

## GENETICS AND THE DEVELOPMENT OF SOCIAL BEHAVIOR IN DOGS

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### INTRODUCTION

As anyone familiar with the facts of embryology knows, behavior is not biologically inherited as such. The fertilized egg shows no activity except that connected with its internal physiological function, and in mammals the first activity of the organism as a whole appears during the fetal period when the developing muscles begin to twitch. Consequently, behavior must be developed, and developed under the combined influence of hereditary and various environmental factors.

Because of this, the developmental method is one of the most meaningful ways to study the action of genetics upon behavior. With this in mind, we (Scott and Fuller, 1964) set up a long term experiment on genetics and the development of behavior in dogs. This paper gives one detailed example of the results—one concerning the development of differences in the behavior of barking.

It is obviously important that every animal in such an experiment be subjected to the same environmental conditions, as it otherwise would be impossible to separate out genetic and environmental effects. The simplest way to do this would be to place each animal in an isolation chamber under controlled physical conditions. However, as Thompson and Heron (1954), Fisher (1955), Fuller (1961), and others have shown, such a restricted environment seriously interferes with the development of behavior. Likewise, the results of all studies of the behavior of animals under natural conditions emphasize the richness of their behavioral development compared to that of animals reared in captivity (Murie, 1944; DeVore, 1963).

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The problem then was to set up a semi-natural but uniform environment in which dogs could develop. Like their ancestors, the wolves, dogs are highly social animals, and their natural social group is the pack. We therefore set up a situation in which puppies would live together with their litter-mates from birth until one year of age, first in large nursery rooms and later in spacious outdoor runs 20 × 75 feet in overall dimensions. Furthermore, dogs, as domestic animals, have as part of their normal social environment contact with human beings. This was provided by daily contacts with caretakers and experimenters. We eventually set up a program which was very much like that of a standardized school system, in that each litter of puppies was put through the same system of testing and training at corresponding ages, but unlike it in that each of our canine pupils was treated in exactly the same way as the others, as nearly as possible.

Such a combined educational and testing program could be organized intelligently only against the background of knowledge of normal development in the puppy. As I have pointed out in other papers (Scott, 1963a), the puppy first goes through a *neonatal period* in which all behavior is adapted to infantile life and particularly to the problem of suckling. The first changes appear when the eyes open at approximately two weeks of age, and there follows a brief *transition period*, during which the puppy goes through a metamorphosis in behavior, so that within five or six days the puppy has developed a great many of the patterns of behavior adapted to adult life. By 18 or 19 days of age, the puppy begins to respond to a variety of social stimuli, and during the *period of socialization* which follows, it forms its primary social relationships with

its litter-mates, mother, and human beings. These weeks comprise a critical period for the process of primary socialization, and the peak for the capacity for forming primary social relationships occurs between six and eight weeks of age. This is therefore the ideal time to take a puppy away from the litter and make it into a pet, and it also coincides with the time of final weaning from the breast.

The next step was to design a series of tests and training situations appropriate to the age of the animals. These tests were given to puppies of five different breeds: basenjis, beagles, cocker spaniels, Shetland sheep dogs, and wire-haired fox terriers. Two of these, the basenjis and cockers, were selected as being most different in as many respects as possible, and they were crossed in a Mendelian experiment. Reciprocal crosses (i.e., cocker males by basenji females and vice-versa) produced two  $F_1$  populations.  $F_1$  males were backcrossed to their mothers, so that comparisons could be made between backcrosses and  $F_1$ 's reared in the same maternal environment. Finally, the same  $F_1$  males were mated to their sisters, producing two  $F_2$  populations. All the hybrids were run through the same testing programs as their purebred ancestors.

If time had permitted, it would have been desirable to produce a second backcross generation, as a test for single-factor inheritance. Likewise, it would have been interesting to include reciprocal backcrosses as a test for the effects of maternal environment, since the  $F_1$  females showed considerable hybrid vigor and hence provided a very different maternal environment from that provided by their mothers.

#### THE DEVELOPMENT OF BARKING

Barking is part of the agonistic system of behavior in dogs, wolves, and other canids. Judging from the behavior of wolves around their dens, barking is primarily an alarm signal evoked by the approach of a strange animal. When analyzed by the sonograph, a bark is seen to be a short, sharp, monotonous sound, highly characteristic for each individual.

These acoustic qualities make a bark very easy to localize, so that from the viewpoint of communication, a bark efficiently conveys information regarding the location of the barking animal. Barking is obviously used by dogs in other ways as well, particularly as a threat in competitive situations. There is a great deal of variation between dog breeds in the amount and quality of barking, but the most extreme variation is seen in the basenji breed, sometimes called the African barkless dog. This characteristic breed difference provided an excellent opportunity for studying the action of genetics upon the development of an important behavior pattern.

