable predictor of behavior, and since most of the behaviors associated with specific breeds are only tangentially related to desirable and undesirable qualities in pet dogs, the practice of relying on breed identification as a primary guide in either pet-dog selection or dangerous-dog designation should be abandoned. As casual attributions of breed ancestry to mixed-breed dogs are inherently misleading, dog professionals should create new schema for referring to this population. The focus of predicting behavior should shift to the particular dog's personality as developing from the interaction of genes and environment and to dogs as multifaceted individuals, bearing in mind that the guardian's choices about how to live with a canine companion are likely to shape the dog's behavior. Public policy decisions should focus on the actual behavior of both the individual dog and the human guardian.

Table of Contents

1. The Issues

- 1.1. Need for predictability in behavior
- 1.2. Conditions necessary for predicting behavior according to breed
 - 1.2.1. Breeds must be identifiable
 - 1.2.2. Behavior must be predictable according to breed
 - 1.2.3. Predictable breed-based behavior must be relevant to companion dog characteristics
 - 1.2.4. Behavior must be predictable according to physical characteristics independent of breed (alternative to 1.2.2 above)

2. Are most dogs readily identifiable as members of a specific breed?

- 2.1. Reliability of visual identification of mixed-breed dogs
- 2.2. Effect of outcrossing on inbreeding

3. Is behavior predictable according to breed?

- 3.1. Genetic influence on behavior
- 3.2. Greyhounds: a breed rigorously selected for ability and motivation to chase a lure at great speed
 - 3.2.1. Selection criteria
 - 3.2.2. Selecting for motivation: the predation sequence
 - 3.2.3. Rate of success in selecting for motivation to chase
- 3.3. Selection for behavior among modern dog breeds
 - 3.3.1. Definition of purebred dog

- 3.3.2. Usefulness for genetic research
- 3.3.3. History of breeds as closed gene pools
- 3.3.4. Breeding for appearance versus breeding for behavior
- 3.4. Types of dogs before the modern purebred:
 - Traditional dog functions
 - 3.4.1. Role of Selection
 - 3.4.2. Effect on morphology (appearance)
- 3.5. Evidence for behavioral uniformity among purebred dogs: aggression

4. Are breed-selected behaviors relevant to desirable companion dog traits?

- 4.1. Selected behaviors and pet dogs
- 4.2. Socialization and Behavior

5. Are specific morphological traits predictive of behavior?

- 5.1. Genetic correlations with aggression
- 5.2. Domestication and behavior: the farm fox experiments

6. Conclusions and recommendations

- 6.1. Education in appropriate husbandry for behavioral health
- 6.2. Public Policy
- 6.3. Mixed-breed dog identification

1. The Issues

1.1. Need for predictability in behavior

There are various reasons why people would like to be able to predict a dog's behavior. One of the most common is in order to select a dog that will make an appropriate pet for the person, and be a good match in terms of temperament and energy level. This might be someone who asks a dog professional how to find a puppy that will grow into a calm and friendly dog because she wants to participate in animal-assisted therapy at local nursing homes. Or it could be someone who is looking for a dog that is likely to be successful in some desired service or competitive role. The person who wants to train a search-and-rescue dog, for example, is looking for particular behaviors, primarily a keen, indefatigable retrieving impulse. In addition, people often would like to be able to predict the behavior of unfamiliar dogs they encounter, especially the likelihood of aggressive behavior toward themselves or people in general. In all these cases, assessments are often made based on the breed of the dog or even on an inferred breed identification based on the appearance (*morphology*) of a dog whose ancestry is unknown.

1.2. Conditions necessary for predicting behavior according to breed

The purpose of this paper is to investigate whether the practice of attempting to predict a dog's behavior based on its breed or on its assumed breed (based on morphological similarities to a breed description) is likely to yield useful results. In order to make such predictions, all four statements below must be demonstrated to be true.

1.2.1. Breeds must be identifiable

This statement requires that one can readily identify by sight the predominant breed or breeds in a given individual without other evidence such as pedigree, breed registration, or DNA analysis. This is particularly important with regard to mixed-breed dogs.

1.2.2. Behavior must be predictable according to breed

This statement requires that dogs of a particular breed can be expected to be substantially more likely to behave a certain way than is typical across the species because they were once (or are still, in the case of working dog^{*} lines) bred to behave that way.

1.2.3. Predictable breed-based behavior must be relevant to companion dog characteristics

This statement requires that the behaviors dogs were bred for (see 1.2.2 above) can be extrapolated to lead to behaviors significant to pet dog owners today.

^{*} Here and throughout this paper, “working dog” refers to any dog whose primary function is one of either competitive or real-world work, e.g., field trials, herding and flock guardians, protection, search-and-rescue, guide dogs, etc. This is not to be confused with the designation of particular breeds as the working group.

1.2.4. Behavior must be predictable according to physical characteristics independent of breed (alternative to 1.2.2 above)

An alternative to 1.2.2, this statement requires that certain physical characteristics can be highly correlated with specific behaviors, eliminating the need to establish relatedness, such as breed membership.

If any of these statements can be shown to be unreliable, then attempts to predict behavior based on breed or appearance must be abandoned.

2. Are most dogs readily identifiable as members of a specific breed?

This first assertion (1.2.1.) is the part of our reasoning that affects our perception of the greatest number of dogs. Difficulties immediately present themselves, as even experienced people cannot reliably identify the breed of any dogs except those of the most popular and phenotypically distinct breeds.

2.1. Reliability of visual identification of mixed breed dogs

For a variety of reasons, people in rescue groups and shelters are in the habit of assigning breed labels to the dogs in their care. DNA identification of breeds,* which is now readily available, has shown that labeling of mixed-breed dogs according to morphology is extremely unreliable.^{1,2} Owners of mixed-breed dogs who have noticed physical characteristics similar to those of one or two breeds in their dog's appearance, are often astonished that the results of these tests come back very different from what they had expected.³ Even if there are only two breeds in a dog's lineage (probably a rare occurrence in the general dog population), as in the most famous study of genetics and dog behavior completed by Scott and Fuller in 1965, the first generation (F1) crosses often do not resemble either of their parents' breeds (see Figures 1a and 1b).⁴ What's more, when Scott and Fuller bred these first-generation crosses to

* DNA analysis (Mars WISDOM™ panel) used to identify the lineage in the shelter study has been shown to be 84% reliable when compared to known parentage of mixed-breed dogs.

each other, none among the resulting (F2) generation puppies looked much like either breed. The photographs accompanying the text showing the F2 generation of Basenji/Cocker crosses reveal a startling diversity among them. Some of the puppies would likely be readily identified by most people as “predominantly” of breeds such as Labrador, Beagle and perhaps Springer, when their actual grandparents were two Cockers and two Basenjies. (see Figure 2).

Moreover, a recent genetic study comparing dogs from eighty breeds, feral dogs, and wolves has shown that a large number of morphological traits in dogs, from length of limbs to skull shape to weight to ear set and coat type, are determined by a very small number of “large effect” genes.⁵ This means that even a small proportion of a particular breed in a dog’s ancestry may result in a strong resemblance to that breed. So we cannot attribute “predominant breed” identification to any dog based on appearance, no matter how striking the resemblance.

