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Evolution and Domestication of the Dog

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Introduction

We ordinarily think of the dog as an animal whose biological history has been determined by artificial selection enforced by human masters, whereas evolution is usually considered a process which takes place without human direction. However, for the greater part of the history of this species, which now can be authentically timed as beginning at least 10,000 to 12,000 years ago, dogs were probably not subject to the conscious selection practised by dog breeders within the last century. Even within this latter period the direction of selection has changed many times. Furthermore, most of the main varieties of dogs were not produced by scientific breeding, but had their origin in the remote historical past as local varieties. It seems most likely that most of these local strains were produced largely by accident and were only later recognized as having valuable special characteristics, after which the variety would be spread over a larger area by travellers and traders.

The dog is, therefore, not in any large degree a conscious product of human ingenuity. Rather, it has evolved under the influence of countless thousands of interactions with human masters. We can therefore think of the dog as a species which, on domestication, entered a new habitat and underwent a process of adaptive radiation similar to that of a wild species entering a vacant ecological niche. It subsequently underwent further modification and diversification as it became divided into small local populations and selection pressure became relaxed in certain directions and increased in others under the influence of the human social environment.

Taxonomy and Distribution of the Genus *Canis*

Linnaeus placed all breeds of domestic dogs in one species, *Canis familiaris,* and modern scientific opinion supports this view. He placed the wolf, *Canis lupus,* in the same genus. Although wolves have in historical times been distributed all over Eurasia and much of North America, they, too, are considered one species (Lawrence, 1967). Other members of the genus are the coyotes of North America (*C. latrans*), and the jackals of the eastern hemisphere.

The black-backed jackal, *C. mesomelas,* is an entirely African species.

The golden jackal, *C. aureus,* lives today in North Africa and Southern Asia, and was once found in Southeastern Europe. Jackals are sufficiently different from other members of the genus that they are sometimes placed in a separate genus, *Thos.* Jackals and coyotes occupy somewhat similar ecological niches on different continents, being plains or desert dwellers living on small game and carrion.

When European explorers came to Australia they found a wild canid, the dingo, which is sometimes temporarily domesticated by the aborigines. It appeared to be a feral domestic dog. Chiefly because of its long isolation from other domestic dogs, it is placed in a separate species, *C. dingo.*

Wolves, coyotes and jackals have a long separate history, being found as bones or fossils as far back as Pliocene times (Matthew, 1930). Other members of the family Canidae are still more remotely related to domestic dogs. The so-called "wild dogs," such as the dhole of India (*Cuon*) and the Cape hunting dog of Africa (*Lycaon*), trace back to a common ancestor with wolves in the Oligocene epoch. The family includes such diverse forms as the foxes (*Vulpes*) and the peculiar "raccoon dog" (*Nyctereutes*) of Europe, as well as various tropical and desert families. In addition to being different from the genus *Canis* in form, other genera vary widely in chromosome numbers (Matthey, 1954).

Origin of the Dog

One of the principal problems of the evolutionary history of the dog is its origin, and three principal theories have been advanced. One of these, popular in the early part of this century (Allen, 1920), is that the dog was domesticated from a wild species which later became extinct. Since no trace of such a wild dog species has ever been found, this hypothesis is no longer taken seriously. Darwin (1859) thought that the dog must have been derived from at least two species, the wolf and the golden jackal, in order to account for the great variation between breeds and individuals. Darwin was working from an assumption of blending inheritance, however, and was ignorant of the degree of variation which is possible through mutation and Mendelian segregation. Early naturalists thought that dogs of the North American Indians might have been domesticated coyotes, on the basis of superficial resemblances in size and color, but anatomical studies on the bones of the Amerind dogs show them to be clearly identical with the European dog breeds. Lorenz (1955) recently revived the theory of the dual origin of the dog, but has since changed his opinion on the basis of behavioral evidence.

This leaves only one tenable theory for the origin of the dog, that it was domesticated from a local variety of small wolf. This immediately raises the question of whether this took place only once or whether dogs were domesticated on several different occasions. As will be seen later, most of the evidence is in favor of a single domestication, although there may have been some subsequent admixture of genes from wild wolf populations on later occasions.

Further Evidence for the Wolf as Ancestor to the Dog

Comparative Anatomy

All members of the genus *Canis* have very similar body proportions, being large-chested, slim-waisted, and long-legged animals. Therefore the body skeleton is of little use in determining the species to which a specimen belongs, and in any case, these bones are frequently not well preserved. The part of the skeleton which is most often preserved is the skull, and especially the teeth, which are the hardest bones of all. Therefore, a great deal of work has been done on tooth characteristics, and one of the outstanding characteristics of the large northern wolves is the size of the teeth in relation to the skull. Some breeds of dogs, such as the St. Bernards, have skulls as wide as those of wolves, and the Irish wolfhound has an even longer skull. Their teeth, however, are considerably smaller (Wagner, 1930; Scott and Fuller, 1965).

The situation is different with respect to the smaller Indian wolf, whose tooth sizes may overlap with that of dogs (Lawrence, 1967). One of the basic characteristics of dogs is, therefore, a set of relatively small teeth. In addition to the genetic heritage of the original ancestor, there must have been, in many cases, a tendency for dog owners to select those animals having smaller teeth and a less fearsome appearance.

It is also reported that wolves bred in captivity tend to show changes in their skull shape, noticeably toward shortening the jaw. Since the teeth are not similarly reduced in size, this results in overlapping of molar teeth. Presumably some of the same effect should be observed in domestic dogs which are normally reared in captivity, but whose teeth are always smaller than those of wolves. These results with alteration of wolf jaws in captivity were obtained from old data gathered before the modern science of nutrition was developed, and it would be interesting to see how wolves reared on modern dog food would compare with them and, indeed, whether modern nutrition has produced differences in the skeletal growth pattern of dogs themselves.

The dog breeds themselves vary considerably in the straightness or curvature of the upper jaw and the crowding of the teeth. For example, in a group of beagles, the sum of the widths of the molar teeth averaged 60 mm whereas the average longest distance from front to back of the jaw was only 57 mm. On the other hand, a group of Shetland sheep dogs tended to have straight jaws with wide spaces between the teeth, with the result that the sum of the tooth measurements added up to only 56 mm compared to 62 mm jaw length (Scott and Fuller, 1965).

One of the difficulties with this kind of evidence is that typological methods do not give clear-cut results, as in almost any measurement there is overlap between populations. One possible answer is that of discriminate-function analysis, in which many measurements are considered at the same time, and are based on entire populations. Using such methods Lawrence and Bossert (1967) have concluded that the red wolf is not a distinct species from *Canis lupus,* but these methods have not yet been applied to the problem of distinguishing the different dog breed populations from populations of wild canids.

Chromosomes

Typological methods are still being used with comparative studies of chromosomes, most authors collecting one or two specimens from a population and drawing conclusions accordingly. Thus Benirschke and Low (1965) reported results from two coyotes, a male and a female, and concluded that the chromosome number was the same as that of the dog (39 pairs), and that the total karyotypes were indistinguishable from those of dogs.

The modern methods of preparing chromosomes have been relatively little used on dogs, but all reports confirm the number established earlier by less adequate techniques, namely 39 pairs (Reiter et al., 1963; Borgaonakar et al., 1967). An early report by Ahmed (1941) indicated that breed differences, again based on small numbers of animals, existed in chromosome shape. Further work should be done with modern techniques on larger populations, as it would appear quite likely that chromosome anomalies might be associated with some of the gross abnormalities of physique found in certain breeds.