While deaf at birth, young puppies are capable of vocalization. No puppies bark during the neonatal period, but they exhibit distress vocalization in response to conditions of pain, hunger, and discomfort. Barking has been observed as early as 18 days of age in puppies playing freely with their litter-mates, and its frequency increases rapidly during the period of socialization.

For the purposes of genetic analysis we needed a standard stimulus situation in which barking could be measured, and this was provided by a series of dominance tests. Pairs of puppies were allowed to compete for a bone for a 10 minute period at 5, 11, and 15 weeks of age, the number of barks being recorded for each puppy.

As shown by the average number of barks (Fig. 1), there is very little barking at 5 weeks of age, but it rises to a peak at 11 weeks and declines again at 15 weeks. These changes are associated with the development of the dominance order, there being very few cases of dominance at five weeks, a somewhat unstable order at 11, and stability becoming greater at 15 weeks. The maximum amount of barking is therefore associated with an unstable dominance relationship, and barking may be done by either the puppy which has the bone or the one which does not. In either case it appears to have the function of a vocal threat.

#### BREED DIFFERENCES IN BARKING

Since the maximum breed differences ap-

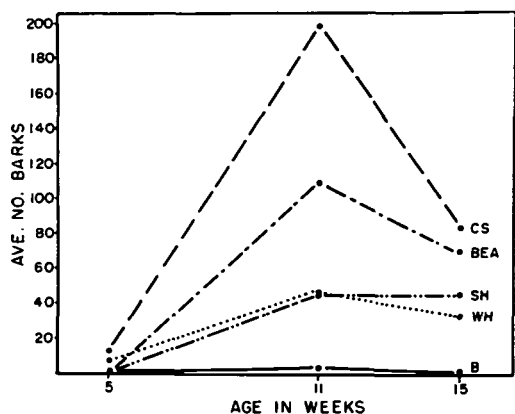


FIG. 1. Average number of barks at different ages for 5 different breeds of dogs.

peared at 11 weeks, this age was chosen for detailed genetic analysis. On closer examination of the data, the cockers and basenjis differed in three ways. The first was in the quality of the barks given, most cockers giving a high pitched "yap," and basenjis merely uttering a low "woof." These differences in pitch, loudness, and harmonics were so complex that no effort was made to measure them.

Second, there was the trait of barking or not barking. Most basenjis and all cockers in our strains barked at some time or other, but not all of them barked in the test situation. As observed, the basenjis seemed to bark only under very strong stimulation, and then to emit sounds with a great deal of effort. This may be described as a difference in threshold of response, basenjis having a much higher threshold than cockers. Stimulation as provided by the dominance test at 11 weeks reaches the threshold for about 95% of cockers and only 55% of basenjis, a difference of 40% (Fig. 2). A slightly greater difference of 48% is obtained by comparing the number of animals barking per opportunity, about 68% in cockers and 20% in basenjis (Table 1).

Finally, there is the pronounced tendency in cockers to go on barking once the threshold is crossed. Basenjis usually stop after two or three barks, but a cocker may go on to give dozens or even hundreds. All basenjis but one gave fewer than 19 barks, and it is possible to draw a line at this point

which will give maximum separation between the two breeds, including 95% of the basenjis and 18% of the cockers, a difference of 77% (Table 2).

It is obvious that somewhat different results are obtained depending on which dimension of behavior is measured. Are these results produced by the same genetic system or by different ones?

BARKING IN HYBRIDS

*Threshold of response.* Table 1 shows an analysis of the data based on the occurrence of barking per opportunity to bark. It is

TABLE 1. Percent of animals barking per opportunity, compared with expected percentage.

Breed	Observed	Expected 1 factor dominant	Expected 2 factor dominant
Basenji	19.6	—	—
Cocker	68.2	—	—
F <sub>1</sub>	60.1	68.2	68.2
F <sub>2</sub>	55.5	56.0	65.2
Backcross to Cocker	65.1	68.2	68.2
Backcross to Basenji	50.0	43.9	56.0

TABLE 2. Percent of animals barking 19 or fewer times at 11 weeks.