Figure 1a.



Ancestral cocker spaniels 0414 V and 0415 z.



Some offspring of the ancestral cocker spaniels used in the cross.

Breeding stock—BCS cross

Mated pair—basenji ♂ and cocker ♀.



BCS F₁ hybrids—♂ and ♀ pair.

Scott, JP, Fuller, JL, *Genetics and the Social Behavior of the Dog*. (Chicago, IL: University of Chicago Press, 1965).

Figure 1b.



Ancestral basenji 739 ♂ and 1090 ♀.

Breeding stock—CSB cross

Mated pair—cocker ♂ and basenji ♀.



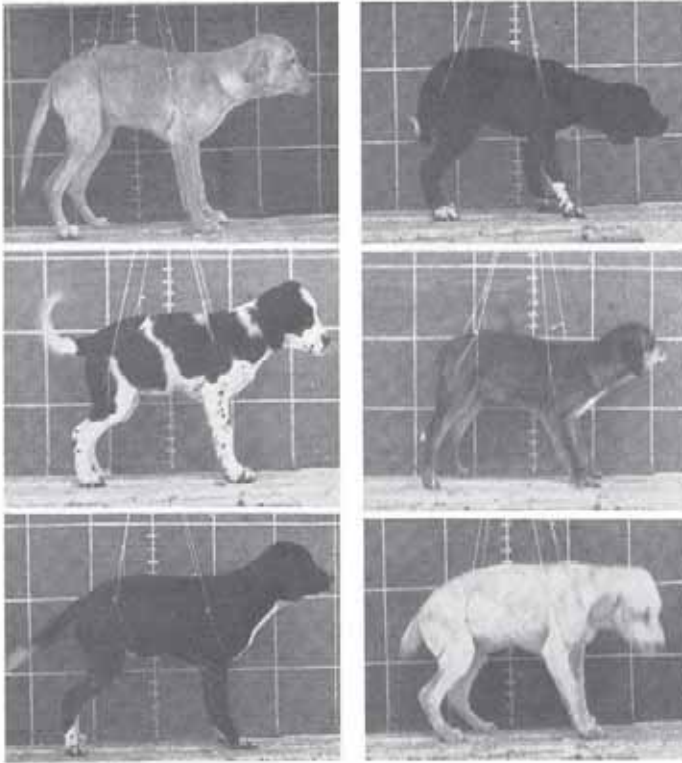
Some offspring used in the cross. ♂ on the right.



CSB F_1 hybrids—♂ and ♀ pair.

Scott, JP, Fuller, JL, *Genetics and the Social Behavior of the Dog*. (Chicago, IL: University of Chicago Press, 1965).

Figure 2.



BCS F_2 litter 3193–3200. Note the great variety of form and color in these animals.

Scott, JP, Fuller, JL, *Genetics and the Social Behavior of the Dog*. (Chicago, IL: University of Chicago Press, 1965).

2.2. Effect of outcrossing on inbreeding

Appearance, like other traits, can only be used to reliably infer membership in a particular group if that group becomes so inbred that the natural diversity of the species has gradually disappeared. Even the results of inbreeding

readily disappear with very slight outcrossing (the introduction of new individuals from outside a closed gene pool). For example, in a wild wolf population in Sweden so extremely inbred that the population was dying out because of fertility problems, the introduction of a single outside individual brought so much diversity that the problem allele (the code written on a gene) was re-randomized into the mix and no longer presents a threat.⁶ Therefore, any given trait, such as a morphological characteristic, is simply a very poor indicator of the breeds in the background of any mixed-breed dog, i.e., any dog either of whose parents was not a purebred of the same breed.

A specific trait illustrates this point. There has been some study of the genetics of skull shape in domestic dogs.^{7,8} Dog skulls vary in several dimensions, and while not on a perfect continuum, some dimensions become larger or longer or wider or narrower in concert with others. One need only think of a Pekingese's head and compare it with that of a Greyhound to form a mental image of the range of diversity. Individuals of any skull shape can be bred gradually in lines that will bring them closer and closer to the other types. No one expects, however, that this change would carry with it any other traits found in different breeds that also have the same skull shape, certainly not behavioral ones. Nor is a similar skull shape indicative of relatedness of two individuals. It carries no implications of common ancestry. To make such an inference would be tantamount to ascribing a specific ethnicity to a human based solely on hair color, e.g., assuming a person with blond hair must be Swedish. There are almost certainly as many genetic pathways to blocky or pointy skulls in dogs as there are to blond hair in humans.

Even in the United States where there are significant populations of purebred dogs, the majority of dogs are almost certainly products of a very diverse gene pool, a virtual genetic sea, as it were. According to our best estimates, there are approximately seventy-seven million domestic dogs in the U.S. as of this writing.⁹ The most recent survey by the American Pet Products Manufacturers Association cites fifty-six percent of the dog owners they surveyed reporting their dogs as “purebred.” However, since only forty percent of these dogs were acquired from breeders or pet stores (the most likely sources of actual purebred dogs) and since even some of these are certainly hybrids of various “designer” breeds, in other words F1 and F1 crosses, the percentage is probably considerably lower, particularly since owners tend to over-report their dogs as purebreds. The only dogs we can document as purebreds are the roughly 1.1 million registered each year in the U.S. by the main registering organizations, the American Kennel Club (AKC)^{*} and the United Kennel Club (UKC).^{10,†} Even if we assume that all of these puppies will make it to adulthood, and we set the average life expectancy of a purebred dog in the U.S. very generously at twelve years, this means about thirteen million registered purebred dogs are alive in the U.S. at any time. And if we—again, very generously—double this number to include possible pockets

^{*} AKC registrations have dropped substantially in recent years, down from 1.3 million in 1996 to 870,000 in 2006. It is not known whether this is due to fewer owners registering their dogs or fewer breeders adhering to the closed lineage pedigrees required for registration.

[†] There is some cross-registration between these agencies, so the 1.1 million total (870,000 AKC and 250,000 UKC in 2009) is probably generous. It is important to limit our discussion of purebred dogs to this population as all the rest may be subject to out-crossing which dramatically undermines the predictability of genetically determined traits in subsequent generations.

of localized closed populations of dogs bred for special purposes but not registered, and those pedigreed dogs whose owners don't bother with registration, we still have a maximum of twenty-six million. The remaining forty to fifty million are certainly subject to outcrossing at the least. Most are probably simply mixes with various breeds in their backgrounds. The physical resemblance of any of these forty-plus million dogs to a "purebred" presents no evidence whatever of its genetic relatedness to the members of the small, stagnant registered breed pools. All of their traits, morphological and behavioral, partake of such a diversity of potential alleles that it is not possible to make any predictions whatsoever about the behavior of these dogs based on the breeds in their backgrounds and certainly not based on any physical resemblance they may have to members of purebred dog breeds.

3. Is behavior predictable according to breed?

This leads us to statement 1.2.2., which concerns predicting the behavior of purebred dogs. Can we expect that dogs of a particular breed will behave in certain ways because they were once (or are still) bred to do specific kinds of work?

