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CANINE BEHAVIORAL GENETICS — A REVIEW

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ABSTRACT

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A chronological review of the history of research in canine behavioral genetics is presented. Prior to the work of Scott and Fuller, many studies attempted to describe observed results in simple Mendelian terms. More recently, a quantitative mode of inheritance has been ascribed to many behavioral traits, and heritabilities have been calculated in different populations. Studies of behavioral traits are complicated by the effects of learning, which may well explain the reports of low heritability of behavioral traits measured on adults. Both genotype and environment have been shown to play major roles in the expression of behavioral traits. Maternal effects and the sex of an individual have important effects on behavior scores. Breeders usually select for both physical and behavioral traits in the same individuals, and this review includes a summary of reported research on the relationships between physical and mental traits.

INTRODUCTION

The success of any breeding program incorporating temperament traits in dogs depends on an understanding of the genetics of behavioral traits. Behavioral differences between breeds and between lines within breeds have been documented, but the genetic bases for these differences are often not well established. Both genotype and environment affect the development of behavioral traits in dogs. The relative importance of these two factors influences the potential success of any breeding and selection program, as does the relationship of behavioral traits to other (physical) traits emphasized by the breeder.

Current knowledge of the genetics of behavioral traits in dogs is summarized in this review. The extensive work by Scott and Fuller (1965), begun in 1945, is often regarded as the major work on canine behavioral genetics. This review is therefore presented in three sections, pre-Scott and Fuller, Scott and Fuller, and post-Scott and Fuller, to trace the chronological development of knowledge in this field.

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Modern genetic theory, first postulated by Gregor Mendel in 1865, was not well accepted until the turn of the century when several researchers, working independently, formulated the same ideas, only to discover that the information had been presented 35 years earlier (Gardner, 1975). As with any infant science, early workers wisely confined their efforts to well-defined variables. It is not surprising, therefore, to find that, although canine intelligence and mentality were being investigated in the early 1900's (Shepherd, 1915), studies on the genetics of canine behavior progressed more slowly.

The task was eventually taken up by E.C. MacDowell at the Carnegie Institution in Washington, DC (1921). Working with Dachshunds, he attempted to teach different litters to make directional choices in response to visual and auditory stimuli. He noted that intensities of reactions were most characteristic, and that extremes were easily recognized. These extremes remained at different ages and appeared under different environmental circumstances. MacDowell felt that his experiments showed the inheritance of a dominant disposition, and that heritable material might be affecting both glandular and nervous tissues (MacDowell, 1921).

L.F. Whitney drew attention to the different behaviors characteristic of certain breeds of dogs. Among these were the bear-hunter's hounds, who kept their distance from the bear until the Airedale Terrier could be brought up by the hunter. The Airedale would then charge in without regard to tactics and engage the bear without support, giving the hunter a better shot. He also mentioned the great inhibition of the Bloodhound when it came to biting humans, and the lower level of inhibition in the German Shepherd regarding the same activity. Scent hounds, sight hounds, and the independent trailing of the English Foxhound were studied. Along with other observations, Whitney stated his belief that certain physical and mental traits were definitely linked (1929a). In the same year, Whitney reported that when experimental crosses were made between eight combinations of open trailers (trailing dogs which vocalize on the trail) and mute trailers (silent on the trail), the first generation progeny were always open trailers but the tone of the voice was that of the mute-trailing parent. He concluded that the open trailing of the hound was a dominantly inherited trait and that the tone of the hound's drawl was a recessively inherited trait. He also reported that physical and mental traits segregated independently in the second generation progeny, contrary to his expectations (Whitney, 1929b).

M.T. Marchlewski studied skull shape and hunting behavior in the dog. Results from experiments with pointers and an accidental mating between a pointer bitch and an Alsatian (German Shepherd) sire indicated that the pointing instinct seemed to be inherited independently from features of body structure, which agreed with Whitney's observations on his second-generation progeny. Marchlewski also reported that high grades of pointing skill seemed to be imperfectly dominant over the lower grades. Air-scenting with the head held high was reported to be dominant to the tendency to hunt with the head held low, as when searching for ground and/or foot scent. In direct contrast to Whitney's findings, Marchlewski found open trailing to be recessive to mute trailing (Marchlewski, 1930).

Iljin studied liveliness and subduedness in 1932. He reported that normal dogs were lively, but that in some dogs there was a factor repressing liveliness. He quoted Adametz as stating that an active, nervous temperament was incompletely dominant to a lethargic temperament (in Whitney, 1971). In 1934, Humphrey described the traits which were important for working dogs, based on the work conducted at Fortunate Fields, Switzerland, with German Shepherds from 1924 to 1934 (Humphrey, 1934). In the same year, Humphrey and Warner reported the results of their investigations. They described gun-shyness (auditory sensitivity) as being controlled by a single locus with two alleles, N and n. Homozygous dominant (NN) produced under-sensitive animals, heterozygous (Nn) produced dogs of medium sensitivity and homozygous recessive (nn) produced over-sensitive (gun-shy) animals. After suggesting the above scheme, they remarked

> "Nevertheless, we think it quite unlikely that sensitivity to sound is actually controlled by but a single factor pair. In actual practice, the instructors are able to subdivide both the NN and Nn groups. Thus a dog may be classified as undersensitive, and yet be almost on the borderline between this and the group of medium sensitivity. Similarly, a dog rated Nn might appear to be almost nn. Probably the shy group could also be subdivided if these dogs were instructed and studied as carefully as the others. There appears to be a continuum from the most to the least shy. Perhaps the effect of environment obscures the sharp grouping that the single factor pair theory requires. It is more likely that if this trait is inherited according to a Mendelian scheme, more than a single factor pair is involved". (Humphrey and Warner, 1934).

It would be difficult for an early Mendelian geneticist to give a more accurate description of a quantitative, or polygenic, trait. Stick-shyness (tactual sensitivity) is described in a similar fashion, with homozygous dominant (SS) producing under-sensitive dogs, heterozygous (Ss) producing dogs of medium sensitivity and homozygous recessive (ss) producing over-sensitive (stick-shy) animals. The ratios obtained were essentially the same as those obtained for auditory sensitivity. Humphrey and Warner cited examples which illustrated that distrust was independent of shyness, since some of their dogs were quite distrustful of strangers yet totally fearless at all times. They also showed the effect of sex by demonstrating that more males were under-sensitive and more females over-sensitive than would have been expected if sex had no effect (Humphrey and Warner, 1934).