Breed	n	%
Basenji	42	95.2
Cocker	49	18.4
F <sub>1</sub>	39	51.3
F <sub>2</sub>	66	53.0
Backcross to Cocker	16	18.8
Backcross to Basenji	35	62.9

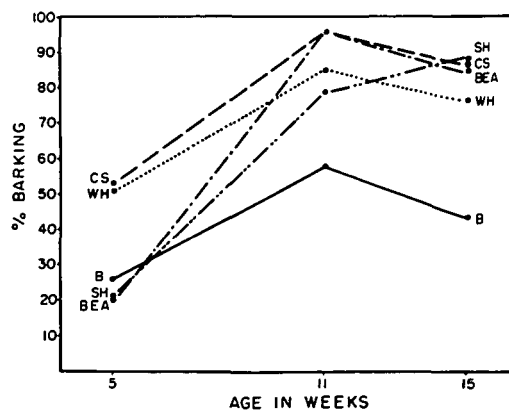


FIG. 2. Percent of animals barking per opportunity to bark, in 5 different breeds.

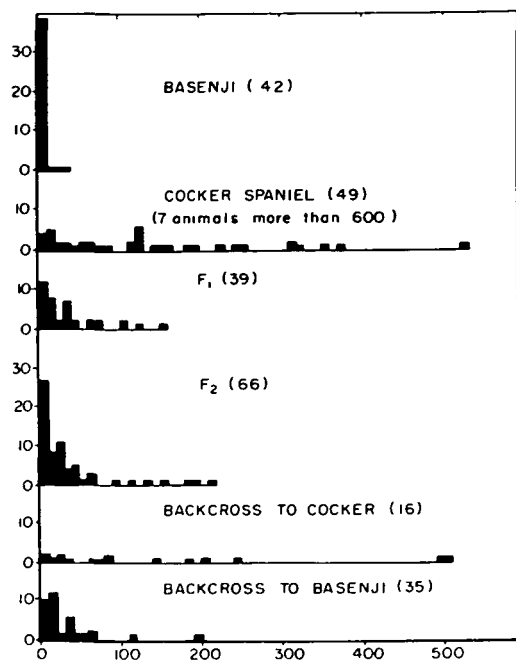


FIG. 3. Distribution of barking to excess at 11 weeks of age, in the pure breeds and hybrids. The figure shows the number of animals producing a given number of barks. Note that almost all basenjis barked less than 10 times.

not legitimate to use conventional statistical tests in this kind of data, in which the performance of a particular dog is not independent of the social relationship with the dog at which he is barking. However, simple comparison with alternate Mendelian models may be instructive. The  $F_1$  figure falls very close to that of the cocker parents, suggesting that dominance is involved. If we calculate the percentages to be expected on the alternate theories of one or two factor dominance, it is obvious that a fairly good fit is obtained on the assumption of one factor. The assumption of no dominance gives a much worse fit than either. It should be pointed out that this analysis is based on a dichotomous distribution of data; i.e., the animals either bark or do not bark. Since no second backcross was made, the conclusion regarding one factor is only tentative.

*Quantity of barking.* The amount of barking shown by each breed and hybrid is shown in Figure 3. Cockers not only show more barking than basenjis, but are

much more variable. The  $F_1$  distribution is intermediate, and that of the  $F_2$  similar and slightly more variable. Backcrosses to the cocker fall between the  $F_1$  and their cocker parents, and the other backcrosses occupy a similar position with respect to the basenjis. The general appearance of the data suggests the hypothesis of no dominance.

This possibility can be checked by dividing the data at the point at which maximum separation of the breeds is obtained (Table 2). The  $F_1$ 's and  $F_2$ 's are approximately intermediate, as would be consistent with the hypothesis of no dominance. The two backcrosses are separated by an amount which would be consistent with the action of one factor (Scott, 1954), but both are shifted in the direction of the cockers much more than are the  $F_1$ 's and  $F_2$ 's. Some sort of complex interaction, either on the behavioral or on the genetic level, is obviously involved. The most that we can conclude is that the data are partially consistent with the action of a single major gene whose action is modified by complex interaction with either environmental factors or other genetic systems. The data also suggest that a different gene system may be involved in controlling the amount of barking as compared to the threshold of response.

#### DISCUSSION

*The action of genetics on behavior.* In the case of the trait of barking or not barking under social stimulation, the obvious explanation is that the one or more genes involved have the effect of altering the threshold of response, a kind of action consistent with many known physiological mechanisms. With respect to gene action upon the amount of barking, the explanation is not so obvious.