3.1. Genetic influence on behavior

Everyone acknowledges that the likelihood of an animal expressing a particular behavior can be influenced by genetic selection. People have been selectively breeding domestic animals for several centuries at least. And the literature of biology is replete with examples of geneticists taking a single closed population (sometimes a single breeding pair) and dividing the offspring into more and more divergent lines in terms of a single characteristic. It often takes only a few dozen generations to alter the selected characteristic. Lines of stickleback fish have been selected to be extremely aggressive.^{11,*} Rats have been successfully separated into lines that fear and attack approaching humans and ones that seek out human contact, as have, most famously, Siberian Silver Foxes.¹⁴

Experimenters have separated Pointers into generally fearful, nervous lines and much calmer ones.¹⁵ In each case, the goal of selective breeding is to isolate some

* When biologists breed for aggression, what they are usually referring to is triggered and more intense aggression toward the animal's own species. For example, they might count how often and in what proximity and for what duration Stickleback fish males attack one another in the tank. It is unlikely that there is a generalized trait for heightened aggression. Rather, there is an intensification of aggressive responses to particular stimuli, e.g., conspecific competitors.^{12,13}

morphological or behavioral characteristic or combination of characteristics that already exist in the population and either increase or decrease their frequency or intensity.

3.2. Greyhounds: a breed rigorously selected for ability and motivation to chase a lure at great speed

Racing Greyhounds are an interesting real-world case in point. They are probably the only remaining example in the United States of a large population of dogs selected strictly for behavior. At least 23,000 racing greyhounds are bred in the United States annually.^{16,*} In racing Greyhounds, as with other purebred dogs, we have a closed gene pool with pedigrees maintained over many generations and no outcrossing permitted.

3.2.1. Selection criteria

As is always the case in real-world selective breeding, the desired behavior has two components: physical aptitude and the inclination to engage in the behavior. In the case of Greyhounds, the physical aptitude is the ability to run faster than any other breed of dog, which involves adaptations in both anatomy and physiology. The inclination is keen motivation to chase rapidly retreating small furry objects.

* There is also an American Kennel Club breed registry for Greyhounds who are shown in conformation competitions – what we normally think of as dog shows – but these animals are not permitted to be interbred with the racing dogs. As with all AKC breeds, the selection criteria are all appearance-based, so it is unlikely that the AKC-registered Greyhounds would be competitive as racing dogs.

This selection is done in the simplest way possible: by breeding only those dogs who win the most races. There is no breeding for appearance. No one cares what color the dogs are, or about the set of their ears, or their dentition, or even their size. No one breeds for the characteristic elongated body and limbs and head and tail—the image imprinted on most of our visual memories by a silhouette on the side of a bus. This anatomy is simply the result of selecting rigorously for the ability in dogs to run fast.

3.2.2. Selecting for motivation: the predation sequence

Of course, none of this physical ability is of any use if the dog is not strongly motivated to chase. The inclination to chase (or rush the prey) is probably the aspect of the predation sequence that is most commonly exhibited across the entire *canis familiaris* species, and so it ought to be relatively easy to select for. The predation sequence, as defined by wolf biologist David Mech, is composed of seven behaviors: search, stalk, rush, grab, kill, dissect, and eat.¹⁷ Such behaviors fall into the ethological category called modal action patterns (*MAPs*), which are behaviors that do not have to be learned, but are immediately fully expressed in the presence of the triggering stimulus, although in some cases the trigger exposure has to occur at a specific developmental stage or the behavior will never manifest. The six-week-old retriever puppy who toddles after the first object that rolls across the floor and picks it up is expressing a modal action pattern. Such behaviors can be modified by learning, but they require only a trigger (e.g., the object rolling across the floor) to be expressed. Much of the selection for behavior across the species has focused on one or more of the predatory components, sometimes also

attempting to weed out others. Breeders of hounds select for search behaviors; herding dog breeders want the stalk and rush, but usually not the grab (except in cattle dogs) and certainly not the kill and dissect; retrievers are supposed to rush and grab; pointers and setters primarily stalk, and so on.

Greyhound breeders don't worry about getting rid of the aspects of the sequence that do not relate to chasing. They don't need to. The kill and dissect behaviors aren't a problem as the racers never have the opportunity to catch the mechanical "prey," and they are unlikely to emit the search or stalk behaviors on the racetrack because the prey appears already in motion, which triggers the chase. The unselected behaviors randomize—some individuals will have them and some won't. But in Greyhounds the rush or chase is ruthlessly selected for. Unsuccessful dogs simply do not reproduce.

3.2.3. Rate of success in selecting for motivation to chase

Even after hundreds of generations of this selection, experts in the field estimate that at least 25% of the pups in racing lines wash out long before they ever get to a race-track where they can be weeded out if they are not fast enough.¹⁸ Remember breeders are selecting for a trait that is already expressed in most dogs across the species. Greyhounds that aren't keen to chase are culled before they can race. As an aside, it's quite possible that this inability to get Greyhounds to fully "breed true" to the chase behavior is a result of the breed's relatively large gene pool.¹⁹ Breeding for a specific behavior, even a very common one, is an iffy

business, no matter if it is done with single-minded rigor. Anything less than strict selection is likely to result in behavior re-randomizing across the gene pool. Since the other parts of the predation sequence aren't selected for or against, some retired racing Greyhounds will, in fact, kill a small animal once they catch it; others will not and may even be injured by an indignant but unscathed cat. Some are inclined to follow scents when at liberty in the open. Others are not interested. Some like to tear up their toys (dissect); others have the same toys undamaged for years.

The consequences of the Greyhound's selective breeding are in stark contrast to what happens with wolves, which are ruthlessly selected by their environment to emit the full predation sequence. The alternative is starvation and failure to reproduce. Since domestic dogs seldom rely on complete predation for survival or for reproduction opportunities, the behaviors tend to drift across the species, with some individuals expressing the entire sequence, others showing fragments, and some showing no inclination to predation at all. There is no way to predict even the probability of how much of the predation sequence will turn up in a domestic dog's genetic profile unless rigorous selection for specific MAPs has occurred.

3.3. Selection for behavior among modern dog breeds

With minor exceptions (such as the Greyhounds described above) there is little, if any, systematic selection for behavior among modern breeds. This is at the heart of the difficulty of statement 1.2.2., which concerns predicting behavior by breed.