Perhaps the most interesting aspect of their work was the correlation study. They calculated product—moment correlations of phenotypic values between 42 physical and 9 behavioral traits. True genetic correlations were not calculated. Of the 378 possible correlations, only 15 were established. The correlations with the behavioral traits are listed in Table I (Humphrey and Warner, 1934). Descriptions of the physical traits may be found in

TABLE I

Phenotypic correlations in German Shepherds (after Humphrey and Warner, 1934)

Trait	Positive	Negative
Temperament	Body sensitivity	—
	Ear sensitivity	—
	Humerus—radius	—
	Distrust	—
	Intelligence	—
	Aggressiveness	—
Body sensitivity	Temperament	Upper teeth
	Aggressiveness	—
	Distrust	—
Ear sensitivity	Temperament	—
	Distrust	—
Intelligence	Upper teeth	Aggressiveness
	Temperament	Eye color
	Willingness	—
	Energy	—
	Nose	—
Willingness	Energy	Aggressiveness
	Intelligence	Eye color
	Nose	—
Energy	Willingness	Eye color
	Croup slope	Pasterns
	Intelligence	Aggressiveness
Aggressiveness	Croup slope	Intelligence
	Temperament	Willingness
	Body sensitivity	Coat
	Distrust	Energy
	—	Proportion
Nose	Forefoot firmness	—
	Intelligence	—
	Willingness	—
	In-breeding	—
Trust	Tail	—
	Hindfoot length	—
	Hindfoot firmness	—
	Temperament	—
	Body sensitivity	—
	Ear sensitivity	—
	Aggressiveness	—

Humphrey and Warner (1934). Temperament was defined as a reflection of shyness, since shyness was the main temperamental problem for working purposes. High temperament scores indicated dogs that were not shy. Intelligence was described as the readiness with which a dog learned and the extent to which it retained and used what it had learned. Willingness was used to describe the dog's reaction to man, and especially to its instructor or master. A high willingness score indicated a dog that persistently responded to its master's requests, with an effort to fulfill them, even though reward or correction was not forthcoming. Energy referred to the speed and extent of the movements made, not in response to command, but in response to internal stimulation and to non-coercive external stimulation. Aggression was described as being high in dogs which would attack easily. Dogs with medium levels could be taught to attack and dogs with low levels could not be taught to attack. Humphrey and Warner noted that even a guide dog must have a moderate level of aggression to be suitable for work in a city, but should not be inclined to snap at strangers. Distrust was apparently a type of aloofness that did not have any bearing on fearfulness. As for the actual scores, they said

> "For functional traits other than sensitivity, the animals were scored on a scale of 1 to 5. The few animals scored 1 for a trait ranked exceptionally high. Most dogs rated 2 or 3. Those receiving 4 or 5 were lacking to a marked degree the trait in question. There is one exception to this rule. Extreme distrust is indicated by 5; minimum distrust by 1". (Humphrey and Warner, 1934).

They stressed that they had found no reliable structure–behavior correlations. This is in agreement with the observations of Whitney (1929b) and Marchlewski (1930). Humphrey and Warner also noted that, among dogs not of their breeding, splendid conformation was, in general, accompanied by deficient temperament and vice versa (Humphrey and Warner, 1934).

From the early 1920's to the early 1950's, L.F. Whitney conducted crossbreeding experiments to study the transmission of several behavioral traits. In addition to the open and mute trailing already mentioned, he examined hunting styles. He agreed with Marchlewski that hunting with the head held high was relatively dominant to hunting with the head held low. The tendency to take easily to the water was described as being imperfectly dominant to the lack of this tendency. The interest in birds and flying things was felt to be dominant to the lack of interest. Smiling (showing the teeth in a non-aggressive manner) was reported as being dominant to not smiling. Perhaps the most interesting observation, however, was that when the experiments were continued for many generations, Mendelian segregation broke down in the later generations (Whitney, 1971). This would be expected if the trait in question was influenced by numerous gene pairs rather than the few pairs assumed in simple Mendelian inheritance. The small sample sizes in the first generations could easily have phenotypes which fit ratios normally associated with small numbers of gene pairs. However, as the sample size increases with further generations, the phenotypes no longer fit the ratios, since the sample is now large enough to reflect the large number of genes actually influencing the trait.

W.M. Dawson noted in 1937 that Humphrey and Warner were able to make marked progress in producing superior animals using only subjective judgements of the trainers. He announced that the U.S. Bureau of Animal Industry was initiating a project to study the inheritance of intelligence and associated characteristics using dogs in the early phases (Dawson, 1937). These tests used herding breeds and continued until the U.S. entered World War II in 1941. Most of the data Dawson collected were never analyzed. He did, however, notice inherited differences in the way the dogs bit sheep during herding tests. Collies tended to nip rather than bite, and hence caused little damage to the sheep. Some German Shepherd × Puli crosses tended to slash and tear when they bit, sometimes causing serious wounds. Turkish dogs (breed unspecified) tended to grab and hold without tearing or injuring the sheep (Dawson, 1965).

F. Schaeller made comparisons of the breeding values of German Shepherds collected by the SV (Schaferhunde Verein, a German dog organization) between 1900 and 1937. The evaluations of the progeny of male and female champions were only slightly above the population mean when performance and conformation were considered. He concluded that the progeny of champions were not superior to the progeny of non-champions. He suggested that using a broader base would be more efficient than breeding only a few champions (Schaeller, 1938, cited in Pfleiderer-Högner, 1979).

H.C. Trimble and C. Keeler reported the following year on the tendencies of Dalmatians to run in a particular position with a coach. They claimed that the tendencies were inherited, but suggested no scheme for the transmission (Trimble and Keeler, 1939).

1941 saw the publication of C. Stockard's classic work on form and behavior in the dog. In it, W.T. James described the results of the behavioral part of the study, which was initiated in 1926 at the Cornell Anatomy Farm near Peekskill, NY. Cross-breeding experiments combined with classical conditioning techniques in a Pavlov stand were used to identify different behavioral types. One type was termed "lethargic", and was typified by the Basset and the Dachshund. The "active" type was typified by the German Shepherd and the Saluki. The active types continued to show conditioned responses for long periods of time and became disturbed by repeated negative stimuli. Lethargic animals, however, became disinterested easily and often became inhibited regardless of the type of stimulus presented. Bulldog behavior seemed to be composed of two factors. Reactions to stimuli were almost violent in nature, yet the dogs would become inhibited during rest periods between stimuli. To study the inheritance of the active and lethargic types, James crossed some of his German Shepherds (active types) with Bassets (lethargic types). The first generation progeny were intermediate in type and better balanced mentally than either of the parents. The progeny most similar in appearance to the Bassets were also the most lethargic. The progeny most like the German Shepherds in appearance were correspondingly the most active. This apparent connection between physical appearance and behavior later broke down, with some animals resembling the German Shepherds physically but exhibiting lethargic behavior. Others resembled the Bassets physically and yet exhibited active behavior. This is more in agreement with the opinions of Humphrey and Warner (1934), Marchlewski (1930), and Whitney (1929b), who did not find a complete linkage between structure and behavior. James also noted several behavioral types distributed between the two extremes. Perhaps the possibility of a continuous distribution should have been considered. He noted that most dogs behaved the same way in their kennel as they did in the Pavlov stand (James, 1941).

The same year, Iljin reported Mendelian segregation in certain aspects of skull shape in wolf—dog crosses. He also noted segregation in the expression of nervous disposition and observed the close similarity in genetic constitution between the dog and the wolf (Iljin, 1941).