Fertile hybrids have been reported between dogs and all three of the closely related species, wolves, coyotes, and jackals. This last report is inconsistent with Matthey's (1954) finding that the yellow jackal has only 37 pairs of chromosomes. On the basis of more recent evidence, Matthey is inclined to think that he was mistaken. It now appears that all members of the genus *Canis* have a diploid chromosome number =78, but this conclusion will obviously be more firm when the chromosome complements of these species have been studied on a population basis.

Evidence from Behavior

Intensive comparative studies of the behavioral patterns of dogs and wolves reveal close resemblances in all patterns observed in both species, and very few patterns that have not been found in both (Scott and Fuller, 1965). The behavioral evidence thus indicates that dogs and wolves are closely related. Similar detailed studies have not yet been done with the coyote and jackal, but such evidence as exists indicates differences from both dogs and wolves. For example, one of the outstanding characteristics of wolves and dogs is their highly social nature. Wolves typically run in packs, which may contain as many as 20 or 25 individuals in the case of packs habitually hunting large herd animals such as moose, and the "lone wolf" is an extreme rarity. Both coyotes and jackals, on the other hand, seldom run in packs, the typical social group being a mated pair with a litter which breaks up when the animals become mature. Jackals are sometimes seen in large numbers around garbage dumps, but these animals do not belong to the same social group.

The evidence is even more clear with respect to patterns of vocalization. Both wolves and dogs show similar patterns of barking and howling. The bark of a wolf is primarily an alarm signal which is readily elicited when a strange animal comes into the territory around the den, whereas the clear howl is used either in chorus with a group of animals or is given by individual animals who become separated on a hunt and howl back and forth.

From hunter's reports, Darwin thought that wolves did not bark, and if they did, learned it from domestic dogs. However, all observers of wolves agree that they bark, no matter what their proximity to or isolation from domestic dogs. The tradition probably got started because hunters relatively rarely came upon the small territory around a wolf den, but frequently heard wolves howling on the hunt.

Coyotes show a typical pattern of vocalization in which barks, howls, yips, and other vocalizations are mingled together in varying pitches and loudness, with a ventriloqual effect. The result is that two animals will sound to the uninitiated listener like a pack of forty. Nothing like this is ever heard in dogs or wolves.

Jackals also make more elaborate noises than dogs or wolves. The African black-backed jackal is reported to make a sound like "ke-ke-ke-kek" when cornered, and in the mating season the female makes a sound described as "a hearty laugh." Jackals howl on occasion, but also make peculiar noises when hunting (Van der Merwe, 1953).

If there is any possibility that jackals have been crossed with dogs, the most likely case would be that of the African basenji. These animals make vocalizations which are distinctly different from other dog breeds. They are supposed by breeders' standards to be barkless, but occasionally do bark, both those in Africa and the improved breed in Europe and this country. Basenjis howl like other dogs and also produce a crowing noise which appears to be a modified and extended bark. Whether or not there is any possibility that basenjis may have been produced by a jackal cross will await further detailed studies and comparison with jackals.

Admixture of Wild Genes

One indication of the common ancestry of our domestic breeds is the universal occurrence in all dogs of a sickle-shaped or curly tail, contrasted with the drooping tail carriage of wild canids. We can hypothesize an early mutation which was preserved because it was useful in distinguishing wild from domestic animals, and that this has been maintained with some variation in all domestic dogs. This does not, however, eliminate the possibility that genes from wild populations may have been introduced from time to time. Degerbøl (1927) points out that the northern dog breeds such as the Siberian Laika, the Scandinavian gray deerhound, and the Esquimo dogs all have relatively large teeth and that this may have resulted from crossing with the northern wolves. Northern travellers frequently bring back stories of such hybrids. It is also possible that the large teeth of northern dogs resulted from accidental selection of animals whose teeth were more competent to deal with large bones. Whether or not there has been the possibility of crossing with jackals to produce the southern variety of dogs is another problem, and one for which we may never find any final answer. In any case, admixture of genes from wild species is likely to have taken place only on the fringes of the species and is unlikely to have produced any major shift in gene frequencies in the total gene pool.

Time of Domestication

Until relatively recently the origin of domestic animals has been only a minor problem for archeologists, who were primarily concerned with human prehistory and origins. Animal bones were often collected in connection with human remains, but were frequently neglected or carelessly classified. Furthermore, the early workers concerned with this problem were dominated by typological techniques so that each new dog skeleton was considered a separate subspecies of *Canis familiaris*. Dahr (1937) was one of the first workers to attack the problem from a population standpoint, and he pointed out that the Stone Age dogs of Europe, far from being specialized breeds, could all be included in one population showing considerably less variation than modern dogs.

For many years the earliest known remains of the Stone Age dogs were those described by Degerbøl (1927) from the Danish kitchen middens. By methods then in use it was estimated that these bones were deposited between 8,000 and 10,000 BC. Since then the more accurate carbon dating method has been developed. With this process these same remains have been dated at 6810 ± 70 BC. Thus the Denmark dogs are probably not older than 9,000 BP (Degerbøl, 1961).

Canine remains were also found at the earlier site of Star Carr, in Yorkshire, England. Degerbøl (1961) has concluded that a skull fragment found at this hunting camp is that of a true dog. Carbon-dating methods place this settlement at 7538 ± 350 BC, so that this dog may have lived as recently as 7200 BC, or as early as 7900 BC, or approximately 10,000 years ago. A contemporary specimen from Turkey has been dated at approximately 7000 BC (Lawrence, 1967), and until recently the timing of these finds was strong evidence that the first domestication of the dog occurred in Europe or Asia.

However, the oldest known dog remains that have been definitely identified come from a specimen in a cave in the Beaverhead mountains in Idaho (Lawrence, 1967). Carbon-14 dates place this specimen at the latest 8300 BC and at the earliest 9500 BC. Similar carbon dating of the earliest human remains in North and South America indicates that a simple hunting culture became established between 14,000 and 9000 BC (Johnson, 1967). Some of these early settlers probably brought the dog with them, which would mean that domestication must have taken place at an earlier date, perhaps around 10,000 BC (Lawrence, 1967). Dogs have thus been domesticated for at least 10,000 years and possibly as long as 12,000.

These conclusions are based on the best evidence available at the moment. While it seems unlikely that the above estimates of timing will be upset by future discoveries, it should be remembered that most parts of the world have been explored by archeologists in only a superficial way, and particularly so with respect to animal remains. Future discoveries should not only pinpoint the time of domestication more closely, but also give more accurate indications of place.

The Place of Domestication

The possible areas in which dogs could have been domesticated are limited by the distribution of the wild species which could have been the possible ancestors. The wolf has an almost world wide distribution in the northern hemisphere, but has never been found south of the Equator. This means that South America and much of Central America can be eliminated, as well as Africa, Australia, and South East Asia, as the known geographical ranges of wolves do not enter into these areas. North America and parts of Eurasia are therefore the only possible centers of origin.

Dogs, on the other hand, were found in historical times associated with man on every continent except Australia, where the wild dingo was found.

According to all anatomical evidence, this species is descended from a dog which escaped from domestication and was able to prosper on the new continent with no competition from other wild species except the native marsupial predators. The distribution of dogs therefore gives no clue as to their point of origin.

Archeological Evidence

New finds are continually being reported from all over the world, and since 1958 it has been possible to date these relatively accurately with the Carbon-14 method. There are many areas of the world which have still not been thoroughly explored, particularly in China and other parts of the Far East, and it is therefore possible that conclusions drawn from the present evidence may be radically changed in the future. As recently as 1948, Haag estimated that the earliest dog remains in the Western Hemisphere were as recent as 1500 BC, but this date has now been pushed back to at least 8300 BC, slightly older than the earliest known dog remains from Europe and closely resembling them. However, it is unlikely that these North American animals represent the original ancestors, on two counts. One is that, as far as is known, the early human migrations were all out of Asia into the empty continent of North America, and not vice versa. Second, and more convincingly, the early American dogs were all small or medium sized animals, quite unlike the large North American wolves. Although there was a smaller variety of wolf in the southeastern part of the United States, formerly classified as a separate species (*Canis niger*), Lawrence (1967) reports that there is no overlap in tooth size between these forms and domestic dogs.