People often expect certain behaviors from a purebred dog, believing that its forebears “have been bred for centuries” to hunt or guard or fight or herd (fill in any common behavior). This is simply not the case with modern dogs. First, the lineages of modern registered breeds are very recent, with most dating back only decades. The “bred for centuries” idea does not apply. Second and more importantly, in the relatively short period since there have been standardized selection criteria for purebred dogs, those criteria have related exclusively to appearance, not to behavior. Breed standards will sometimes give lip service to desired temperament but these qualities are never defined in a way that can be applied by a judge to the dog in a show ring. Because purebred dogs are judged entirely by how they look, morphological qualities are what breeders select for. There are breeders who specialize in dogs bred for specific competitions, such as hunting and herding, where the concern is for performance rather than appearance, but these dogs almost certainly represent a small subset of the purebred population. One recent study of purebred dogs in Sweden confirms that the emphasis on breeding for appearance has all but erased any behavioral selection that existed in the past, and this study included members of the breeds that were still being used in working dog trials of various kinds! When dogs of thirty-one breeds were compared for qualities like playfulness, sociability and curiosity/fearlessness, some differences among breeds were indeed found. However, nearly the full range of behavior across all the breeds studied occurred within every breed, suggesting that most work-related behaviors have long since randomized across the species. Most significantly, when the

breeds were grouped according to their original functions (terrier, herding and guarding*), the breeds from each group were equally distributed on all the qualities.²⁰

It remains to be seen whether trainers' and behaviorists' reports of clustering of behavior associated with particular breeds will one day be borne out by controlled studies, or whether any of the noted behavioral characteristics could then be tied back to a breed's original function. These reports may, of course, be found to be artifacts of differences in owner responses to behaviors, as was the case in one ground-breaking study of aggression in pet dogs which found that a bite of the same severity was considered more serious by the owner when the dog was a large male than when the dog was small or female.²¹ In addition, any study of breed differences in behavior would have to find a way around the confounding variable of the owners themselves, whose own expectations of a breed are likely to influence their treatment of a dog, and whose expectations of how to treat a dog are likely to influence their choice of breed. The person who chooses a dog with the expectation that it will be an enthusiastic watchdog is likely to treat that dog differently than he would treat a dog he had chosen with the expectation that it will be rambunctiously friendly with everyone it meets. Studies that take such variables into account have yet to be accomplished. However, as the genetic research progresses, a complex personality trait,

* Svartberg uses the term "working" to designate breeds traditionally used for guarding of property or livestock. I have changed it to "guarding" here to avoid confusion with the more generic use of "working" to mean any dog who works, i.e. performs a function other than companion or conformation show dog, which would encompass all the groups Svartberg refers to.

such as level of “sociability,” may well be found to be the result of an interaction among multiple genetic predispositions that occur more frequently among particular breeds than among the species as a whole, combined with equally variable social opportunities that affect the actual expression of the genetic potential.

3.3.1. Definition of purebred dog

To see why multiple genetic predispositions occur more frequently among particular breeds than among the species as a whole, we must examine what we mean by a breed. In the contemporary dog world, we generally mean purebred dogs, members of a gene pool closed for many generations with documented pedigree records. Or, as the American Kennel Club puts it, “a dog whose sire and dam belong to the same breed and who are themselves of unmixed descent since recognition of the breed.”²²

3.3.2. Usefulness for genetic research

This is certainly what geneticists mean by the term purebred, and this definition holds for all the research currently underway using dogs as a laboratory for trying to pinpoint the genetic aspects of all sorts of traits, physical and behavioral. This is the only useful definition from the geneticist’s viewpoint, as the advantage of a closed gene pool over any freely reproducing or even outcrossed group is that the genetic diversity is limited. This makes it easier to find the sources of differences among individuals.

These closed gene pools account for why purebred dogs have been the subject of something of a boom in genetic research over the last decade and a half. If you know that

two individuals are closely related (as are all purebred dogs of the same breed), and their morphology (appearance) is very similar, it simplifies efforts to correlate their genetic differences with the small physical differences and usually broader behavioral differences among them. For example, if they all share long golden hair, you don't have to waste your time worrying about whether the gene you think may hold the location for hip joints (which is an area of common weakness—and thus variability—in Golden Retrievers) is actually the location for coat color. If, on the other hand, you are trying to pinpoint differences between breeds, you look at genes whose alleles (the codes on the genes) are the same within the breed, but differ between breeds. In other words, these closed gene pools called breeds help scientists figure out where to look for alleles related to specific characteristics (all of which put together make up an individual's *phenotype*) in the dizzying complexity that is the *genotype* (the entire genetic makeup of an individual).

3.3.3. History of breeds as closed gene pools

This idea of a breed as a completely closed gene pool is quite recent.

It dates back only to the early 1880's, about a decade after the first multi-breed dog show competitions were held. These competitions originated in England, then quickly spread to the rest of Europe and the United States. Various clubs for owners of particular types of dogs had held earlier competitions, but this was the first attempt to bring together different types of dogs in single competitions. These competitions eventually led to the formation of modern breed associations, which, in turn, began to narrowly define the desired appearance of each breed, to select for this

appearance and to close the breeding pool to members of any other group. It is worth noting that these early associations included only a small fraction of the 161 breeds recognized today by the American Kennel Club, the umbrella organization for breed clubs in the U.S. In fact, only 35 breeds were represented at the first Westminster Kennel Club show in 1877. The remaining 126 breeds are thus much younger closed registries.

The idea of maintaining pedigree records and including only dogs of “unmixed descent” began a little later, in the late 1880’s. The AKC recognized its first few breeds in 1884 (nine breeds, all gun dogs, including retrievers, setters, and spaniels). Before this, pedigrees were not required for participation in shows. The owner simply arrived with his dog and paid his \$2. In fact, in the first Westminster show, there was a “Miscellaneous Class,” which included dogs described as “a cross between a St. Bernard and a Russian Setter and a dog named Nellie, born with two legs only.”²³ At first, the main reason for establishing centralized stud books and registration was simply to have a means to distinguish among the various Bobs and Jets and Vics and Nettles that appeared in the program.²⁴

3.3.4. Breeding for appearance versus breeding for behavior

Thus purebred dogs as they exist today are quite new to the species. And they are the only groups for which we have any scientific data showing their actual genetic relatedness. They have been selected exclusively for appearance. But what about dogs who seem by appearance or behavior or both to be examples of a certain “type” of dog? What was generally meant by breeds before our modern concept of the

purebred was developed in the show ring? Do such dogs still exist?

Of course, the original stock that went into the founding of the breeds of dogs now bred for appearance had themselves been selected for physical and behavioral aptitudes for certain kinds of work. However, once you begin to select for a morphological characteristic, your chances of carrying the behavioral characteristics along for the ride immediately begin to diminish. The biologist Ray Coppinger points out, that he must see a dog “running under load” to be able to tell anything about its physical ability or its inclination, i.e., its behavioral aptitude to pull a sled. The behavior exhibited in the show ring is standing; having a certain appearance while standing still is what purebred Huskies and Malamutes have been bred for for many generations. “In a few generations of selecting for specific size, color or other *superficial reminders* [emphasis mine] of the ancestral working dogs,” Coppinger maintains, “any of the innate predispositions for the ancestral work almost certainly deteriorate.”²⁵ Coppinger’s contention is, in fact, borne out by the results of the Swedish study mentioned earlier (see Section 3.3.).

Various genetic phenomena certainly occur in inbred populations that can create consistently passed-on traits. For example, when a closed population is too small for normal randomizing of genetic diversity, the scene is set for mechanisms such as genetic drift, meaning that the overall diversity of alleles tends to diminish over time, i.e., the members become more and more alike in more and more ways. And when breeding is managed to select for very specific traits, whatever other traits are found on that chromosome will come along for the ride. These mechanisms account for the high incidence of various health

problems within purebred populations, such as the recently studied autoimmune disease (similar to human Lupus) in Duck Tolling Retrievers.²⁶ It is important to emphasize that this effect occurs by chance. It would be pure coincidence if these phenomena happened to accentuate behavioral traits that humans had hoped to increase.