Three years later, F.C. Thorne added to his 1940 study on approach and withdrawal behavior by examining the genetic relationships of the dogs studied. He credited Cornell Medical College for allowing him to study the data, since they were collected during Stockard's study prior to his death. It is unclear if James collected the data or not. Thorne noted that in the study of 178 dogs, 82 were extremely shy. Of the 82 shy animals, 43 (52%) were direct descendants of an exceedingly shy Basset bitch. Other descendants of this particular bitch were studied, and it was noted that 73% of them were shy, unfriendly animals. Thorne concluded that such excessive shyness was caused by the inheritance of a dominant characteristic (Thorne, 1944). This is similar to the descriptions of MacDowell (1921) and Adametz (in Iljin, 1941), but contradictory to the ideas of Humphrey and Warner (1934), who described shyness in terms of a recessive trait. Thorne also remarked that such a characteristic would therefore not be susceptible to modification through learning and training (Thorne, 1944). Later investigators accepted the hypothesis that shy behavior had a genetic basis, but the concept that the environment could not modify behavior would eventually be challenged.

R. Kelley found, when studying "collie eye" (a herding behavior), that the mean score of Collie progeny was near the mean of the parents' scores. He suggested that the trait was controlled by many additive genes (Kelley, 1947, cited in Burns and Fraser, 1966).

B.E. Ginsburg and M.J. Zamis studied the reactions of naïve dogs to a field of goats in 1949. Out of 95 dogs from 13 breeds and 3 cross-breeds, only 2 showed spontaneous herding behavior. One was a Great Pyrenees male and the other a Springer Spaniel female. Most of the dogs showed aggression, some ignored the goats and others actively avoided them (Ginsburg and Zamis, 1944). James (1951) illustrated that genetic effects can survive different environments. He cross-fostered puppies between a Terrier bitch and a Beagle bitch so that each raised half of her own litter and half of the other's.

The results indicated that the social organization of the dogs was based on behavioral dominance and submission. In each litter, the Terriers were behaviorally dominant over the Beagles. Beagles seemed to prefer the company of other Beagles, who were easier to get along with, and Terriers preferred the company of Beagles also, since they could dominate them more easily than another Terrier (James, 1951).

The next year, R. Melzack demonstrated that irrational fears which were independent of learning could exist in dogs. He also showed that moving objects created a greater percentage of avoidance than stationary objects (Melzack, 1952).

Vauk reported breed differences in puppies' attitudes towards potential prey. Dachshunds showed interest in pigeons as prey objects from 22 days of age, Chows showed the same behavior but at a later age, 46 days. Pointers, on the other hand, showed inhibition towards prey, pointing at 35 days of age. Poodles had lost the instinct to chase prey and showed no interest at all, either anxious or playful (Vauk, 1953, cited in Burns and Fraser, 1966). Rech also reported his study on aggressiveness towards man in 1953. He looked at morphology and function in 2000 dogs classed as biters. Guard and sheep dogs were described as most aggressive, followed by gun dogs, that were more excitable than hunting dogs. Surprisingly, Terriers were irritable but showed only medium aggression, while Bulldogs and Mastiffs were less aggressive than their appearances suggested (Rech, 1953, cited in Burns and Fraser, 1966).

The following year, J. King reported more breed differences regarding aggressiveness. He stated that Basenjis have a more distinct social hierarchy than the normally less aggressive American Cocker Spaniels. Basenjis were more aggressive and rejected more strangers, while in both breeds these characteristics were more noticeable in males than in females (King, 1954, cited in Burns and Fraser, 1966). This agrees with Humphrey and Warner's (1934) finding that there were sex differences in some behaviors. King noted that aggression was stronger towards dogs of the same sex and breed than towards less similar individuals. He suggested that aggressiveness was a genetic trait (King, 1954).

In 1958, Marchlewski reported his observations on Doberman × English Pointer crosses, English Pointer crosses with dingo × Border Collie bitches and field-trial pointers. The performances of the cross-breds confirmed that pointing is a complex genetic trait with considerable variation even within breeds. Cross-breds had good hunting instincts, but only one showed any tendency to point game. Progeny of superior field-trial performers were not necessarily superior to average dogs, even if both the parents had achieved distinction (Marchlewski, 1958, cited in Burns and Fraser, 1966). This would seem to support Schaeller's (1938) study, and casts doubt on the value of performance scores taken after significant amounts of training have been done, at least in the formulation of breeding strategies. Marchlewski continued by saying that a certain amount of heterozygosity seemed to be the norm for animals yielding high performances in field trials. He suggested that the best use of field trials would not be the identification of animals suitable for breeding, but rather be to identify the most suitable matings within a breeding population. He also suggested that, within similar genotypes, pointing may have been dominant to some extent (Marchlewski, 1958).

The same year, H. Mahut reported the results of her study on breed differences for emotional responses. She selected some of the test objects that Melzack (1952) had already proved to be fear-eliciting in some dogs. Home-reared dogs of 10 different breeds were compared in six different behavior classifications regarding strange objects. These classifications were:

no response;

curiosity (brief investigation of the object);

teasing (immediate and excited approach to, and seeking contact with, the object, worrying and teasing it);

approach—avoidance (excitement with alternating approach and avoidance, stalking and keeping the object well within reach);

wariness (tenseness and trembling of the body, keeping an eye on the object from a safe distance, frequently accompanied by growling);

avoidance (clear-cut avoidance and escape from the test situation).

Only the initial reaction during the first 10 s was recorded. Two separate groups of Scottish Terriers and Boxers, which were reared in restricted environments (cage-reared, free in laboratory and kennel-reared), were also tested. All animals were tested in familiar environments with either their owner or caretaker present, except the cage-reared (isolated) dogs, which were merely tested in a familiar setting. The 10 breeds differed significantly in five of the six responses possible. Only in "curiosity" were there no differences. It was possible to identify two basic groups on the basis of the avoidance and wariness scores. One group, termed the "fearful" group, was composed of working and hunting types such as Collies, German Shepherds, Miniature and Standard Poodles, Corgis and Dachshunds. All of these breeds had high scores for "avoidance" and "wariness" responses. The other group, termed the "fearless" group, was made up of fighters, killers and ratters such as Boxers and three types of Terriers (Boston, Bedlington and Scottish). These breeds had lower "avoidance" and "wariness" scores even though size differences were equally distributed throughout both groups. The two groups differed in all four measures of emotional behavior and even in the "curiosity" responses, where individual breeds had not shown significant differences. Severe restriction affected the Scotties and Boxers differently, with Scotties making significantly more avoidance responses (in the restricted groups). Mahut remarked that:

> "The results obtained with the restricted groups of dogs illustrate the complex interaction of constitutional and environmental factors in determining patterns of emotional behavior. In a perceptually rich environment, Boxers and Scottish Terriers are similar in that they are both fearless and aggressive, though each breed has its own characteristic pattern of response. However, when reared in a more restricted environment,

> both breeds became more fearful and they no longer differed with respect to the patterns of response — though the quantitative difference referred to above (more avoidance by Scotties) still remained." (Mahut, 1958).

Combining Mahut's findings with earlier studies, it became clear that many behaviors were indeed a complex interaction between both genetic and environmental factors.