Otherwise, the oldest remains of true dogs are found in western Europe, in England and Denmark respectively. Again, it is not likely that these dogs were domesticated locally, as the northern wolves of Europe are large in size and have very large teeth compared to those of dogs.

In the Near East and Southern Asia, there are two subspecies of small wolves, the Indian wolf *Canis lupus pallipes,* and the Arabian wolf *Canis lupus arabs*. Both of these varieties show close resemblances to dogs, and Lawrence suspects that *arabs* may actually be a hybrid between domestic dogs and the Indian wolf. This area in the Near and Middle East therefore seems to be the most likely center for the original domestication of the dog.

The dog remains that have been located in the Near and Middle East are all associated with agricultural communities (Reed, 1959). Currently, the earliest known remains from this general area of Asia come from a Turkish site which has been dated around 7000 BC. Another set of remains were found in Jericho, dated at approximately 6500 BC, and in the contemporary farming village of Jarmo several canine clay figurines with curly tails indicate that the artists were acquainted with dogs. However, judging from the association of dogs with the prehistoric hunters of Star Carr, the dog was probably domesticated by hunters and food gatherers before the beginning of the agricultural revolution.

This does not eliminate the Far East as a possible center of origin. According to Lawrence (1967), there was a now extinct subspecies of wolf in China which closely resembled the Indian wolf and which could have been a possible ancestor, and there are also a few reports of very early dog remains in Japan which have not yet been thoroughly studied. However, on the basis of present evidence it is most likely that the dog was first domesticated somewhere in the vicinity of the Near East or Central Europe and spread out in all directions from this point.

The Process of Domestication

All domestic mammals and birds are highly social animals, with the possible exception of cats, which have a tendency to become attached to places rather than people and so arrive at domestication by a somewhat different road. A correspondingly high degree of sociality is found in the wild species from which they were derived. Among birds, mallard ducks, Indian jungle fowl, wild geese, and wild turkeys are all animals that constantly live in social groups. The wild ancestors of some of the herd animals, such as horses and cattle, are now extinct, but all information that we have indicates that they lived in herds like their domestic descendents. The wild species of pigs, sheep, and goats are highly social, and wolves are no exception to the rule. Even the European rabbit, the presumed ancestor of our domestic forms, is a group-living animal and much more social than the North American forms which have never been domesticated (Hale, 1962).

One characteristic of these highly social mammals and birds is a short period in early life in which social relationships can be readily formed, normally with the members of the same species, but also with other species with whom they come into contact. Most of the domestic animals readily become attached to human beings as well as their own species during this critical period of primary socialization.

This phenomenon was first noticed scientifically in young chicks and its general importance in birds was first appreciated by Lorenz (1937), who gave it the name of imprinting. A similar phenomenon takes place in the herd animals like sheep and goats, where the mother forms a more specific attachment to her young than vice versa (Hersher et al., 1963), and the process has been extensively studied in the dog.

The Process of Primary Socialization in the Dog

Reproduction and the development of behavior in the dog and wolf is obviously adapted to the life of a hunting animal. The period of pregnancy is short, some 63 days, and implantation is delayed so that the fetus does not begin rapid growth until pregnancy is halfway along. The pups are born in a small and immature state, weighing perhaps half a pound each at birth in a medium sized dog. The size of the litter tends to be relatively small, averaging 4 or 5, although litters may be much larger in some of the big domestic breeds. The result is that the female is handicapped in hunting activity for only a relatively short period toward the end of pregnancy. Although not particularly useful to a household pet, this has obvious adaptive value for a wolf or a hunting dog.

When the pups are born the mother takes constant care of them during the first few days, when nursing is being established, and then begins to leave them for longer and longer periods. In the wild species the mother during this period can obtain food readily from meat cached around the den or brought back by other members of the pack. When the pups are approximately three weeks of age the mother supplements the milk with regurgitated food from her own stomach, and the pups are usually weaned between 7 and 10 weeks of age. In wolves, adults of both sexes feed the pups in this way, whether or not they are the actual parents. While the pups at this age are by no means mature themselves, the mother is left free to leave them for long periods.

Behavioral development in dogs and wolves has evolved in two directions. During the first two weeks of life (the neonatal period), behavior patterns are adapted for neonatal nutrition, or nursing, and for an existence in which all care and protection is provided by the mother. Even urination and defecation are induced in a reflex fashion by the licking of the mother, an adaptation which has the effect of keeping the den clean. Otherwise, their social behavior is limited to distress vocalization, or care-soliciting behavior, and a slow crawl, throwing the head from side to side, which is a primitive form of investigative behavior.

The pups are both blind and deaf and thus have relatively little sensory contact with the outside world. Puppies in this period are slow learners and require many more repetitions of experience to form fixed habits than do older dogs.

The neonatal patterns of behavior are so different from those of an adult dog that one would have great difficulty in recognizing puppies as members of the same species from their behavior alone. A similar phenomenon is, of course, well known in those insects whose larvae and adults live in different habitats, such as the caterpillar which metamorphoses into an adult butterfly.

In dogs, the first overt change in behavior takes place on the average at about two weeks, when the eyes open and the pups first begin to crawl backward as well as forward. Within the next five or six days, comprising the transition period in development, the puppy changes quickly but not entirely from the neonatal to the adult forms of behavior. In sensory capacities, both the ears and eyes open and become at least partially functional. In motor development, the puppies stand and run, begin to cut their teeth and, associated with this, begin to mouth and chew objects as well as to suck them. By 19 or 20 days of age they become capable of being conditioned at a rate similar to that of an adult. Most significantly, they begin to show many adult patterns of social behavior in immature form, such as playful fighting, running in groups, and even immature sexual behavior.

At this time the pups also become capable of rapidly forming social attachments. The first indication that this has taken place is the response of distress vocalization when isolated in the home pen, indicating that the puppies notice the absence of familiar individuals (Scott and Bronson, 1964). At the same time they begin to react with distress to being placed in strange surroundings, indicating that an attachment has been formed to particular places.

From approximately 3 until 12 weeks of age is the critical or sensitive period for rapid establishment of social relationships, with a peak in this phenomenon between 6 and 8 weeks of age. Various isolation experiments indicate that the period is brought to a close by the development of a fear response to strange individuals, beginning about seven weeks of age. Up until this time puppies ordinarily give only momentary fear responses to strange individuals, and their chief emotional response is distress vocalization caused by the absence of the familiar.

If a puppy is taken from the litter at the beginning of the period of socialization and raised entirely by human beings from this point onward, he will develop all social relations with human beings and will later show very few responses to other dogs other than those of fear and antagonism. If, on the other hand, he is reared exclusively with dogs for the entire period of socialization, i.e., as long as 14 weeks of age, he will develop social attachments only with dogs and will respond to human beings in a fearful fashion, forming attachments only with great difficulty. Finally, if a puppy is left with the litter and removed to human companionship between 6 and 8 weeks of age, he has had the opportunity to form relationships with dogs and still capable of doing this easily with people. The general result is an animal which is considered a normal dog, being a part of both dog and human society.