3.4. Types of dogs before the modern purebred: Traditional dog functions

Perhaps the expectation of predicting behavior by lineage is based on an attempt to identify the general working type in the dog's ancestry, apart from whether the dog is classified as a modern purebred dog. We have historical and anthropological documentation of dogs having varied dramatically in shape, size, and coat for several thousand years. The amazing plasticity of the species is nothing new and much of this is almost certainly due to selective pressures from humans. Moreover, historical records dating back many centuries mention specific types of dogs, usually referring to the type of work the dogs were used for. These dog types existed long before our modern concept of a purebred came into being. People have indisputably been selecting for specific physical and behavioral aptitudes in dogs for much longer than the modern idea of a purebred has existed.

One of the most fruitful ways to look at this question is Coppinger's anthropological approach, an observational study of human/dog interactions in parts of the world where these relationships seem to retain much of their ancient character. He has applied this approach to dogs used to guard livestock, to herd livestock, to hunt, and to pull sleds. Coppinger's observation is that the more casual forms of

artificial selection that take place in these function-driven settings consist primarily of culling and selective favoritism, rather than establishing truly closed gene pools. Sometimes even this rudimentary genetic pressure is absent. He describes the common practice in developing both flock guardian and some hunting dogs as “starting with any village dog,” and “socializing it to your purpose.”

Coppinger conducted interviews with various dog owners in communities where these ancient functions for dogs are still active. In the case of flock guardians, the socializing means raising the puppy with sheep as its sole companions. In the case of hunting dogs (Coppinger calls them “walking hounds”), it means raising them with farmyard animals (from chickens to goats) so the dogs won’t get distracted by them when chasing the intended prey through farmyards. With the hunting dogs, Coppinger found that the accepted practice is to use lots of social facilitation to show the puppies that chasing and playing with the intended prey is loads of fun, e.g., “dragging of a carcass lure,” and just bringing the young dog along on a hunt, so he discovers what a great time is to be had chasing stuff with the other dogs.

Coppinger also discusses the genetic selection for the more specialized hunting tasks, such as those that distinguish pointers from retrievers, for example, and the particular physical and motivational traits of successful sled-dog teams. In fact, a new study has found that the small, very specialized world of competitive sled dog racing has developed a genetically identifiable breed, the Alaskan sled dog, a hybrid of Siberian Husky, Alaskan Malamute, Pointer, Saluki, Anatolian Shepherd and Weimeraner. The most successful dogs in this sport are to be found within this new

breed, although the study included no data on how “true” the members of this new gene pool breed for the desired behavior and sub-sets of behavior.²⁷ So while the most successful sled racers were members of this breed, this does not mean that all, or even a majority, of the members of the breed are found to be suitable for the work they are bred for.

3.4.1. Role of Selection

Artificial selection has a role in all this, and a locale that regularly practices group hunts of specific “pest” or “varmint” species will soon develop its own version of a “mink hound” or an “otter hound” linked to the specific prey object. The dogs that do well at the activity will tend to be selected for special treatment and may even be deliberately bred to other successful individuals. Their progeny, in turn, are more likely to be selected for the socialization and “training” described above. “Huntsmen not only give good dogs more care but they give the puppies of good dogs more care. These puppies have value. Whether hounds or shepherd dogs, puppies from notable dogs can be easily sold.” But note that Coppinger is referring here to the immediate progeny of known successful individuals.

Before the standardized appearance-based pure breeds of today, most selection amounted to breeding to a locally known “good” dog. A person looking for a dog to do a certain job would try to find a pup whose parents had been good at the job he had in mind. However, since everyone knew there was no guarantee any puppy would have the desired traits, he would search, if he could afford it, for an already proven dog to buy. No one presumed that just any collie-looking or hound-looking dog would do, nor were these

looks uniform in any case, or even very similar outside the particular locality or the individual breeder's stock. And this remains the case today with field-bred lines of various breeds differing much more widely in appearance than their show-bred counterparts.

Interestingly, this practice of searching for a promising working dog among adult dogs, rather than relying on breeding programs, is becoming more and more common today. Professionals seeking all manner of real-world working dogs to do everything from police protection and search work to assistance for the hearing-impaired are finding their untrained candidates among shelter dogs. Breeding programs are often too expensive and too unreliable when compared to actually meeting an adult dog and assessing his readiness for whatever training is involved. Current adult behavior is always the best predictor of future behavior. This certainly holds true for companion dogs as well. One of the advantages of adopting an adult dog over a puppy is that one can see his actual behavior, starting with friendliness. This is much less risky than trying to predict a puppy's behavior potential.

3.4.2. Effect on morphology (appearance)

Local dogs will also tend to cluster around a physical norm, as similar size and athletic ability will help them stay together on a hunt or pull the sled with uniform force and direction. They become, in effect, an extended family with the level of similarity that you would expect in such a group. In fact, Coppinger notes that local breeders of working dogs often prided themselves on developing a distinctive look for the dogs they bred. This distinctive "look" however, in no way

approached the idea of a modern “breed standard” based on a uniform look that all breeders in the breed strive to match.

3.5. Evidence for behavioral uniformity among purebred dogs: aggression

One aspect of canine behavior that is of undeniable relevance to the choice of a companion animal is aggression, particularly aggression that rises to the level of biting and injuring human beings. Researchers have certainly attempted to find differences among breeds on this important aspect of behavior. The Swedish breed comparison study referred to earlier (see Section 3.3.) also presented some conclusions regarding breed and aggression. However, the aggression section of the test used in that study was shown to be invalid by the author’s own analysis. The only studies that can be shown to be both reliable and valid bear out the expectation that dogs bred for appearance are unlikely to maintain much behavioral uniformity. Only very modest differences in aggression levels have been documented between breeds. One large study in Germany found no significant levels of inappropriate aggression among eleven breeds that had been designated by the government of Lower Saxony as particularly dangerous.^{28,*} A follow-up study then compared members of these breeds with Golden Retrievers and again found no significant differences.^{29,†}

* As distinguished from “appropriate” aggression, i.e., reacting with growling, snarling, snapping when directly, overtly threatened, e.g., a stranger waving a stick at a dog.

† The results of this study actually resulted in the repeal of breed-specific legislation in Lower Saxony.

One large study of owner-reported behavior that did not make the distinction between appropriate and inappropriate aggression did find some differences among breeds in stranger-directed, owner-directed, and dog-directed aggression.³⁰ This study confirmed the finding of two earlier studies that showed the greatest variation in aggression is between small (more aggressive) and larger (less aggressive) breeds.^{31,32} The striking finding here, however, is that the rate of aggression toward humans was extremely low across all breeds. The mean on all human-directed aggression for every breed included was between “no” and “moderate” aggression. And only very small percentages of any breed were reported as ever showing what the study defined as “serious” aggression (“snaps, bites, or attempts to bite”).^{*} The difference between one or five dogs in a hundred is not particularly instructive for the potential pet owner seeking a single dog. Moreover, what differences there were appeared as much between the “working” and “conformation” lines within breeds as they did between breeds. For example, conformation lines of Springer Spaniels tested as slightly more aggressive than the field lines of the same breed. Such differences could be easily attributed to different husbandry decisions as show dogs and field competition dogs generally lead very different lives.