In 1958, B.E. Ginsburg added to Humphrey and Warner's (1934) remarks about conformation and behavior. He noted that in working strains of the Border Collie, selection was rigorous for behavior, resulting in highly uniform behavior and considerable variability in bodily characteristics. He claimed that, in dogs bred primarily for conformation, the reverse was true. He also illustrated the powerful and diverse effects of genetics by mentioning the work of R. Mencl in producing the Dog of Canaan, which would react at different flight distances in response to genetic selection (Ginsburg, 1958).

1962 was the year that the shadow of Lysenko (the great advocate of the inheritance of acquired characteristics) appeared in the literature. The work of the Russian L.V. Krushinski was finally published in English and related conclusions drawn from several Pavlovian studies dating from the late 1930's. In contrast to Iljin (also a Russian, but who spoke in Mendelian terms), Krushinski (1962, cited in Burns and Fraser, 1966), described the inheritance of acquired characteristics, a concept which had been convincingly challenged by Weismann prior to 1914 (Strickberger, 1968). However, Krushinski did show that "apporting", what we call the fetch or retrieve, had a genetic basis. He also paid close attention to what he termed "active" and "passive" defense reactions. The active form appeared to be a form of confident aggression and the passive form one of fearful aggression. He crossed dogs with different combinations of active—passive reactions and obtained individuals with different forms of defensive behavior in each litter. He therefore suggested that the determining components of this behavior may be inherited independently. He felt that the active defense reaction was correlated with "strong" nervous systems, but was dependent upon some form of experience to be manifested. He also noted that the active defense reaction was greater in males and the passive greater in females, but not significantly so (Krushinski, 1962). Although he used different schemes and mechanisms, Krushinski showed indications that he felt genetics and experience both played a part in the production of behavior, and that there might be a difference between the sexes in some cases. This was really not so different from the beliefs of his western counterparts.

In 1963, S.F.J. Hodgman reported that excessively abnormal temperament was not only a problem in pedigree dogs in the British Isles, but was also genetic in origin (Hodgman, 1963).

SCOTT AND FULLER

In 1945, one of the most influential projects on the genetics of canine behavior began at the Jackson Memorial Laboratory in Bar Harbor, Maine. J.

P. Scott and J.L. Fuller would continue collecting data with several co-workers for many years, culminating in their publication of Genetics and the Social Behavior of the Dog (now known as Dog Behavior — the Genetic Basis) in 1965. Their objective was to compare different breeds of dogs under environmentally similar conditions so that any behavioral differences between breeds could be attributed to genetics rather than genetics plus environment. The size of the breed differences was supposed to reflect how important a role genetics played in the behavior being considered. It became one of the few projects to study a large number of traits in a controlled colony with a reasonably large number of animals. In addition to this, many of the traits were studied developmentally for the first time, allowing a far more comprehensive evaluation.

Scott and Fuller discovered breed differences in traits such as emotional reactivity (to being stimulated while restricted in a Pavlov stand), being quiet while being weighed, crude leash training, and sitting on and jumping off a platform on command. Half of the problem-solving tests revealed no differences between breeds, which was attributed to sampling bias due to applying learning criteria to dogs before allowing them to be tested (this gave unequal samples with regard to breeds) and complications due to unusual fear of the apparatus in many dogs. Only in circumventing barriers, maze-tests and spatial orientation (selecting which ramp led to the reward) were breed differences noted. They stated the belief that genetic control of problem-solving behavior was largely a matter of non-allelic interactions with relatively small additive effects (Scott and Fuller, 1965). They crossed Basenjis and American Cocker Spaniels and attempted to describe certain behaviors in Mendelian terms. Scott and Fuller had to use threshold theories to make their descriptions plausible and failed to provide a second backcross which, they noted, would have been necessary to prove their theory of a small number of alleles working in Mendelian fashion with thresholds. It is interesting to note that in some traits they stated that a large number of genes could not be ruled out (Scott and Fuller, 1965). It would have been informative to see these experiments continued for several generations, since earlier studies indicated that single gene-pair explanations could survive the first few generations only to break down completely in later generations (Whitney, 1971). Scott and Fuller also noted that, when they applied analysis of variance techniques on more specific scores, rather than on total complex scores, the simple Mendelian explanation did not fit at all well (Scott and Fuller, 1965).

Consequently, they became the first workers to list heritability estimates for canine behavioral traits. Some of the traits studied showed very low heritability estimates, while others had estimates which were quite high. Some of the traits indicating a high degree of genetic influence in pure breeds are listed in Table II. They noted that emotional or motivational characteristics seemed to have the most effect on performance scores. Factor analysis of performance tests showed only five major factors, one due to

TABLE II

Proportion of total variance due to breed differences between Basenjis and Cocker Spaniels (after Scott and Fuller, 1965)

Variable	Proportion
Posture in Pavlov stand	0.43
Investigative behavior in Pavlov stand	0.46
Escape attempts while in Pavlov stand	0.56
Human avoidance and vocalization at 5 weeks	0.59
Playful fighting at 13—15 weeks	0.42
Leash fighting	0.77
Docility during sit-training	0.48
Running time for long barrier	0.78
Vocalization on U-shaped barrier	0.47

similarity of certain tests, and another a result of the tendency of many animals to show position preferences, which will lower scores on maze tests. The remaining three factors were felt to be more emotional than intellectual, and were termed "impulsiveness", "docility" and "visual observation". A similar analysis on all tests revealed a comparably small number of major factors, which were termed "body size", "activity-success", "heart rate" and "general activity". Although there seemed to be a small number of factors, correlations in the F_2 generations did not support the concept of a few major genes affecting them all through pleiotropy. There was, however, some degree of genetic variation in the great majority of tests performed, both between and within breeds (Scott and Fuller, 1965).

Scott and Fuller then looked at the correlations between physical and mental traits. They agreed with Humphrey and Warner (1934) that there were no reliable correlations between physical and mental characteristics. This was also in basic agreement with the findings of Whitney (1929b), Marchlewski (1930), James (1941) and Rech (1953). Within pure breeds, Scott and Fuller felt that there might have been a tendency for size to affect certain behavior traits, but the association was not consistent and seemed to have a different pattern in each breed. They felt that their results disputed the "breed" concept (that all members of a given breed will have the same pattern of behavior). This is of particular interest since many people use the breed differences reported by Scott and Fuller to defend their belief in such breed stereotypes. However, if they were to actually read Scott and Fuller, they would notice that the authors found great variation within each breed, as described on p. 203.

> "After emphasizing differences between the breeds in the form and intensity of emotional expression, we wish to caution the reader against accepting the idea of a breed stereotype. Typically the range of scores for a breed extended over 5 or 6

points, and occasionally over the entire 9 points of the stanine scale. Basenjis and Cocker Spaniels had mean stanines of 6.0 and 3.03, respectively, at one year; but 65% of the Basenjis and 41% of the spaniels overlapped in the middle range of 4 to 6." (Scott and Fuller, 1965).