Socialization in the Wolf

Numerous examples of persons who have reared wolf cubs and made pets of them are present in the scientific literature, from the day of Buffon (1804) down to the present (Fentress, 1967). Unless the cubs are obtained from a zoo it is impossible to determine their exact age, but as far as it is known, the course of development runs the same time sequence as that in the dog. If the wolf cub is obtained about the time the eyes open it can be raised like a puppy and grows up looking and acting very much like a large dog. With few exceptions the end result is an animal that becomes very much attached to people and behaves in a fashion indistinguishable from that of a normally reared pet dog, with the exception that wolves appear to be more reactive to slight noises and sudden movements. The owners are able to take the animals on the streets without attracting any attention, so dog-like is their appearance and behavior.

Wolf cubs appear to develop strong fear reactions sooner than puppies, which usually discourages people from adopting them at later ages than the period when the eyes are just open. However, Woolpy and Ginsburg (1967) have been able to socialize wild-caught adult wolves by patient and careful contact over a long period of time. The essentials of the method are confinement and passive contact. The wolf is penned in a solitary cage, and the experimenter enters and remains quietly for a long period each day. At first the wolf shows every sign of extreme fear, urinating, defecating, salivating, and attempting to climb the walls to escape. He gradually becomes more quiet and after a period of several weeks may finally make a positive approach to the experimenter. If the latter reacts appropriately at this time, neither frightening the wolf nor acting fearful himself, the wolf will establish a tolerant and friendly relationship which is extended to other human beings as well. This relationship, although amicable and tolerant, is different from that which a wolf cub develops with a human being, especially in that the wolf does not occupy a subordinate position. The relationship is also different from that which it enjoys with other wolves.

These results indicate that the process of forming an emotional attachment can take place at any age, but that it requires a much longer period than in infancy, because of the length of time required to overcome the interfering fear responses. The ability of the wolf to adapt to people also has some significance in connection with possible contacts between wild wolves and prehistoric human hunters and food gatherers.

Similar Ecological Niches of Man and the Wolf

In Eurasia and North America wolves occupy the ecological niche of hunters of the large herd animals, and the size of the packs seems to be partially correlated with the size of the prey, very large packs developing when the prey is moose, and smaller ones for mountain sheep, deer, or caribou. However, wolves do not confine their diet to these prey animals and at different seasons of the year will eat mammals as small as mice and a certain amount of vegetable material such as berries. They will also eat carrion. They thus show considerable adaptibility in their food habits, although perhaps not as great as that of man.

However, as hunters of the large herd mammals, wolves occupy the same ecological niche as early man, and, indeed, must have been active competitors in prehistoric Eurasia and North America. We have, therefore, the theoretically interesting situation of two different species each occupying the niche of a dominant predator. We have no evidence of what actually happened when the two species came in contact except from historical records of hunters in North America a century or so ago. There are frequent records of wolves hanging around hunting camps and eating the remains of animals killed by the hunters. There are also many records of wolves following hunters, who sometimes became very frightened. Investigating all of these cases, Young and Goldman (1944) were able to find only one authentic case of a North American wolf attacking a human being. Like most carnivores, wolves appear to be highly traditional concerning their prey species, although they adapt very well to domestic live stock which are similar to the wild prey animals.

The situation may be somewhat different in Eurasian wolves, where there are not only numerous legends of man-killing wolves, but also, according to Pulliainen (1967, private communication), authentic cases of wolf attacks on human beings in contemporary Finland and Russia. Further information is obviously needed, but it looks as if the North American and Eurasian wolves may be either genetically or culturally different from each other.

The point here is that an early hunting society in Eurasia would easily come into contact with wolves, and that in some circumstances wolves are capable of forming a tolerant relationship with people if this is permitted, especially if there is sufficient food for both.

It is obvious that stone age hunters were not able to exterminate wolves in North America. Indeed, even with modern weapons and poisoning techniques, modern men have only been able to push wolves back toward the Arctic, assuming the position of sole dominant predator only in areas where domestic stock are reared. In the long period before the domestication of herd animals, when the two species were engaged in similar occupations in the same area, the usefulness of a domestic wolf in hunting would become immediately apparent.

Mutually Understandable Behavior Patterns

Besides being highly sociable and occupying similar ecological niches under certain conditions, human beings and both dogs and wolves have other points in common, especially the existence of behavior patterns which are mutually recognizable. With respect to agonistic behavior, it is easy for a human being to recognize the intent of a growling and snarling dog, and it is easy for a dog to understand a shouting and threatening human being. Living in groups as they do, both species have evolved the capacity to develop dominance-subordination relationships, with the result that individuals can learn to live in close association without destructive violence.

Even more striking are the resemblances in allelomimetic behavior and the motivation connected with it. Both people and dogs are strongly motivated toward companionship and doing what the other individual does, with some degree of mutual imitation (Scott, 1967b), and both species are capable of making group attacks on an individual, whether of the same or a different species. Certain other kinds of behavior have no counterparts, such as the sexual tie in dogs and reaction of the male dog to the urine of a female in estrus. However, the behavior patterns of dogs and wolves are sufficiently similar to those of human beings that it can be said that wolves and men were strongly preadapted for life in a combined social group. To put this in other words, the wolf is preadapted for domestication.

Polymorphism in the Wolf

As a dominant predator the wolf is protected from certain kinds of selection pressure, thus permitting the survival of individuals with a considerable variation from the mean. As a highly social species, wolves should be subject to selection favoring variation useful in cooperative enterprises, as a greater degree of variation permits a greater degree of division of labor. For an example, a wolf pack might benefit both by the presence of individuals that were highly timid and reacted to danger quickly and effectively, and also by the presence of other more stolid individuals who did not run away but stayed to investigate the perhaps nonexistent danger.

Although there is still little more than anecdotal evidence to support the existence of such behavioral polymorphism, the existence of anatomical polymorphism is much better verified. Murie (1944) was easily able to distinguish the individuals in a wolf pack by their different appearance in form and color. In addition, local populations of wolves vary considerably in form and size, with a general tendency for the northern or Arctic wolves to be larger than the southern variety (Jolicoeur, 1959).

Assuming that behavioral as well as anatomical polymorphism existed in the wild wolf populations of 12,000 years ago, there must have been a considerable variety of individuals and subpopulations from which the first domestic dogs could have been selected. If one attempt did not succeed, another might, and it is very likely that the first successfully domesticated animals were smaller, less aggressive, and less fearful than the average wild wolf.

Polymorphism also carries the implication that the gene pool of the species is adapted to permit viable variants. One can hypothesize a condition in which almost any variation from the standard gene complement would be distinctly nonviable, and other situations in which the genetic complement was buffered against the effects of variation.

Probable Method of Domestication

The archeological evidence indicates that the wolf was first domesticated by Stone Age hunters sometime between 8000 and 10,000 BC. At this time the Ice Age was coming to an end, the supply of game was plentiful, and the human population quite small. These Stone Age hunters therefore must have lived under prosperous conditions similar to those of the North American plains Indians during the early part of the 19th century, with the exception that the Eurasian hunters did not have the horse.

Scavenging wolves would have come around the hunting camps, looking for offal and attempting to steal stored supplies of meat. The hunters may, on occasion, have even hunted wolves and dug the young cubs out of their dens. Some of these may have been brought home alive and escaped the soup pot perhaps by attracting the attention of a woman who had lost her baby and was suffering discomfort from persistent lactation. Such a wolf cub could be very easily reared on the breast by a human mother for a few weeks, after which it could subsist on scraps and bits of cooked food. In a time of ample meat supplies there would have been plenty to go around. The adopted cub would have become rapidly attached to human beings, as wolf cubs do today, if taken at the right time, and it would have been friendly and playful with the children. By the time it was three months old it would have been largely self-sufficient, living on scraps of food and becoming a member of the human group. And unless human behavior has changed markedly, the foster mother would have become strongly attached to it.