In an ideal Mendelian experiment involving crosses between highly inbred strains, there is no genetic variation within the parent and  $F_1$  strains, such variation appearing in the  $F_2$  and backcross populations where random assortment of the genes takes place. Consequently, the segregating generations in such experiments should be more variable than the parent and  $F_1$  populations. The data in Figure 3 obviously do

not fit this model. One of the parent strains, the basenji, shows little variability, but the other is highly variable. The  $F_1$  is moderately variable, or intermediate, as is the  $F_2$ . The backcross to the basenji is less variable than the backcross to the cocker. The data thus suggest that what is inherited is not the capacity to develop a particular amount of barking, but rather the capacity to be variable in behavior. This would mean that variation would result both from the distribution of genes, and from direct gene action, a hypothesis that can be tested by repeated measurements of the same individual. This was not done in the dominance test at 11 weeks, repeated tests being made only with different individuals.

However, we have data on other tests given repeatedly over long periods of development (Scott, 1963b). They show that while the young puppy has few patterns of behavior in the beginning, the expression of these patterns is highly variable, and consistent invariable behavior develops only as a result of long periods of training. This leads to quite a different conclusion from the usual view that heredity functions to set limits upon the development of behavioral capacities. The primary function of behavior is, after all, adaptation to environmental change, and one of the requirements of successful adaptation is variability. All the evolutionary evidence indicates a trend toward greater and greater capacities for behavioral variation. We can say, therefore, that the function of heredity with respect to behavior is not only to produce variation between individuals, but also to increase the capacity for behavioral variation within an individual. It is not heredity but over-severe training which puts behavior in a straightjacket.

*Genetics and the development of behavior.* Returning to the problem of the effect of genetics upon the development of behavior, we can draw the following conclusions from this example. In the first place, the expression of the genetic differences involved in barking varies from one period in life to another, being absent at birth, reaching a maximum later on, and declin-

ing thereafter. Second, the expression of the behavioral difference is dependent upon the stimulus situation. Dogs will not bark under every sort of condition. Finally, this apparently simple difference in behavior is in reality quite complex. The two breeds differ in the threshold of stimulation, the tendency to continue barking when aroused, and in the sound of the barking itself. Not only are the differences complex, but their expression as social behavior is dependent upon the development of the social relationship of dominance.

The data also suggest a theoretical point of great interest, involving the highly specific effects of genetics on behavior. Not only does barking not appear in the neonatal period in any breed, but the amounts of other sorts of vocalization given at this early period do not predict future breed differences. Basenjis give one of the highest rates of distress vocalization of any breed while being weighed on the scales. I pointed out above that behavior in the neonatal period is almost entirely adapted to the circumstances of neonatal life, and that the puppy undergoes a behavioral metamorphosis during the transition period, after which behavior begins to be adapted to the circumstances of adult life. Behavior in the dog has evolved in two directions, toward adaptation for the special circumstances of the neonatal existence on the one hand, and toward adaptation for the adult social environment on the other.

This challenges one of the older and simpler concepts of behavioral development, namely that development is a sort of unfolding or unflowering and that consequently everything that happens at one stage of development leads up to something else. The general course of development in the puppy suggests that certain lines of behavioral development may lead nowhere except that they are necessary for neonatal survival, and that they are abandoned at a later age.

*Genetics and the social environment.* I have pointed out elsewhere (Scott, 1962) that behavioral development in the dog and wolf is closely related to adult social organization as well as to the general ecology of

the species. Ordinarily, the mother pays a great deal of attention to the pups during the neonatal period, necessarily short in a hunting animal. The mother begins to leave them unattended about the time when the puppy begins to develop the capacity for rapid socialization, which means that the strongest social bonds are developed with the litter mates rather than the parents. This forms the foundation for the typical social group of adult wolves, the pack.

Domestication has greatly altered the social environment of dogs, so that they live within and respond to human societies as well as their own. Variations in behavioral development such as that described here have presumably evolved in response to the demands or lack of demands of the human social environment. In the case of the "barkless" trait of the basenji, we only know that these animals were formerly extensively used for hunting in the jungles of Central Africa. It is possible that under these conditions, where predators such as leopards are common, that a noise such as a bark, which has the effect of pin-pointing the location of the barking animal, is a non-adaptive trait. Basenjis have instead developed various "yowling" noises, varying in pitch and volume, in their system of vocal communication. Like the noises made by coyotes, these are likely to be misleading as to the direction of their origin. However, this can only be a matter of speculation in the absence of records.

*The magnitude of genetic effects on behavior.* One of the conclusions that can be drawn from the experiment on barklessness is that the expression of behavioral differences varies throughout behavioral development. In this particular case there is an initial period of no differences, followed by a peak and a gradual decline. Other cases may show an initial difference followed by a decline, or the development of a difference which is maintained. Training also has an important effect upon the expression of genetic differences in behavior. It may either magnify differences, as when successful adjustment is rewarded in some animals but not in others, or to decrease them as all individuals achieve successful adjust-

ment to a common problem. However, as Fuller (Fuller and Scott, 1954) has shown, the proportion of variance attributable to genetic differences may remain constant even as the total variation of the population is reduced.