Speaking of the more complex tasks, they stated on p. 367 that:

"Taking any two breeds at random, one would expect a large number of significant differences between mean scores. However, there are genetically overlapping individuals in each of these breeds, so that in many traits one breed could be made like the other within a very short time by selection. This means that the dog breeds have retained a great deal of genetic variation." (Scott and Fuller, 1965).

This belief in large genetic variation is similar to that expressed by Marchlewski (1958).

Other interesting observations of Scott and Fuller include the idea that strong maternal effects may be present in emotional traits if the puppies are kept with the bitch long enough for them to learn from her. They felt that improved training and upbringing were as important as genetics in producing good behavior. Since the first-generation hybrids performed better than either of their pure-bred parents in problem-solving situations, Scott and Fuller recommended that cross-breds be considered as working dogs, provided that the pure-bred lines were properly maintained. Maintenance of the pure-bred lines seems important since they stated that the heterosis (hybrid vigor) lasted only for one generation. Consequently, inter-breeding of the hybrids should not result in any improvement in problem-solving ability. They also recommended against breeding one champion sire to many bitches, since they felt that good breeding programs need to consider multiple criteria to be effective (Scott and Fuller, 1965). The last piece of advice is quite similar to that of Schaeller (1938).

The influence of this project is difficult to estimate. Several studies listed previously were undoubtedly inspired and/or aided by the contributions of Scott and Fuller, and several other workers published papers from studies connected with them, such as M.S. Charles Higgins (Scott and Charles, 1954), A. Anastasi and J.R. Schmitt (Anastasi et al., 1955), D.G. Freedman (Freedman, 1957), O. Elliot (Elliot and Scott, 1961, 1963), S.B. Schnitzer and M.E. Schnitzer (Schnitzer et al., 1962) and R. Plutchik (Plutchik, 1971). Most of their results are incorporated in Scott and Fuller (1965).

POST-SCOTT AND FULLER

Also in 1965, C. Keeler and E. Fromm noticed differences in activity and fear between wild red foxes and their tame amber counterparts (Keeler and Fromm, 1965). Their idea that a small number of genes controlled both color and wildness (pleiotropy) is not in agreement with previous workers (Whitney, 1929b; Marchlewski, 1930; Humphrey and Warner, 1934; James, 1941; Rech, 1953; Scott and Fuller, 1965), who found no complete linkages between physical and mental traits. J.H. Woolpy and B.E. Ginsburg studied genetic wildness in the wolf in 1967 and found that social conditioning conducted with the aid of tranquilizers did not last well, succumbing to genetic programming more rapidly than socializing done without chemical assistance (Woolpy and Ginsburg, 1967).

E. Went suggested changes in the rules for creating breeding values of German hunting dogs. He asserted that the performance of the dam and the progeny must be considered as equally important as that of the sire (Went, 1968, cited in Pfleiderer-Högner, 1979). The same year, J. Steinitz noted that breeding controls for pointers in Czechoslovakia included progeny evaluation. Sires with progeny far below the population mean were culled (Steinitz, 1968, cited in Pfleiderer-Högner, 1979). H. Briest suggested that dog-breeders utilize modern animal-breeding techniques (Briest, 1969, cited in Pfleiderer-Högner, 1979). At the same time, H. Herzog advocated the use of statistical methods in the breeding of working dogs also, emphasizing the progeny test as the most appropriate method of evaluation (Herzog, 1969, cited in Pfleiderer-Högner, 1979). However, W. Petri felt that the application of livestock-breeding techniques to the dog would not be a simple task. The reasons given were that canine sires have fewer records, not all of their progeny are tested, environmental conditions are not as easily standardized, the effect of the trainer is difficult to estimate, and finally that the performances are measured subjectively, not objectively as milk yield is in dairy cattle (Petri, 1969, cited in Pfleiderer-Högner, 1979).

The next year, B. Sacher applied statistical genetic techniques to the breeding-books of certain types of pointers. He found that scores were not normally distributed within prize classes, the mean being closer to the highest grade. He stated that the scores were too high and did not reflect reality. He criticized the minimum requirements and the way prize classes were divided, and suggested that the prize classes be eliminated. He felt that heritability estimates were not possible since the data were not good enough, but noted that such estimates were prerequisites for breeding-value estimations (Sacher, 1970, cited in Pfleiderer-Högner, 1979). In the same year, the U.S. Army reported that their Biosensor dog-breeding program was using a breeding index based on data collected from each litter. The information included the percentage of hip dysplasia, the average of puppy evaluation scores, the temperament of the litter, the size of the litter at birth, the number weaned, the percentage of long-haired puppies and the percentage of floppy-eared puppies (Castleberry et al., 1970). J.F. Wiedeking repeated Briest's suggestion of using modern animal-breeding techniques in dog breeding (Wiedeking, 1971. cited in Pfleiderer-Högner, 1979).

G. Geiger investigated the breeding-book of Dachshunds in Germany in 1973 and found the scores better distributed than the data studied by Sacher, perhaps due to the 12-point system used as opposed to the 4-point system used in the pointer prize classes. He conducted a three-level nested analysis of variance on 1463 full- and half-sib progeny of 21 sires. In contrast to the earlier findings of Humphrey and Warner (1934), King (1954) and Mahut (1958), his results showed maternal effects but no effect due to sex. The heritabilities are shown in Table III (Geiger, 1973, cited in Pfleiderer-Högner, 1979).

TABLE III

Heritability estimates in Dachshunds (after Geiger, 1973)

Trait	Sire	Dam
Hare tracking	0.03	0.46
Nose	0.01	0.39
Seek	0.00	0.41
Obedience	0.01	0.19

A second study of additive genetic variation in 1973 came from the Army Dog Training Center in Solleftea, Sweden. C. Reuterwall and N. Ryman reported on their study of 958 German Shepherds from 29 sires. The eight behavioral traits studied were labelled A–H:

Trait A was termed "Affability" (tested by having an unknown person confront the dog);

Trait B was termed "Disposition for Self Defense" (tested by having an unknown person attack the dog);

Trait C was termed "Disposition for Self Defense and Defense of Handler" (tested by having an unknown person attack the dog and handler);

Trait D was termed "Disposition for Fighting in a Playful Manner" (tested by asking the dog to fight for a sleeve or stick);

Trait E was termed "Courage" (tested by having a man-shaped figure approach the dog);

Trait F was termed "Ability to Meet with Sudden Strong Auditory Disturbance" (tested by firing shots at some distance and making a noise with tin cans just behind the dog);

Trait G was termed "Disposition for Forgetting Unpleasant Incidents" (tested by scaring the dog at a certain place and then asking the dog to pass the place again);

Trait H was termed "Adaptiveness to Different Situations and Environments" (tested by observations during the other parts of the test).

In contrast to Geiger's findings, Reuterwall and Ryman reported significant differences between the sexes, males handling noise (Trait F) better and exhibiting more controlled defense (part of Trait C) and playful fighting (Trait D). Sex differences had also been noted by Humphrey and Warner (1934), King (1954) and Mahut (1958). Reuterwall and Ryman noted that, in all the traits studied, the additive genetic variation was small (Reuterwall and Ryman, 1973). The heritability estimates listed in Table IV were reported by Willis based on the information found in Reuterwall and Ryman (Willis, 1977). It should be noted that the scores used by Reuterwall and Ryman were transformed and extremely complex. Some workers in Sweden today, working on the genetics of the breeding program at the Statens Hundskola, feel that the findings of Reuterwall and Ryman's study are based on scores too complex to have much meaning (L. Fält, personal communication, 1982).