If the original puppy was a female it could have mated with a wild male and brought up her own puppies within the camp, or perhaps a mate was provided by bringing in other puppies in subsequent years. Or the adoption and taming of wolf cubs could have become a standard part of the magical and religious practices of the tribe. Once such a tame wolf reached maturity the practical advantages of possessing one would be immediately apparent. It would act as if the hunting camp were its den and its boundaries a territory. It would respond at night to both strange animals and human beings entering the area, and give the alarm by barking. Furthermore, if taken on a hunt it would join in group attacks on a game animal without any particular training and also aid in locating small game, whether birds or mammals.

In short, the original domesticated wolf must have immediately been appreciated as an extremely useful social invention, and once a breeding population had been established it must have spread rapidly from tribe to tribe. In fact, the archeological evidence indicates that the dog spread throughout the world wherever people were living within a thousand years or so.

Considering the ease with which wolves can be tamed, it is, of course, possible that domestication took place on many occasions. Against this is the evidence of the common characteristic of all dogs, the curly tail, which may have been a very early mutation by which domestic animals could be distinguished from wild ones. There is also the evidence that all dogs have relatively small teeth and are basically smaller animals. Even the giant breeds, such as St. Bernards and Great Danes, do not have the bodily proportions of Arctic wolves but are obviously overgrown dogs, clumsy as the result of their large size. Until better evidence is available, we can adopt the hypothesis of a single domestication, with possible admixture of genes from wild populations of wolves from time to time.

Evolution of the Wolf

The major controlling factors in evolutionary change are mutation pressure, selection pressure, isolation, and inbreeding. Wright (1931, 1965) has pointed out that the ideal conditions for rapid evolution, based on the assumption of polygenic effects and differential effects of genes in different combinations, are provided by a species which is divided into a number of small local subpopulations that are nearly but not completely isolated and small enough so that a moderate degree of inbreeding takes place. Selection pressure should also be moderate, otherwise each population will become stabilized around the particular gene combination which is most advantageous. As local populations become extinct, evolutionary changes will inevitably occur, guided by the genetic make-up of the surviving populations. The division of a species into two or more subspecies is of course dependent on complete isolation being achieved in some way.

The organization of wild populations of wolves is in many ways closely comparable to this ideal situation. As dominant predators and adaptable animals able to live in a variety of habitats, wolves are ordinarily subject to only a moderate selection pressure. While the mating system of wolves is known only by inference, it appears that new groups are probably formed by litters leaving an older pack in a body and hence having a considerable opportunity for inbreeding. In any case, the social group itself is always small and semi-isolated from others by distance and territorial boundaries.

On the other hand, there is no evidence that local populations of wolves frequently became extinct except as the result of intensive extermination programs by their human competitors. Wolves are large and mobile animals and are restricted by few natural barriers except oceans and deserts. If one area becomes unlivable, they can easily migrate into another. This same mobility prevents any complete isolation between populations, and taxonomists consider that all wolves belong to the same species, although the connection between North American and Eurasian wolves at the Bering Strait must be a tenuous one. Rather than becoming divided into separate species, wolves have evolved along the lines of numerous local populations, each intergrading with the next. The overall result has been considerable stability for the species, and fossil wolves are not reported to be greatly different from modern ones. The only area of the world where wolves have come close to separating into two species is South Asia, where the Indian wolves are separated from the northern ones by the great barrier of the Himalayas and adjacent deserts and are sufficiently different to be considered a subspecies. It is this same population, or one closely similar to it, which is the most probable ancestor of the dog and therefore formed the raw material for the further evolution by the dog in the new habitat provided by human culture.

Evolution of the Dog

Domestication of the dog by early hunting and agricultural populations did not drastically change the organization of populations from that seen in the wolf. The dogs in a hunting tribe or agricultural village comprise a small local population with a considerable amount of inbreeding and some opportunity for cross-breeding with groups from adjacent tribes. Yet there has been a much greater differentiation of local populations than in the parent species.

The obvious explanation is deliberate selection for unusual variation, such as is practised by many modern dog breeders. This is at best only a partial explanation, and the origin of diversity in dogs can be viewed in more general terms as the result of penetration of a species into a vacant habitat, in this case the human cultural environment. Human cultures themselves evolve and differentiate, and from the viewpoint of the dog represent a great variety of habitats. Each culture represents a different habitat, exercising a different sort of selection pressure, and as the original populations of dogs entered such habitats the small numbers in each new group gave a great opportunity for accidental selection of unusual variations as well as for deliberate selection pressure exerted by the human masters.

Dogs can reproduce at one year of age, and it is theoretically possible to pass through a generation once every year. Estimating the average dog generation as a conservative two years, dogs have had perhaps 5,000 generations in which to accumulate mutations and to differentiate into subpopulation. While this has been going on, human cultures have also changed and differentiated, and the Stone Age hunting camp has been replaced first by agricultural villages and latterly by the towns and cities of our modern industrial society.

Historical records of what has actually happened to dogs in this time are incomplete and not always reliable. The best historians are usually uninterested in dogs, and even the crudest written records extend over little more than half of the period of domestication. The first extensive treatise on dogs was written not quite 400 years ago (Caius, 1576). Nevertheless, some general conclusions can be drawn, and we can also make some enlightened guesses on the basis of some of the more reliable information.

In the first place, the Stone Age dogs appear to have been medium-sized animals, similar in form and probably serving as all-purpose hunting and guard dogs. Their center of origin was probably somewhere in Central Europe or the Middle East. In Mesopotamia today there are two kinds of dogs: the salukis, which are used for gazelle hunting, and a large, stockily-built, long-haired dog which is used to guard flocks of sheep and goats (Hatt, 1959). Early carvings indicate that these same two kinds of animals were present in the pre-Christian civilizations of that area, and that the large animals were then used for war dogs.

The salukis appear to have been the ancestors of the modern greyhounds and were first brought back to western Europe by the returning Crusaders. The Afghan hounds of nearby Afghanistan and the borzois of Russia were probably also derived from this original Mesopotamian stock.

Judging from the resemblances between African basenjis and Australian dingos, and the occurrence of similar dog breeds in southeastern Asia and the East Indies (Werth, 1944), we can postulate the early origin of a short-haired dog adapted to tropical living and that it was taken into Africa and across southern Asia, eventually reaching Australia.

There is also a northern group of dogs with some characteristics in common; these include the sled dogs of the Eskimos in both Eurasia and North America. Whether these have a common origin or not, they go back to a relatively recent date, according to the timing of skeletons associated with those of prehistoric Eskimos.

A third group of early dogs reached the Americas, and the earliest remains so far discovered indicate that they were similar to the undifferentiated Stone Age dogs of Europe (Lawrence, 1967). At the time the white explorers reached the Americas there were dogs living all over the two continents, from Hudson's Bay to Tierra del Fuego. These rapidly disappeared under the pressure from European immigrants, and the introduction of the European breeds. Studying their remains, Allen (1920) described three groups, chiefly distinguishable on the basis of size. These included the large Eskimo dogs, medium-sized dogs in at least eight varieties, and small-sized dogs of at least five distinguishable populations. The Eskimo dogs or Huskies and Mexican hairless are the sole surviving breeds, and even their ancestry is in some doubt.