^{*} Whether or not one agrees to classify anything other than an actual bite as “serious,” the greater difficulty with this survey instrument is that respondents are instructed to count any “recent” (no timeline specified) incident as a positive for this behavior. This is analogous to considering any human who has ever had a shouting match with anyone as abnormally aggressive.

4. Are breed-selected behaviors relevant to desirable companion dog traits?

4.1. Selected behaviors and pet dogs

For the moment let's say that the ability and the inclination of dogs to do the work that they were selected for centuries ago were still more frequently expressed among members of those breeds than in the general canine population. What implications would this have for their suitability as companion animals today? As discussed above, many of these behaviors are fragmentary expressions of predation. If a dog is particularly inclined to chase small animals (or tennis balls for that matter), this may influence the kinds of games that he and his human guardian are likely to enjoy together. It is also possible that a dog with an extremely heightened inclination to perform any of these behaviors, such as those that may be seen in working lines of various breeds, may have difficulties in a typical pet dog home, e.g., the retriever who seemingly endlessly presents the ball to be thrown, or the cattle dog who nips at the heels of runners, or the pointer who spends hours quartering the local off-leash space looking for birds. All these behaviors originally needed to be expressed for many hours at a time; the work, whether herding sheep or cattle, or searching out and retrieving game, was likely to go on all day. Unless a person is looking for a long-distance-running companion dog or a competitive Frisbee® dog, the energy level and motivation to sustain such physically strenuous work for a long duration can be a challenge to the pet owner seeking to keep his companion occupied.

The Swedish study mentioned earlier (see Section 3.3.) found differences among breeds with regard to how boisterously the dogs greeted and played active games like tug of war with a stranger and how upset the dog became when confronted with very loud noises (gunshots and chains beating on metal) or the sudden appearance of scary human-size dummies. This may be a fruitful line of inquiry, although it presumes that boisterous greeting and play are more preferable to pet owners than more moderate behavior. Of course, it is possible that genetic predispositions exist for behaviors that do have unquestionable relevance to a relationship with a companion animal, behaviors such as resource guarding (possessive behavior toward toys, food, sleeping locations, etc.) and Neophobia (fear of novelty, e.g., fear and aggression toward strangers), even perhaps ease of housetraining and general energy level.

Insofar as such studies have been undertaken to date, they have relied on general breed observations by dog professionals, which presents the obvious difficulties of overgeneralization and bias that are inherent in such surveys.^{33,34,35} Direct owner surveys about individual dogs that are validated by hands-on behavior evaluations (see Section 3.5.) might yield more credible results. But even if such predispositions could be shown to be prevalent in specific breeds, breed inclinations are probably not the most fruitful area of inquiry since their predictive value will never be reliable at the individual level. A person looking for a pet is looking for an individual, not a breed. Thus genetic markers for behavior might be useful in assessing individual dogs, but may or may not turn out to occur consistently in the large genetic families known as breeds, particularly since selection for behavior has become the exception among

purebred dogs. The active field of behavior genetics may, of course, uncover genetic markers for relevant behaviors, but probably the most fruitful area of all for research in helping people live more happily with their canine companions would focus on identifying the husbandry techniques that best foster good relationships.

Even if all of the predispositions among purebred dogs discussed here can eventually be documented, it is important to remember that they would not be relevant to people seeking to choose an adult dog where a behavioral history and observation of current behavior are available. Prior behavior is a much more reliable predictor of future behavior than is a genetic predisposition, which may or may not ever manifest itself. People seeking a dog most commonly choose a puppy that of course has no history of prior behavior and little relevant current behavior, as puppy evaluations to date have been shown to be completely unreliable. Even so, the actual behavior of the particular puppy's parents is likely to yield much more reliable information about the puppy's behavioral potential than general breed characteristics can.

4.2. Socialization and Behavior

Even the study most often cited in support of breed-specific differences in behavior contains support for the primacy of socialization in developing dogs as suitable companions for people. This is the major work completed in 1965 by Scott and Fuller that compares Beagle, Basenji, Shetland Sheepdog, and Fox Terrier puppies raised in a controlled kennel environment on a variety of problem-solving tests and

various other assessments, including aggression toward dogs and humans.³⁶ The study found some significant differences among the breeds when the puppies were raised in kennels. But the most striking finding is seldom mentioned. It concerns a few puppies that were raised in homes as family pets, rather than in the relatively socially impoverished kennel setting. Regardless of breed, these puppies became, as adults the most confident, social, and affiliative with humans at the top of the scale among all the breeds in these qualities. They did not, however, differ dramatically from their kennel-raised peers on the problem-solving tests that were central to the project.

A more recent small study of twenty-eight dogs of fourteen breeds distributed among the sporting, working, and terrier groups offers dramatic evidence of the power of dog/human relationships in influencing a dog's behavior. Dogs who lived in homes and were considered family members by their owners were compared with dogs who lived outside (in kennels or unconfined) and were considered to be primarily working or guarding animals.³⁷ Those in the first group, who had had an opportunity to form bonds with at least one human being, were found to be dramatically more friendly to humans in general, more inclined to stay close to people, more playful, and more likely to look to their human companions for help and encouragement when confronted with a problem-solving task than the dogs in the second group. Breed differences had no significance with regard to this behavioral division between the two groups. This finding lends powerful support to the position that differences in socialization may be more powerful than the genetic potential of a dog when it comes to qualities that actually affect the human/dog relationship.

5. Are specific morphological traits predictive of behavior?

5.1. Genetic correlations with aggression

Finally, we must consider statement 1.2.4., which, if established, would offer a way around the problems with 1.2.2. and 1.2.3. Can it be shown that certain physical characteristics are linked to specific behaviors, thus eliminating the need to place an animal within a particular gene pool where the behavioral characteristics have been selected for? Some findings among various species initially suggest that this might be the case. Albino mice, for example, have repeatedly been found to be more fearful than normally pigmented mice.^{38,39*}

5.2. Domestication and behavior: the farm fox experiments

The well-known Siberian Silver Fox experiments in Russia have shown that various morphological characteristics cropped up when selecting for the behavioral quality the experimenters have labeled *tameness*, meaning friendliness and actively affiliative behavior toward humans. The farm fox experimenters took a group of captive but undomesticated Silver Foxes and selected those that were least fearful into one line, gradually selecting for more and

* It is interesting to note that neither the albino mice and rat studies, nor any other studies of genetically determined traits correlating with elevated rates of aggression have successfully ruled out the possibility of the aggression as a secondary effect of the identified trait, e.g., causing discomfort that would be likely to increase general irritability.

more affiliative individuals. In about forty generations, they succeeded in producing a line of foxes, seventy to eighty percent of whom would enthusiastically approach and seek contact with unfamiliar humans, much as very friendly puppies would do. In this tame line, gradual changes also occurred in pigmentation (the foxes typically had large patches of white fur instead of the uniform blue/gray of the original line), in ear set (often showing folded ears rather than the upright ears of the original population), in skull shape (widened skulls and shortened snouts), and in tails (shortened and curled over).⁴⁰

The farm fox experimenters found that these same morphological changes can be seen in the fossil remains of the earliest dogs when they first diverged from wolves. Thus the common ancestors of all modern domestic dogs crossed the tameness Rubicon at the very beginning of the species. All domestic dogs have this genetic behavioral base. Researchers now believe that the dog's ability to notice and respond to human gestures and communication is part of this same tameness transformation.⁴¹

In any case, all domestic dogs share similar morphological differences from wolves. What this suggests is that the farm fox experiments have genetically duplicated in foxes the domestication process, i.e., becoming tame, that dogs experienced millennia ago, the process that actually defines them all as *canis familiaris* and not as wolves. Of course, the farm fox experiments do not imply that we should expect to find the friendliest dogs among those with piebald (as opposed to solid) coats, or folded down ears, or curled over tails. Rather, dogs made their behavioral transformation into

domestic, i.e., tame, animals millennia ago.* Only after this profound change occurred did humans begin to exploit the extraordinary plasticity of the species to change its appearance in myriad directions. There is no evidence that this morphological manipulation could in any way reverse or even affect the behavioral change toward tameness that had already occurred.† These tame behavioral characteristics are precisely what make a dog a dog and not a wolf.