This brings up the question of the importance of genetic effects upon any behavior. Obviously, the environment will make highly important contributions to variance if it is deliberately altered, as when animals are given different sorts of training and treatment, and the proportion of variance of this sort reaches a maximum when heredity is kept completely constant, as in an inbred strain. At the other extreme, environmental conditions can be kept constant and a maximum amount of hereditary variation can be introduced, as in the present case. Consequently the relative proportion of variance attributable to environment and heredity has little meaning except in particular cases.

However, the proportion of variance due to genetic differences, ordinarily called heritability, is highly important to the practical problem of artificial selection for behavioral differences. Obviously, this kind of variance will be maximized where environmental conditions are kept constant and as nearly ideal as possible.

As part of our general program of research on the genetics of behavior in dogs, we analyzed the variation of 34 measures of behavior and compared them with 10 measures of physical size. All of these variables were selected in the expectation that breed differences would appear, and measurements were made on five different breeds. Variance components were then estimated by the method of Gower (1962), and the percentages of variance attributable to breed differences were calculated (Table 3). The resulting figures ranged from zero in one of the physical measurements (femur diameter) to 66% in one of the heart rate measurements (the arrhythmia index). However, the average figures came out almost exactly the same for the physical and behavioral measurements, namely 27%. This figure is conservative as a total estimate of heritability, since other estimates

TABLE 3. *Proportion of variance attributable to breed differences.*

No. variables	Kind of measurement	Mean percentage
10	Physical size	27
5	Heart rates	38
8	Expression of emotion	23
3	Social relationships with dogs and humans	21
6	Trainability	28
12	Problem solving	27
34	All behavioral measures	27

showed that there was at least another 12% of the variance attributable to matings within breeds and hence also genetic.

Again, these figures have little general meaning since the proportion of variance due to breeds could have been raised by deliberately selecting breeds which contrasted greatly in their behavior. However, they do demonstrate that it would be as easy to select for differences in behavior among a population of animals as it is to select for differences in size. It is often alleged that the environmentally caused variation in behavior makes it almost impossible to work with genetically, but this is not true. Behavior is no more difficult to measure than are other quantitative characteristics; the special difficulties lie in relating primary gene action to its final expression in behavioral adaptation.

#### CONCLUSION

The nature of the effect of genetics upon behavior is one of the basic problems of psychology, in that no causal explanation of behavior is complete without heredity. It is also one of the basic problems of biology, in the sense that the theory of evolution depends upon the selection of adaptive characteristics, and for animals behavior is one of the principal means of adaptation. No theory of evolution of animals is complete without a consideration of behavior, and this has been recognized by all evolutionists beginning with Darwin.

What do we know about genetics and behavior? In the first place, it is well established that certain individual genes with major biochemical or anatomical effects can produce major crippling effects on behav-

ior, such as feeble-mindedness resulting from metabolic disorders in man. Second, it has been shown that a particular behavioral trait can be affected by many genes (Hirsch, 1962). Third, it has been demonstrated in this paper and by the work of many other authors that the distribution of differences in behavior resulting from Mendelian crosses conforms in a general way to Mendelian theory. The same papers demonstrate enormous complexity of gene action, resulting not only from interaction between genes at the physiological level, but also from the process of adaptation at the behavioral level and interaction between individuals on the social level. Trying to relate such results to gene distribution is a fascinating intellectual puzzle which may be attacked in various ways.

One method is to attempt to infer gene action from the data as Broadhurst and Jinks (1961) have done, the result being a hypothetical model which gives a reasonably adequate explanation of the results. Another is to attempt to trace the pathway of causation between gene and behavior, which can be done in various ways, starting either with important behavioral differences and working backward through physiology, or starting at the other end with the biochemistry of the gene and working out its consequences.

The developmental method is intermediate between the two. Here we start not with the gene but with the earliest apparent action of the genes upon behavior. This has the advantage that it emphasizes the fact that every action of genes upon behavior has a history. As I said at the beginning of this paper, behavior is never inherited as such, but is developed under the combined influences of various organized systems, both genetic and environmental (Scott, 1963b). In the long run the study of the developmental genetics of behavior should give us more realistic models of gene action, and it has already given me, at least, an illuminating insight into the role of heredity as a cause of behavior, not as a purely negative and limiting factor, but as a major source of variation within individuals as well as between them.

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