Beyond these scanty historical indications and what we can infer from prehistoric remains, there is little authentic information about ancient dogs. The modern breed associations are of quite recent origin, and accurate written information began to be collected less than 100 years ago. The Kennel Club of England was founded in 1873, and the American Kennel Club in 1884. It was only at this time that breeders began to limit cross-breeding, to set standards for the selection of parents, and to keep complete pedigrees. Dog breeding as a modern pastime has been practiced chiefly in Great Britain and the United States, and to a lesser extent in western European countries. The classification of breeds reflects the cultures of the country. In Great Britain the emphasis is on sport, or hunting, and the Kennel Club of England recognizes two major classes of breeds, the sporting dogs, including hounds, gun dogs, and terriers, and the nonsporting breeds which include working dogs, toys, and others. The French list recognizes hunting dogs but also watch dogs, running dogs, 17 kinds of shepherd dogs, and 24 "ladies" dogs, including mostly toy and lap dogs. The German list emphasizes working dogs and watch dogs of a relatively ferocious sort, whereas the Swedish one recognizes nine different Spitz breeds.

The American Kennel Club lists over a hundred breeds, originating from all over the world, and classifies them into six groups, chiefly on the basis of function rather than ancestry. In some cases a group includes breeds that are historically known to be genetically related, but the same group may also include animals with similar uses coming from opposite ends of the earth. These groups are worth looking at, however, as an example of the numerous ways in which dogs are now used.

In this classification, the *sporting breeds* chiefly include the bird dogs, or gun dogs, of which we have many historical records in England. The modern setters and pointers were developed from the medieval spaniels. By tradition, the spaniels were named because they originally came from Spain, and there are many modern breeds bearing the same name. Pointers are known to have some admixture of hound ancestry, and it is possible that this has occurred in other breeds as well.

The *hound breeds* are traditionally divided into sight hounds and scent hounds. The former includes the greyhounds and their various relatives, and probably comprises a natural group with a common ancestor similar to the gazelle hounds or Salukis of the Middle East. Among scent hounds, there is a group of English breeds, including the fox hounds and beagles, made up of similar dogs which probably have considerable common ancestry. The fox hounds and coon hounds of the United States have also been chiefly derived from these breeds. However, hound breeds from other parts of the world have probably been developed independently, as we have no records of transportation of these animals from one country to another. The Norwegian elkhound, for example, is most similar to the Spitz and other northern breeds.

The *working breeds* include three main kinds of dogs from all over the world. One of these includes shepherd and farm dogs, such as the Scottish collie, Old English sheepdog and German shepherd. There is probably no common ancestry except in animals coming from neighboring areas. Another group of working dogs is made up of the guard dogs, of miscellaneous origin and including various giant breeds such as the mastiff, Great Dane, and St. Bernard. The third group includes the sled dogs from various Arctic regions. As indicated above there is some evidence that these last animals have remote common ancestry in an early variety of dogs adapted for life in a far northern climate.

Terriers, as indicated by their names (Scottish terrier, Welsh terrier, Irish terrier, etc.), are largely dogs from the British Isles. From medieval times hunting has been a popular sport in these countries, but only the nobility were allowed to hunt deer and use hounds. The common people had to content themselves with hunting ignoble game, or vermin, and for this purpose the smaller terriers were developed. As a group, terriers are the most aggressive of all the dog breeds, and some of them were used in the once popular sport of dog fighting.

The *toy breeds* have miscellaneous origins from widely different geographic regions and have in common chiefly their small size. They are true dwarfs rather than a separate species, as they have disproportionately large brains and genital organs. The puppies are also disproportionately large compared to the adults.

The American Kennel Club's final group is the *nonsporting breeds,* which include a variety of animals now used entirely as companions and show dogs. Some of these formerly had special uses. Dalmatians were coach dogs, and bulldogs were once used in bull-baiting.

As well as recognized breeds, there are a large number of varieties of dogs in the United States which have either never been under the control of professional breeders or which have never been entered in the American Kennel Club. In almost every part of the world there are local native varieties of dogs, often distinctly different from the commonly recognized breeds, although many of these are disappearing under pressure of European breeds brought in by explorers and immigrants. Most of the native varieties of dogs in South Africa were destroyed during an epidemic of rabies and have been replaced by either European breeds or dogs of mixed ancestry. Almost all of the Amerindian breeds have long since disappeared, and the aboriginal dogs of Malaysia are rapidly declining in numbers.

Most primitive cultures support only one kind of dog, or at most two, so that the early differentiation of dog populations had a largely geographic basis. At the present time, a large urban culture can support and keep separate dozens of breeds (the American Kennel Club recognizes over 100), maintained as separate populations by restrictions in a way which is reminiscent of caste systems in human societies.

Such breed populations are often quite large, containing 40,000 individuals or more, but many are quite small. Selection for breed standards is based on typological ideas, and changes from time to time according to the current ideas of the breeders, with the result that great changes of form have taken place since accurate records have been kept. The popularity of different breeds waxes and wanes according to human cultural changes. The genetic situation is not a stable one, and we can predict that dogs will continue to change in the future in both appearance and behavior.

Evolution of Behavior in Dogs and Wolves

One of the most important factors affecting evolution in a highly social animal is that of the nature of the social environment itself. Darwin chiefly thought of this problem in terms of sexual selection, referring to competition between members of the same sex for the opportunity to reproduce, and the tendency for an animal to prefer one kind of mate over another. These phenomena are examples of a broader phenomenon which may be called *social selection,* and which may be defined as any sort of selection exerted by the social environment and including the selective survival of individuals of any age, irrespective of sex. Social selection is an obviously important factor in the wolf (Scott, 1967a) and even more important in the dog, which belongs to two societies, canine and human.

Social Selection in the Dog and Wolf

We have already pointed out that the evolution of behavior in dogs and wolves has proceeded in two different directions in early and late development, with puppies in the neonatal period being selected for behavior adapted to survival under conditions of highly protective maternal care, and later behavior evolving toward adaptation to the adult social situation involving greater independence of the individual, but also considerable social cooperation and caregiving behavior. In between there is a brief transition period accompanied by a metamorphosis of behavior almost as spectacular as that which accompanies metamorphosis from the tadpole to the frog.

These general evolutionary tendencies have not been seriously modified by social selection from the human social environment, probably because similar, though not as clear-cut, tendencies are found in human development. In human infants the process of primary socialization takes place before most of the transition processes, and these are not concentrated in one brief period as they are in the dog (Scott, 1963). However, there is in early human development a neonatal period very similar to that of the dog, whose behavioral development has been modified least of all in the neonatal period. There is likewise little difference in the transition period between the behavior of wolves and dogs. For the most part, the early care of puppies is still left to their canine mothers, and it is only after the transition period is over (at approximately three weeks) and the puppy begins to take supplemental food, that human care begins to have an important effect.

In the period of socialization there has evolved in the wolf the capacity to form rapid emotional attachments to familiar objects and individuals, an attachment that is strengthened over a period of several weeks. This process is so fundamental for the survival of a highly social animal born in an immature state that there is no reported variation in wolves, and even in dogs it takes place with great uniformity with respect to time.

The nature of this process is such that it permits the formation of attachments to different species, even though in the normal course of development of a wolf no contact with animals other than the parent species would be possible during the appropriate period. As indicated above, the existence of such a process is a major factor determining the fitness of any animal species for domestication.

Certain modifications of the primary socialization process seem to have occurred in dogs as a result of human social selection. One is a less rapid development of the fear response to strangers which tends to bring the period of socialization to an end by preventing close and prolonged contact with strange animals. More complete studies of wolf development will determine how far development in dogs has changed from that in the ancestral species.

Most dogs are valued for their capacity to make rapid and close attachment to human beings, but there is some variation between breeds. In the strain of African basenjis studied by us there was both a tendency for fear responses to appear more readily in the early part of the period of socialization, and a tendency for less close emotional attachments to develop when basenjis were given the same amount of human handling as other breeds (Scott and Fuller, 1965).