The study described in Section 2.1. comparing wolves, feral dogs, and purebreds of eighty breeds confirms this. The geneticists found a clear genetic “bottleneck” (meaning all members of the group, in this case domestic dogs) separating wolves from feral dogs, with all the specific breeds descending from the ferals.⁴² Moreover, since the only traits they found to cluster together were morphological, there is no evidence at all that even a strong physical resemblance to a given breed would carry with it any particular behavior tendencies.

* Coppinger hypothesizes that the morphological norm for domestic dogs is something like the prototypical “village dog,” of his observations around the world: a smallish dog with a short coat and tulip ears.

† It is difficult, however, not to notice the irony in the fact that widened skulls and shortened snouts, relative to the population of dogs overall, are the morphological characteristics currently most associated with aggression toward humans in the popular media and general public perception today.

6. Conclusions and recommendations

The failure of one of the premises for predicting behavior by breed would be enough to render the practice useless. The fact that none of the four bases holds up to scrutiny leads us to the inevitable conclusion that the practice should be abandoned in the case of mixed-breed dogs and should be suspended in the case of purebred dogs unless and until genuine genetic breed-specific predispositions for relevant behavior can be documented.

And even such documentation, if it is accomplished, should not supersede the actual observed behavior of an individual dog. Presuming that a particular dog is more likely to behave in a certain way because of real or presumed breed identification does harm in at least two ways. It can lead people to presume that a dog is predestined to be so reliable that they need not worry about good behavioral husbandry, including diligent socialization. It also leads people to reject and even ban dogs with absolutely no valid scientific evidence indicating that this practice will result in fewer incidents of canine aggression.

6.1. Education in appropriate husbandry for behavioral health

Thus pet dog selection should focus on the dog as a multi-faceted individual. A prospective pet owner should look at the dog's behavior history and place it in context as much as possible. The actual observed personality always trumps any presumed potential. And because a pet dog lives in a relationship with humans, public education must also include how the guardian's choices about how to live with a canine

companion are likely to shape the dog's behavior. Education is necessary to help people learn what kind of care is needed to facilitate a dog's smooth integration into a human household.

6.2. Public Policy

Public policy decisions should focus on the actual behavior of both the dog and the human guardian. This is particularly important in the area of dangerous-dog law, where the ineffectiveness of correlating breed with aggression toward humans and other dogs has been well substantiated.

6.3. Mixed-breed dog identification

Since casual attributions of breed ancestry to mixed-breed dogs are inherently misleading, dog professionals should create new schema for referring to this majority of the domestic dog population. Various alternative names have been suggested elsewhere. A model practice might be one proposed last year at the 7th International Veterinary Behavior Meeting in Edinburgh. Potential adopters would be presented with behavioral profiles of potential pets, which rate each one for friendliness, fear, arousal, and aggression based on evaluations of the dog's actual behavior. These profiles along with such considerations as size, gender, age, and coat type would be used to help match people with appropriate companions.⁴³ An appropriate match could then be supported by good instruction on how to live successfully with the dog, how to provide sufficient social opportunities, mental and physical stimulation, and how to guide and modify behavior as needed. Even if the practice of DNA identification were to become routine among those working to home and rehome this population, breed attribution should

still be avoided as it serves to reinforce misconceptions among the general public about realistic expectations for the dogs carrying such labels.

Notes

1. Voith,V, Ingram,E, Mitsouras,K, Irizarry,K, “Comparison of Adoption Agency Identification and DNA Breed Identification of Dogs, *Journal of Applied Animal Welfare Science*, 2009, 12(3): 253-262.
2. Voith, V, “A comparison of visual and DNA identification of breeds of dogs”. *Proceedings of Annual AVMA Convention*, Seattle, WA, July 14, 2009.
3. Brackman,J, “Can DNA Decipher the Mix? Unraveling the genetic tapestry provides clues to breeds and their mixes.” *The Bark*, 2008, (50).
4. Scott,JP, Fuller,JL, *Genetics and the Social Behavior of the Dog*. (Chicago, IL: University of Chicago Press, 1965).
5. Boyko,AR, Quignon, P, Li, L, Schoenebeck, JJ, Degenhardt, JD, et al, “A Simple Genetic Architecture Underlies Morphological Variation in Dogs,” *PLoS Biol*, 2010, 8(8): e1000451. doi:10.1371/journal.pbio.1000451
6. Kojola,I, Casulli,A, Sand,H, Wabakken,E, Ellegren,H, Vilà,C Sundqvist,A, Flagstad,Ø, Seddon,J, Björnerfeldt,S, “Rescue of severely bottlenecked wolf population by a single immigrant,” *Proceedings of the Royal Society*, London, 2003, 91-97, <http://www.rspb.royalsocietypublishing.org>.
7. Drake,A, Klingenberg,C, “Large-Scale Diversification of Skull Shape in Domestic Dogs: Disparity and Modularity,” *The American Naturalist*, 2010, 175(3) 289-301.
8. Bannasch, D, Young, A, Myers, J, Truve´, K, Dickinson, P, “Localization of Canine Brachycephaly Using an Across Breed Mapping Approach,” *PLoS ONE*, 2010, 5(3).
9. American Pet Products Manufacturers Association, *2009-2010 National Pet Owners Survey*.
10. American Veterinary Medical Association, *U.S. Pet Ownership & Demographics Sourcebook*, (Schaumburg, IL 2007).
11. Bakker,T, “Aggressiveness in Sticklebacks (*Gasterosteus aculeatus* L.): A Behaviour-Genetic Study,” *Behaviour*, 1986, 98(1/4): 1-144.
12. Bakker,T, Sevenster,P, “Determinants of Dominance in Male Sticklebacks (*Gasterosteus aculeatus* L.), *Behaviour*, 1983, 86(2/3): 55-71.