TABLE IV

Heritabilities in German Shepherds (after Reuterwall and Ryman, 1973)

Trait	Males	Females
A	0.17	0.09
B	−0.11	0.26
C	0.04	0.16
D	0.16	0.21
E	0.05	0.13
F	−0.04	0.15
G	0.10	0.17
H	0.00	0.04

A = Affability
B = Disposition for self-defense
C = Disposition for self-defense and defense of handler
D = Disposition for fighting in a playful manner
E = Courage
F = Ability to meet with sudden strong auditory disturbance
G = Disposition for forgetting unpleasant incidents
H = Adaptiveness to different situations and environments

Also in 1973, R.B. Cattell, C.R. Bolz and B. Korth reported on their study of behavior types and breeds. They measured 42 behavioral variables in 101 dogs of five different breeds and then reduced the variables to 15 factors. Using these, they achieved a separation roughly corresponding to the five participating breeds. They suggested a genetic basis for the behaviors studied (exuberance, aggressiveness, excitation, self-sufficiency, obedient cooperation, competence, timidity, calmness, aloofness, emotionality and apprehension) (Cattell et al., 1973).

The next year, M.E. Goddard and R.G. Beilharz stated their belief that fearfulness and dog distraction were heritable in Australian guide dogs (Goddard and Beilharz, 1974). In 1982, Goddard and Beilharz reported further on the genetics of Australian guide dogs. They noted that sex had an important effect, with males suffering a higher rejection rate due to dog distraction and a lower rejection rate due to fearfulness than females. Variation in environment prior to 6 weeks of age, breed differences, age of placement in private homes, and age when males were castrated had little effect on overall success in Goddard and Beilharz's study, whereas year and source of dog (their own breeding program or outside population) had significant effects. Fearfulness emerged as the most important and most highly heritable component of success. Estimates of heritabilities based on scores of 394 Labrador Retrievers computed from sire components, dam components and the two combined are listed in Table V (Goddard and Beilharz, 1982). In contrast to reports by Scott and Bielfelt (1976), Geiger (1973) and Scott and Fuller (1965), no strong maternal effects were evident (Goddard and Beilharz, 1982). In a separate paper, Goddard and Beilharz reported heritabilities and genetic correlations between 10 traits, which were:

nervousness (N) (fear, usually shown by withdrawal or inhibited movement, of people, traffic or strange places);
suspicion (S) (approach—withdrawal conflict towards unusual objects);
concentration (C) (attention to the stimuli to which the dog is being trained to respond);
willingness (W) (keenness to work and to carry out commands);
distraction (D) (attention to other irrelevant stimuli);
dog distraction (DD) (attention and attraction towards other dogs);
nose distraction (ND) (attention and attraction towards scents);
sound-shy (SS) (fear of loud noises);
hearing sensitivity (HS) (strong response to sounds, including the trainer's voice);
body sensitivity (BS) (strong response to touch and leash corrections).

TABLE V

Heritability estimates in Australian Labradors (after Goddard and Beilharz, 1982)

Trait	Sire	Dam	Combined
Success	0.46	0.42	0.44
Fear	0.67	0.25	0.46
Dog distraction	−0.04	0.23	0.09
Excitability	0.00	0.17	0.09
Health	0.40	0.10	0.25
Hip dysplasia	0.08	0.20	0.14

Estimates of heritabilities based on scores of 249 Labrador Retrievers, calculated from combined sire and dam components, are listed in Table VI (Goddard and Beilharz, 1983). Nervousness had the highest heritability and was the only trait with a significant sire component. Estimates of genetic correlations between the traits are listed in Table VII (Goddard and Beilharz, 1983).

In contrast to other workers (Castleberry et al., 1976; Bartlett, 1976;

TABLE VI

Heritability estimates in Australian Labradors (after Goddard and Beilharz, 1983)

Trait	Heritability
Nervousness (N)	0.58
Suspicion (S)	0.10
Concentration (C)	0.28
Willingness (W)	0.22
Distraction (D)	0.08
Dog distraction (DD)	0.27
Nose distraction (ND)	0.00
Sound-shy (SS)	0.14
Hearing sensitivity (HS)	0.00
Body sensitivity (BS)	0.33

TABLE VII

Genetic correlations in Australian Labradors (after Goddard and Beilharz, 1983)

Trait	N	S	C	W	DD	SS
S	0.53					
C	−0.01	−0.31				
W	−0.57	−0.20	0.67			
DD	0.11	0.63	−0.47	−0.41		
SS	0.89	0.47	0.33	−0.78	0.28	
BS	0.72	0.51	−0.29	−0.74	−0.21	0.59

N = Nervousness
S = Suspicion
C = Concentration
W = Willingness
DD = Dog distraction
SS = Sound-shy
BS = Body sensitivity

Rosberg and Olausson, 1976), Goddard and Beilharz (1983) found no negative correlations between important traits. However, they did not list correlations for hip dysplasia. They also noted the importance of sex; females being more fearful and distracted by scents but less aggressive and distracted by dogs than males. Sex differences were also noted by Humphrey and Warner (1934), King (1954), Mahut (1958), Reuterwall and Ryman (1973) and Pfleiderer-Högner (1979). G. Queinnec, B. Queinnec and R. Darre reported on their work with French racing greyhounds (Queinnec et al., 1974). Breeding values for greyhounds were based 40% on the animal's own performance and 60% on the performance of its progeny, both over 3 racing seasons to account for repeatability.

In 1975, the U.S. Army Biosensor Project reported a heritability estimate of 0.70 for their intermediate temperament evaluations. They also stated their intention to use heritability estimates of both hip dysplasia (previously estimated in their colony as 0.22) and temperament in the calculation of breeding values (Castleberry et al., 1975). The following year, they reported the first known estimate of the genetic correlation between temperament and hip dysplasia (considered by many to be the two major problems in breeding dogs for military or police work). Before listing the estimate, they noted that previous dysplasia-free litters had shown undesirable temperaments. Their estimate of the phenotypic correlation between the two traits was −0.25 and that of the genetic correlation was −0.35 (Castleberry et al., 1976).