Once the puppies have been partially weaned from the breast there is a tendency in human societies to replace the parental care of the dogs with human care, and in a puppy taken from a litter and adopted as a pet, parental care is taken over completely. As a result, there has been a relaxation of selection for animals that give the puppies later parental care. While dogs still bring back food to their home areas and attempt to cache it, there is seldom any effort to hook this up with feeding younger animals, and the feeding of vomited food to pups by adult males is almost never seen.

Nevertheless, when the adult behavior patterns of dogs and wolves are compared there is no evidence of any fundamental change in behavioral organization, since almost every behavior pattern that is observed in wolves can also be seen in dogs, at least in a low frequency. Rather than completely suppressing some behavior patterns, or creating new ones, domestication has had the effect of exaggerating or diminishing the frequency of occurrence of behavior patterns in different populations of dogs, with a resulting enormous increase in variation. The other result is that dogs are almost never given the opportunity of developing among themselves the high degree of social organization seen in wolf packs.

In addition to care-giving and parental behavior, dogs exhibit extended variation in three other major behavioral systems. For example, dogs and wolves have similar patterns of agonistic behavior, but in beagles and certain other hound breeds the occurrence of actual fighting is reduced almost to zero, probably as a result of selection for individuals that will tolerate each other in pack hunting. Two strange adult males can usually be placed together with little result other than a certain amount of barking and growling. At the opposite extreme, the terrier breeds have been selected for insensitivity to pain and ease of arousal for attack, so that they become highly intolerant of each other. When wirehaired fox terrier puppies were raised with their mothers throughout the period of socialization we found that they would not tolerate each other in groups larger than three, even as early as seven weeks of age (Fuller, 1953). Thus beagles are much more peaceful than wolves and terriers are much more aggressive, although the actual behavior patterns of agonistic behavior remain relatively unchanged.

In sexual behavior, dogs still show the same patterns of courtship and mating as wolves, given the opportunity to express them. Both the time of sexual maturity and the seasonal cycle, however, have been altered. Female dogs of various strains and breeds will come into the first estrus as early as five or six months and ordinarily not later than 15 months, whereas wolves show the first estrus not earlier than the end of the second year, and sometimes not until the third year. The normal annual cycle of wolf sexual behavior comes in the spring, with the pups being born in late April or May, and similar cycles take place in both the coyote and jackal. The cycle in the dog has been modified in two directions. In basenjis and dingos the estrus period has been shifted to the autumn of the year rather than the spring, but an annual cycle has been maintained, influenced by declining day length (Fuller, 1956). In all other known breeds of dogs the estrus periods of females are not related to the season of the year and occur at roughly six month intervals. This again is an argument for common ancestry of all dogs, with an early split between the southern varieties and the rest of the species.

Perhaps the greatest modification has occurred in investigative behavior, which is closely related to the hunting and predation which are the major activities of a carnivorous mammal. Wolves hunt birds, when they are available, and mammals in all sizes from mice to moose. Various dog breeds have been selected for specialized hunting activities, the scent hounds and bird dogs for finding game, the sight hounds for pursuit, and the terriers for attack. Shepherd dogs have been selected for their ability to learn to herd large mammals, a practise sometimes seen in wolves in the course of hunting. All these activities are specializations of behavior patterns seen in wolves. While most dogs have more general capacities than is commonly supposed (many shepherd dogs will readily learn to hunt deer), the general result of selection has been to exaggerate the frequency of certain patterns of investigative behavior in some breeds and to diminish it in others.

Thus the general effect of human selection upon domestic dogs has been to increase enormously the amount of variation seen in the wild species. This human selection, whether conscious or not, is equivalent to the phenomenon of social selection seen in any animal society, and we can now consider its theoretical basis.

Theoretical Considerations

Variation and Selection

As Wright (1931) has pointed out, the theoretical effect of strong selection pressure of a consistent sort is to limit variation within a population and consequently to inhibit evolutionary change. However, in any natural situation there are always a large number of selection pressures operating upon a population, and these are not always consistent from generation to generation.

From the viewpoint of genetics, the important basic phenomenon is the differential survival of genes, which are subject to selection pressures from several sources. The first of these is the genic environment, since the action of a gene is dependent on the nature of the gene complex of the individual which is in turn determined by the nature of the gene pool of the species. Any gene whose action is incompatible with that of others will be selected against. A second source of selection pressures is the prenatal environment. In mammals, homeostatic processes keep this environment relatively stable under most conditions, and one would expect a consequent restriction in the range of variation of processes going on in prenatal development. The postnatal social environment likewise tends to be stable because of maternal care and the protection provided by social groups, especially in the more highly social mammals.

The biotic environment, from which a large number of selection pressures originate in the form of competing species and available food supplies, is only relatively stable. The "balance of nature" is a shifting and unsteady balance of forces rather than a steady state. Likewise, climatic and other factors in the physical environment vary widely from year to year as well as from season to season.

Because of the complexity of these selection pressures, no gene or gene complex is likely to contribute equally to survival under all the conditions which are experienced by an individual or population. Opposing selection pressures should lead to the preservation of variation. Further, because many selection pressures vary widely from time to time, there is a tendency in any species population to preserve those genes and gene combinations which are buffered against the effects of selection, the phenomenon which Lerner (1958) has called genetic homeostasis. Thus, while selection has the theoretical effect of limiting variation under certain simple situations, it can also have the effect of preserving and maintaining variation under more complex conditions.

While the survival of the gene is the ultimate effect determined by selection, its pressures are exerted directly against gene carriers at different levels of organization: the individual at all times in development, the social group to which it belongs, the subspecies population made up of social groups in a certain geographic area, and the entire species population including all individuals. This brings up the possibility that certain characteristics may have different and even conflicting survival values for the units of organization at different levels. While the number of theoretical conflicts is quite large, the general principles involved are illustrated by situations in which behavior that contributes to the survival of a social group may be dangerous to the individual involved, and vice versa.

Group Survival and Individual Survival

This problem is usually posed in the form of the evolution of altruistic behavior, in which an animal sacrifices his own safety for the benefit of his social group. The actual problem is much more general and complex, but we can present it in broad outline by adding three other simplified theoretical possibilities. The first of these is the evolution of behavior which promotes both group and individual survival. An example of this is allelomimetic behavior in dogs and wolves, where cooperative group action increases success in hunting, allows successful defense of a den (in wolves), and alerts the whole group to sources of danger. Every individual in the group benefits by his own behavior and contributes to the survival of others. This is perhaps the commonest, and certainly the strongest, situation which would lead to evolution of social behavior and organization, and selection would obviously favor it under almost any circumstances.

A second theoretical situation is one in which behavior promotes individual survival and group death. An example of this is the occasional cannibalism of newborn infants seen in dogs, and there should be strong selection pressure against the survival of genes that contribute to this kind of behavior. The obverse of this situation is one in which behavior results in individual death but group survival ("altruistic" behavior), and an example is seen in the defense of the den by wolves against predators such as bears. As Hamilton (1964) has pointed out, this situation should theoretically result in some sort of balance between the two pressures, and what we actually see in wolves is a vigorous but at the same time somewhat cautious defense of the den. The same sort of cautious behavior is seen in predation, where dangerous animals such as moose are approached carefully and only attacked if sufficiently weak to be killed without danger to the individual.

Finally, there is the theoretical possibility of behavior that promotes the death of both the individual and the group. This is the result of violent fighting, and there are almost no instances of unrestrained destructive fighting in wild animal societies (Lorenz, 1964; Scott, 1962). In the terrier breeds of dogs which have been selected for their ability to fight in this manner, these animals have to be protected from each other in order to survive (Scott and Fuller, 1965).