13. Wootton,RJ, "Measures of the Aggression of Parental Male Three-Spined Sticklebacks," *Behaviour*, 1971, 40(3/4): 228-262.
14. Trut, LN, "Early Canid Domestication: the farm-fox experiment, *American Scientist*, 1999, 87: 160-169.
15. Murphree,OD, Peters,JE, Dykman,RA, "Behavioral comparisons of nervous, stable, and crossbred pointers at ages 2, 3, 6, 9, and 12 months," *Integrative Psychological and Behavioral Science*, 1969, 4(1): 20-23.
16. *American Greyhound Council*, <http://www.agcouncil.com/node/17>.
17. MacNulty,D, Mech,LD, Smith,DW, "A Proposed Ethogram of Large-Carnivore Predatory Behavior Exemplified by the Wolf," *Journal of Mammalogy*, 2007; 88(3):595–605.
18. Greyt2KUSA FactSheet, http://www.animalperson.net/animal_person/files/national_fact_sheet.pdf
19. Federico,CF, Calboli,J, Sampson,J, Fretwell,N, Balding, DJ, "Population Structure and Inbreeding From Pedigree Analysis of Purebred Dogs," *Genetics*, 2008, 179: 593-601.
20. Svartberg, K, "Breed-typical behaviour in dogs—Historical remnants or recent constructs?" *Applied Animal Behaviour Science*, 2006, 96: 293–313.
21. Guy, NC, Luescher, UA, Dohooa, SE, Spanglerc, Millerd, EJ, Dohooc, IR, Batea, LA, "A case series of biting dogs: characteristics of the dogs, their behaviour, and their victims," *Applied Animal Behavior Science*, 2001, 74(1), 43-57.
22. American Kennel Club, http://www.akc.org/classified/support/obc_glossary.cfm
23. Westminster Kennel Club, <http://www.westminsterkennelclub.org/about/amshow.html>
24. Sampson,J, Binns, MM, "The Kennel Club and the Early History of Dog Shows and Breed Clubs," *The Dog and its Genome*, Cold Spring Harbor NY: Cold Spring Harbor Laboratory Press, 2006, eds. Ostrander,EA, Giger,U, Lindblad-Toh,K, 19-30.

25. Coppinger,R, Coppinger,L, *Dogs: A Startling New Understanding of Canine Origin, Behavior, and Evolution* (New York: Simon and Schuster, 2001).
26. Wilbe,M, Jokinen,P, Truvé,K, Seppala,EH, Karlsson,EK, Biagi,T, Hughes,A, Bannasch,D, Andersson,G, Hansson-Hamlin,H, Lohi,H, Lindblad-Toh,K “Genome-wide association mapping identifies multiple loci for a canine SLE-related disease complex,” *Nature Genetics*, 2010, 42: 250 – 254.
27. Hudson,HJ, Parker,HG, Runstadler,J, Ostrander,EA, “A Genetic Dissection of Breed Composition and Performance Enhancement in the Alaskan Sled Dog,” *Genetics*, 2010, 11:71.
28. Schalke,E, Ott,SA, von Gaerner,A, Hackbarth,H, Mittmann,A, “Is Breed Specific Legislation Justified? Study of the results of the temperament test of Lower Saxony,” *Journal of Veterinary Behavior*, 2008, 3(3): 97-103.
29. Ott,SA, Schalke,E, von Gaertner,A, Hackbarth,H, “Is there a difference? Comparison of golden retrievers and dogs affected by breed-specific legislation regarding aggressive behavior,” *Journal of Veterinary Behavior*, 2008, 3(3): 134-140.
30. Duffy,DL, Hsu,Y, Serpell,JA, “Breed Differences in Canine Aggression,” *Applied Animal Behaviour Science*, 2008, 114(3): 441-460.
31. Guy,NC, Luescher,UA, Dohoo,SE, Spangler,E, Miller,JB, Dohoo,IR, Bate, LA, “Demographic and aggressive characteristics of dogs in a general veterinary caseload,” *Applied Animal Behaviour Science*, 2001, 74(1); 15-28.
32. Arhant,C, Bubna-Littitz,H, Bartels,A, Futschik,A, Troxler,J, “Behavior of smaller and larger dogs: Effects of training methods, inconsistency of owner behavior and level of engagement in activities with the dog,” *Applied Animal Behaviour Science*, 2010, 123(3): 131-142.
33. Hart,BL, Hart,LA, “Selecting pet dogs on the basis of cluster analysis of breed behavior profiles and gender,” *Journal of the American Veterinary Medical Association*, 1985, 186: 1181-5.
34. Hart,BL, Hart,LA, “Behavioral profiles of dog breeds,” *Journal of the American Veterinary Medical Association*, 1985, 186: 1175-80.
35. Tortora,DL, *The Right Dog for You*. (New York: Simon and Shuster, 1986).

36. Scott,JP, Fuller,JL, *Genetics and the Social Behavior of the Dog*. (Chicago, IL: University of Chicago Press, 1965).
37. Topál,J, Miklósi,A, Csányi,V, "Dog-Human Relationship Affects Problem Solving Behavior in the dog," *Anthrozoos*, 1997, 10(4); 214-224.
38. Fuller,JL, "Effects of the Albino Gene Upon the Behavior of Mice," *Animal Behavior*, 1967, 15(4); 467-470.
39. DeFries,JC, Hegman,JP, Weir,MW, "Open-Field Behavior in Mice: Evidence for a major gene effect mediated by the visual system," *Science*, 1966, 154(3756): 1577-1579.
40. Trut,LN, "Experimental Studies of Early Canid Domestication," *The Genetics of the Dog*, eds. Ruvinsky, A, Sampson J (Wallingford, UK; CABI, 2001) 15-43.
41. Trut,LN, Kharlamova, AV, Kukekova, AV, Acland, GM, Carrier, DR, Chase,K, Lark, KG "Morphology and Behavior: Are They Coupled at the Genome Level?," *The Dog and its Genome*, eds. Ostrander, E, Giger, U, Lindblad-Toh, K, (Cold Spring Harbor, NY: Cold Spring Harbor Press, 2006) 81-93.
42. Boyko, et al, 2010.
43. Marder,A, Voith,V, "The American Shelter Dog: Identification of dogs by personality," *Proceedings of the 7th International Veterinary Behaviour Meeting*, Edinburgh, 2009, 23-26.

About the Author

After more than two decades teaching college courses in several disciplines and working with adult students in the process of career change, Janis Bradley brought her skills in counseling and curriculum design to the San Francisco SPCA Academy for Dog Trainers. For a decade there she was one of the main architects of a uniquely student centered curriculum, preparing more than four hundred students for careers as professional dog trainers. She is among the first to apply modern educational and counseling techniques to the design of pet dog training classes and to the process of working with clients who need help resolving their dogs' behavior issues. Bradley is the author of a popular book on dog aggression, *Dogs Bite, but balloons and slippers are more dangerous*, and of *Dog Bites: Problems and Solutions* for the Animals and Society Institute, a position paper widely used by legislators investigating the dog bite issue.

The **National Canine Research Council** is committed to preserving the human-canine bond. We publish, underwrite, and reprint accurate, documented, reliable research to promote a better understanding of our relationship with dogs.

We make grants to universities, independent research organizations and independent scholars. We also conduct our own research on contemporary issues that impact the human-canine bond, including the dynamics of popular attitudes toward dogs and canine aggression; public health reporting on dog bites; public policy concerning companion animals; and media reporting on dogs.

An NCRC Vision Series Publication

www.nationalcanineresearchcouncil.com

ISBN 978-0-9835085-0-2