In 1976, C.R. Bartlett reported heritabilities and genetic correlations between traits studied in American guide dogs. The traits listed were hip dysplasia, body sensitivity (judged by how hard a jerk on the choke-chain leash the new dog could tolerate; low scores indicating a lack of sensitivity), ear sensitivity (judged by how loud a vocal correction the new dog required; low scores indicating lack of sensitivity), nose (olfactory acuity leading to distraction problems for all but the best trainers; low scores indicating greatest use of the nose), intelligence (the ability of the dog to understand things from its own viewpoint, not implying a willingness to obey; low scores indicating great intelligence, which may be a problem to all but the best trainers), willingness (willingness to do what the dog's master asks of it, regardless of distractions; low scores indicating the most willing dogs), energy (activity versus laziness; low scores indicating active, energetic dogs), self right (the belief of the dog that it has a right to be where it is; negative scores indicating a tendency to give way to another), confidence (confidence shown with strange people or in strange environments; low scores indicating more confident dogs), fighting instinct (tendency to fight; low positive scores in-

TABLE VIII

Heritability estimates in American guide dogs (after Bartlett, 1976)

Trait	Males	Females	Combined
Hips	0.72	0.46	0.54
Body sensitivity	0.26	0.05	0.10
Ear sensitivity	0.49	0.14	0.25
Nose	0.30	0.05	0.12
Intelligence	0.17	−0.07	−0.06
Willingness	−0.14	−0.04	−0.03
Energy	−0.03	0.06	0.05
Self-right	0.15	0.25	0.22
Confidence	0.04	0.26	0.16
Fighting instinct	−0.05	−0.08	−0.04
Protective instinct	−0.21	−0.13	−0.12

dicating the tendency to avoid fights, negative scores indicating even less tendency to fight, passing into submission) and protective instinct (a desire of the dog to protect its own; low positive scores indicating a dog which will speak if a stranger approaches its master with menace, but will not fight to protect the master). Heritability estimates of these traits, based on over 700 records for males and over 1000 records for females, both calculated by paternal half-sib analysis, are listed in Table VIII (Bartlett, 1976).

It is not clear which of the eight breeds mentioned in Bartlett's work are included in this analysis. Estimates of the genetic correlations between some of the traits and hip dysplasia are listed in Table IX (Bartlett, 1976). Of these, only the correlation between hip dysplasia and ear sensitivity was found to be significant.

TABLE IX

Genetic correlations with hip dysplasia (after Bartlett, 1976)

Trait	Correlation
Body sensitivity	0.15
Ear sensitivity	0.52
Nose	−0.11
Intelligence	0.00
Willingness	0.00
Energy	−0.26
Self-right	−0.03
Confidence	−0.22
Fighting instinct	0.00
Protective instinct	0.00

Estimates of genetic correlations between temperament traits are listed in Table X (Bartlett, 1976). Correlations between ear sensitivity and energy, body sensitivity and nose, self right and confidence, ear sensitivity and confidence, and ear sensitivity and nose were all found to be significant. All correlation coefficients listed for intelligence, willingness, protective instinct and fighting instinct were zero (Bartlett, 1976). Low scores were good in willingness, energy, hip dysplasia and confidence, low positive scores (negative scores were possible) were good in fighting instinct and protective instinct. On the other hand, high scores were good in nose, intelligence and self right, with medium scores being good for sensitivity traits. Also, body sensitivity, ear sensitivity, nose, intelligence, willingness, energy and confidence were scored on a scale from +1 to +5, whereas self right, fighting instinct and protective instinct were scored on a scale from −5 to +5. The results, however, are in basic agreement with Humphrey and Warner (1934). Although most heritability estimates were small, it is interesting to note that four of the genetic correlation estimates between hip dysplasia and behavior traits were negative, two of them between −0.2 and −0.3. Although

TABLE X

Genetic correlations between temperament traits (after Bartlett, 1976)

Trait	BS	ES	N	E	SR	C
ES	1.00					
N	0.75	0.58				
E	−0.38	−0.77	−0.14			
SR	−0.15	−0.13	0.12	−0.14		
C	1.32	0.60	0.34	−0.04	−0.74	—

BS = Body sensitivity
ES = Ear sensitivity
N = Nose
E = Energy
SR = Self-right
C = Confidence

they were not statistically significant, the possibility of a trend should be considered, particularly in light of the U.S. Army Biosensor project's findings and those of S. Rosberg and A. Olausson (completed in 1976 but not published). Rosberg and Olausson reported low heritability estimates for mental traits in the dogs at the Swedish Army Dog Center in Solleftea, Sweden. All dogs included in the study were German Shepherds. Phenotypic correlations between the mental traits they were studying and hip dysplasia were small, but negative. Genetic correlations were negative, ranging up to −0.55, but the authors felt they were unreliable due to problems with the material studied (Rosberg and Olausson, 1976).

A study of the genetics of American guide dogs was completed in 1976 by C.J. Pfaffenberger, J.P. Scott, J.L. Fuller, B.E. Ginsburg and S.W. Bielfelt. They followed up Scott and Fuller's (1965) work in behavior and obtained estimates of heritability for their puppy tests. The traits reported by Scott and Bielfelt (1976) in their chapter on analysis of the puppy-testing program included the following:

sit (three repetitions of a forced sit with a vocal command);

come (five repetitions of the handler moving away, kneeling down, calling the puppy by name (followed by the command "come" while clapping the hands);

fetch (three repetitions of playful retrieving with vocal command);

trained response (a complex score, indicating if the puppy was afraid of the tester or not, was over-excited or cooperated calmly, did or did not pay attention to moving objects, adjusted slowly or readily to the new environment, showed no curiosity or was curious about new objects and people, did or did not remember previous experience, tried to do what the tester wanted or not, and showed persistence or not in performing a task);

willing in training (also a complex score, indicating if the puppy was fear-

ful or at ease, afraid to move or moved freely, was indifferent or friendly to the tester, was unresponsive or responsive to encouragement, urinated or was continent, was upset by the new situation or was confident, and was obstinate or willing in its responses);
body sensitivity (another complex score, indicating if the puppy stood erect or cowered, turned head away or not, looked at or away from the tester, showed pain by action or not, came back after pain or attempted to escape, tucked in the tail or not, wagged tail or not after pain, and growled or not when in pain);
ear sensitivity (similar to body sensitivity, except in relation to sound instead of pain);
new-experience response (similar to trained response, but this time an emotional response to novel stimuli, not training);
willing in new experience (similar to willing in training, except related to novel stimuli instead of training);
traffic (indicates if puppy can avoid a moving and stationary cart without becoming fearful);
footing-crossing (indicates if puppy noticed differences in footing between curbs and metal patches in the sidewalk);
closeness (how close the puppy passed to obstructions);
heel (how well the puppy accepted leash training).

Eleven of the 13 traits, whose heritability estimates are listed in Table XI, had dam components much larger than the sire components, indicating strong maternal effects (Scott and Bielfelt, 1976). This agrees with the findings of Scott and Fuller (1965) and Geiger (1973). As part of the same study, J.L. Fuller examined the relationship between physical measurements and behavior. Once again, no substantial correlations were found (Fuller, 1976).

TABLE XI

Heritability estimates for California guide dogs (after Scott and Bielfelt, 1976)

Trait	Heritability
Sit	0.06
Come	0.14
Fetch	0.24
Trained response	0.08
Willing in training	0.12
Body sensitivity	0.16
Ear sensitivity	0.00
New-experience response	0.06
Willing new experience	0.24
Traffic	0.12
Footing-crossing	0.06
Closeness	0.04
Heel	0.10

Comparing Scott and Fuller's 1965 estimates with those of the U.S. Army Biosensor project (Castleberry et al., 1975), it seems possible that certain components of behavior may be highly heritable. The failure of other workers to find high estimates may indicate that such estimates are quite sensitive to the quality of the tests, size of the samples and statistical methodology.