The results of this analysis are clear. Where selection pressures at two levels of organization coincide (and this would have to be extended to all levels of organization to establish a clear-cut case), the effect is to produce strong selection pressure and to limit variation. Where there is a conflict between two pressures, the net effect is to set up a balanced situation. This could be achieved in a number of ways, one being intermediate behavior pattern based on a fixed gene combination, and another being a balanced gene frequency in the population. In the latter case, the conflict in selection pressures should have the effect of preserving variation.

The Origin of Variation in the Dog

The above considerations apply to a wild social species such as the wolf from which the dog was derived. The dog has become, however, a different animal from the ancestral species in one outstanding way—through an enormous increase in variation, not only in behavior but also in physical form and appearance. To take a dramatic example, a full grown Chihuahua may weigh as little as 4 pounds, while a St. Bernard may weigh as much as 120. This degree of variation is not exceeded by any other domestic species, including man himself.

This phenomenon is related to several theoretical considerations. In a highly social animal such as the dog, important environmental selection pressures are exercised by three groups of factors, those belonging to the physical, biotic, and social environments. As pointed out above, the social environment (including the prenatal environment) in the highly social species of wild mammals tends to be more stable than the other two over periods of many generations, and hence to exert constant rather than varying and fluctuating selection pressures. A lamb always grows up in the environment of a sheep flock, generation after generation, and wolf cubs normally grow up among members of a wolf pack. The result is that social behavior tends to become conservative in an evolutionary sense, being stable over long periods and less variable at any given time.

This rule is violated in the dog because the species has become involved with the phenomenon of human cultural evolution. Instead of remaining constant generation after generation, the human social environment varies from one generation to the next and from place to place. These changes produce shifting selection pressures on the dog and in part account for the great genetic diversity of form and behavior in this species.

Social selection indirectly increases variation in another way. The social group most likely to survive is one whose members contribute most effectively to social organization. One of the obvious effects of social organization is to increase the chances of survival of individuals by lessening the selective pressure from physical and biotic factors. The result of this relaxation of selection pressure should be an increase in variation in those adaptive characteristics related to the physical and biotic environments. This relaxation can be maintained only as long as effective social organization is maintained, and the latter is itself dependent upon social selection pressure. Thus there is a reciprocal or compensating relationship between social selection pressure and selection pressure arising from other parts of the environment.

This result in the dog is complicated by the fact that the major factor exerting social selection pressure is human social organization, but the results of the relaxation of other pressures are essentially the same. Breeds such as the Chihuahua with its tiny size and paper-thin skull obviously could not survive without the protection of human society, and individuals with physical defects from any breed often live to a ripe old age.

There is still another way in which social selection contributes to the origin of variation. Social organization implies division of labor, and once a useful diversity has arisen within a social group, there must be strong selection pressure in favor of maintaining this diversity.

Synergistic Relationship between Genetic Variation and Complexity of Social Organization

The existence of different varieties of animals within a social group makes greater division of labor and diversification of social behavior possible, and thus contributes to social organization. In turn, increasing complexity of organization provides useful niches or social roles for a still greater variety of individuals. This suggests that a synergistic relationship exists between complexity of social organisation and genetic variation. Once such a relationship is established it should set in motion a process of continuous change, limited only by whatever other factors limit the development of social organization.

In the case of dog and man, it is probable that most of the increased variation in dogs has come from changes in human social organization, with relatively little effect of genetic changes in dogs upon the organization of human behavior. In the early prehistory of man, genetic variation in the dog may have made an important contribution to human social organization, by making the domestication of herd animals possible through the use of shepherd dogs. Today, variation in dogs is chiefly a response to human social change. As soon as a new social niche for dogs appears, it is easy to find an animal suitable for the purpose, and it is easy for our prosperous human society to support a variety of breeds having no special use.

There is another qualification to this principle, arising from conflicting tendencies in social selection pressure. In a relatively stable animal society such as that of the wolf there must be strong selection pressure in favor of behavior that maintains social organization, with a consequent tendency to decrease variation in the area of social behavior. Only those social variants whose behavior is neutral or immediately useful would be permitted to survive. A large or rapid increase of genetically determined variation in social behavior is therefore dependent on the relaxation of social selection pressures. It is only when social organization becomes relatively independent of genetics, as it has in human cultural evolution, that a strong synergistic relationship between genetic variation and complexity of social organization becomes possible.

Genetics and the Evolution of Human Social Organization

The evolution of form and behavior in the domestic dog cannot be understood except with reference to the human societies of which the dog has become a part. One of the outstanding characteristics of human societies is verbal communication that vastly increases the possibilities of cultural transmission of information from one generation to the next. This in turn makes cultural evolution a major phenomenon in human societies. While this process has many similarities to biological evolution, it has become almost entirely independent of it, except with respect to the synergistic relationship between genetic variation and complexity of social organization described above.

Much of our progress toward understanding the process of biological evolution has come about because of the discovery of the mechanism by which genetic information is transmitted, namely, the genes and chromosomes. Likewise, the nature of cultural evolution can only be appreciated by taking into account the nature of its transmittal mechanism, that of learning. Unlike the chromosomal system, which transmits the same quantity of genic material from generation to generation, the learning mechanism produces a cumulative effect, and the theoretical extent of accumulation of information is almost unlimited, depending only on physical capacities for the storing of written records. Since little is lost, this could lead to an increasingly stable situation except for a built-in factor of instability, the fact that each individual in every generation must learn everything anew and must start from a different point in time. Because learning is an organizational process, this inevitably produces a reorganization of information in each new individual. And, unlike genetic information, which is transmitted only at the initiation of development, cultural information can be transmitted and accumulated by an individual throughout his lifetime.

The result is a rate of change which vastly outstrips that of genetic change. Major cultural changes often take place within the lifetime of an individual, whereas biological changes produced by selection usually take several generations to accomplish. The result is that social selection pressures generated by cultural conditions are likely to fluctuate and change direction from generation to generation, or even within the same generation. The dog, with its short generation span, can respond biologically to these shifts in selection pressures, but the longer-lived human being cannot. This in itself is one explanation of the fact that the human species is less variable than that of the dog.

In addition, there are no human populations that have been subjected to deliberate genetic manipulations and control as have the different breeds of dogs. The so-called human "races" are not genetically equivalent to dog breeds, nor are any other human populations. If there is any genetic correspondence between dog and human, it is that the dog breeds may be taken as models of the kind of genetic variation *between individuals* that exists within human populations.

As in the dog, the outstanding characteristic of human populations is the immense amount of variation in form and behavior compared to other animal species. Excluding deliberate selection, much the same factors account for it: adaptive radiation in prehistoric man, the relaxation of selection pressures from the physical and biotic environments as the result of effective social organization, and, finally, the synergistic relationship between the development of complex social organization and the survival of genetically variant individuals who can make a contribution to social organization by making increased division of labor possible.

I am suggesting that there is not only a positive relationship between social organization and genetic variation, but that this relationship is in part a reciprocal one. Once this process is set in motion, there is no reason why it should stop, barring a complete breakdown of social organization and its replacement by a simpler form. From this viewpoint, mankind's genetic future should be one of increasing individual diversity and greater complexity of organization, but involving no fundamental shifts in averages. Genes will be added that will extend variation in all directions, but very few will be lost from the gene pool. Social selection resulting from cultural change occurs so rapidly and in such a fluctuating fashion that there is little opportunity for making great changes in the genetic constitution of the species. In any case, the immense size of modern human populations in itself assures genetic stability.

As for dogs, they should continue to respond to the shifts and changes of human cultural evolution, but in a more extreme fashion than we do ourselves. As we look at them we shall see an exaggerated reflection of our own genetic condition, but true only to the extent that we extrapolate correctly. We can do this on the broad general dimension of variation, but not in its details, for dogs are still dogs, with genetic constitutions most similar to other members of the family Canidae, even after 12,000 years as a part of human society.

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