In 1977, L.E. Smiley, C.S. Schotte and B.E. Ginsburg reported their work (started in 1975) on communication systems of coyotes and Beagles. Beagles threaten with the familiar snarl, whereas coyotes threaten with a gape—hiss. Results of cross-breeding experiments indicated that the two types of threats segregated in a Mendelian fashion, with the coyote gape—hiss being a genetic recessive to the Beagle snarl. Other vocalizations were reported as mosaics of parental components (Smiley et al., 1977). Schotte and Ginsburg subsequently reported that third-generation hybrids produced from gape-hissing second-generation hybrids (presumed to be homozygous recessive) all showed the recessive gape-hiss, adding credence to their original single-gene hypothesis (Schotte and Ginsburg, 1979). In 1982, A.A. Moon and B.E. Ginsburg reported complications in the coyote—Beagle hybrid study. An exception to their previous findings was noted in that a number of second-generation hybrids which showed snarl threats as puppies began showing the gape-hiss threat when they reached maturity, almost doubling the ratio of gapers to non-gapers. The authors suggest the presence of a second recessive gene which is not expressed in the first-generation hybrids, where it was only present in the heterozygous condition (Moon and Ginsburg, 1982). They later noted (along with M. Fine) the definition of three distinct sub-sets regarding the time of gape—hiss onset (Moon et al., 1982). It would be interesting to have this experiment carried out through many generations to determine if Mendelian segregation would completely break down in later generations, as it did in early studies of behavior (Whitney, 1971).

The effect of in-breeding on behavior was reported by C.J. Brown, O.D. Murphree and J.E.O. Newton in 1978. They developed two strains of pointers by selective breeding, one highly in-bred and exhibiting human-aversion behavior, and the other non-in-bred and displaying normal, friendly behavior towards humans. They concluded that most of the variability in traits associated with human-aversion in their timid strain was the result of additive gene action (Brown et al., 1978). This is interesting in light of Marchlewski's (1958) remarks about high-performing pointers usually having a fair amount of heterozygosity. J.E.O. Newton, R.A. Dykman and J.L. Chapin also found that combining behavioral and autonomic measures could separate the two strains with complete accuracy whereas either set of measures by itself was only 95% accurate (Newton et al., 1978).

J.E.O. Newton and L.A. Lucas reported more work on the nervous and normal pointer strains in 1982. They noted that dogs of the nervous strain had reduced heart rates in the presence of humans and while being petted. Dogs from the normal strains showed increased heart rates when humans were present and a reduction of heart rate towards baseline levels while being petted. Reciprocal crosses between the two strains showed the pattern of the male parent at 3 months of age, while at 6 months of age both types of hybrid showed some characteristics of both parents, but no hybrids showed all the characteristics of either parent. The authors suggest that genetics explained "markedly different physiologic effects of an emotion-provoking stimulus, which elicits what appears to be a negative emotional effect in one line and a positive emotional effect in the other line" (Newton and Lucas, 1982). From these results and those of Moon and Ginsburg (Moon et al., 1982) and Wright (1980), it would seem that either the effect of genetic components on behavior can change over time, or that different genes may be activated at different stages of physical development.

In 1979, M. Pfleiderer-Högner estimated heritabilities of Schutzhund scores in Germany. She analyzed 2046 test results in 1291 German Shepherds from 37 sires, all tested animals being born in 1973. The four criteria studied were tracking, obedience, man-work and character. She found sex and the number of dogs competing in a given trial to be significant, but not age or month of trial. Sex differences were previously noted by Humphrey and Warner (1934), King (1954), Mahut (1958) and Reuterwall and Ryman (1973). Estimates of heritabilities from sire components, dam components and their combination are listed in Table XII (Pfleiderer-Högner, 1979).

TABLE XII

Heritability estimates for German Schutzhund scores (after Pfleiderer-Högner, 1979)

Trait	Sire	Dam	Combined
Tracking	0.01	0.20	0.10
Obedience	0.04	0.13	0.09
Man-work	0.04	0.07	0.06
Character	0.05	0.17	0.12

The only significant correlation was between man-work and character, so she suggested the use of a selection index based on the tracking and man-work scores. She advocated the use of performance tests on the animal being evaluated and its siblings, not progeny tests, since that method increases the generation interval (Pfleiderer-Högner, 1979).

In 1982, L. Fält, L. Swenson and E. Wilsson reported their unpublished work on heritability estimates for behavioral traits studied at the National Dog School (Statens Hundskola) in Solleftea, Sweden. The traits studied in 8-week-old German Shepherd puppies included: yelp (time from first separation from litter to first distress call); shriek (time from the same separation to the first serious, emphatic distress call); contact 1 (tendency to approach a strange person in a strange place after separation); fetch (pursue a ball and pick it up in the mouth); retrieve (bringing the ball back after picking it up);

reaction (to a strange object in a strange place); social competition (actually a form of tug-of-war); activity (number of squares entered when left in a marked arena); contact 2 (time spent near a strange person sitting passively in a chair in the middle of the marked arena); exploratory behavior (number of visits to strange objects placed in the corners of the marked arena). Estimates of heritabilities for the traits, calculated from sire components and dam components separately, are listed in Table XIII (Fält et al., 1982). Although some specific behaviors had low heritability estimates, others had quite high estimates.

TABLE XIII

Heritability estimates for Swedish German Shepherds (after Fält et al., 1982)

Trait	Sire	Dam
Yelp	0.66	0.73
Shriek	0.22	0.71
Contact 1	0.77	1.01
Fetch	0.73	0.10
Retrieve	0.19	0.51
Reaction	0.09	1.06
Social competition	0.11	0.76
Activity	0.43	0.76
Contact 2	0.05	1.11
Exploratory behavior	0.31	0.83

SUMMARY

Early attempts to define the inheritance of canine behavior in simple Mendelian terms often ran into complications. Modern attempts to do so seem to require the assistance of threshold theories or epistatic interactions in order to be plausible, and studies have not been carried out on sufficient generations to determine how long Mendelian explanations remain viable. Several studies have described canine behavior in terms suggesting a quantitative (polygenic) mode of inheritance, with both genetic and environmental factors playing major roles in the expression of the trait.

Maternal effects and the sex of a dog have been shown to have important effects on behavior scores. It has even been suggested that, within breeds, the size of a puppy may be an important factor in determining behavior.

Some studies suggest that the progeny of superior performers are not necessarily superior to the progeny of average performers. This suggestion is supported by the finding that German Schutzhund scores are lowly heritable, indicating that such performance scores are not an accurate reflection of the animal's genetic make-up. Breeders may have to use scores assigned before training commences in order to select properly.

Finally, early workers found no reliable correlations between physical and mental traits, but none of them considered hip dysplasia specifically. The studies which have correlated hip dysplasia scores with behavior scores have all listed at least some negative estimates. The evidence is inconclusive, since none of the estimates are statistically significant, but the possibility of a trend should be considered.

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