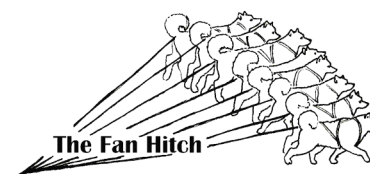


Selected reading from....

The Fan Hitch Journal of the Inuit Sled Dog International



Published March 2009 in Volume 11, Number 2



Aboriginal Kamchatka Sleddogs. Finnish expedition, 1920.
Picture donated by Inkeri & Petri Kangasvuo

Evolutionary Changes in Domesticated Dogs: The Broken Covenant of the Wild, Part 1

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Introduction

It all started during the Stone Age. As human populations increased and expanded their geographical range, a new ecological niche became available to scavenging animals, in the form of piles of refuse near human camps. The idea that wolves became domesticated through adaptation to scavenging human refuse, proposed by R. Coppinger (2001), is based on sound archeological and zoological data, and it provides the most plausible explanation of why and how wolves evolved into domesticated dogs, *Canis familiaris*. The removal and hand-rearing of puppies as tame companions may also have helped, but that became practicable only after the scavenging wolf had changed enough, becoming more docile and compatible with life near people. In the beginning, under the conditions of a mild southern environment, people did not really need dogs, except for companionship, or for being useful as meat. Most likely this event took place in Southeast Asia (Olsen, S. J and J. W. Olsen, 1977; Savolainen, 2002). The custom of eating dog meat is very old in Southeast Asia and China and has remained widespread to the present day. When both species began to populate regions with a harsh environment and marked seasonal changes, such as arid plains, high mountains, boreal forests, tundra and polar deserts, they

needed each other for survival. This became particularly obvious in the north, where people and dogs simply could not survive separately. First hunting by itself, and then hunting combined with the management of domesticated herbivorous mammals, opened new directions for the uses and evolution of dogs. In the process the dogs changed, becoming friendlier and less fearful of people, less predatory, more discriminating in their relationships with different kinds of animals, and better able to communicate with humans emotionally and physically and during work. Their anatomical features have also changed, in adaptation to the local environment and to different kinds of work. Once fully domesticated, dogs underwent further evolutionary changes in different parts of the world, considerably influenced by the continuing increase of density and expansion of the human population.

R. Coppinger (2001) observed the life of feral dogs and their relationships with local people in Africa. He called them "village dogs". It remains uncertain whether those village dogs were indigenous feral dogs or mixes with recent imports. In this context, that question is of minor importance, because any domesticated dogs, if abandoned, can revert to a similar way of life, provided the climate is mild enough and there are no wolves. As Coppinger explains, the village dogs and the villagers coexisted without antagonism and the dogs were ownerless. Both shared the same space, just as we share the same space with other commensalist animals. In those relationships between village dogs and humans, however, one important additional element was present. Although people did not own the dogs, they easily tolerated their close presence and moreover enjoyed watching dogs eating handouts. They also encouraged the dogs to chase and kill small predators, and both shared that activity. These two forms of interactions with dogs, feeding and hunting, had been important factors driving evolution from scavenging wolves to feral generalist-type dogs, and further to dogs specialized for different functions and highly serviceable to people. Similar relationships between local people and indigenous Dingo-like feral dogs still persist over large areas of rural Africa, India, Southeast Asia and Australasia. This is what the relationships between the Dingo and Australian aborigines were like when Europeans first arrived. This oldest form of ownerless relationship between dogs and people reemerges easily under favorable conditions, whenever dogs are abandoned and revert to a feral way of life. A basic behavioral adaptation of dogs to survive, feral or not, is staying with people, who treat them kindly enough and feed them, at least sometimes. All aboriginal dog types

specialized for performing specific work evolved naturally out of more primitive Dingo-like feral dogs; this is why we call them natural breeds. They still retain many wild traits of their ancestors, dogs capable of permanent feral life. At the same time, they possess unique working qualities, which became their new survival adaptation, actively cooperating with people and helping them in hunting, in managing other animals and in pulling sleds. This became a crucial factor for survival of both species in extreme environments. The uniqueness of the dog lies in its extraordinary cognitive ability, allowing this animal to share in our lives emotionally both at work and at leisure. This is a specific adaptation of dogs to live with people and influence them to its own advantage, which helped the dog, *Canis familiaris*, to inject itself into human society. This peculiar trait cannot be traced directly in the fossil record, but ancient joint burials of people with dogs and artifacts indicate that the transformation of wolf into dog was completed as early as 15,000 years ago. A "covenant of the wild" was made between dogs and humans, and from then on both stood together against the rest of the world. Natural dogs became adapted to live with people and serve them, and at the same time remained members of the local geographic fauna - until an emerging and expanding civilization began destroying them all.



A lighter built type of the Caucasian Mountain Dog used for livestock protection.
Picture donated by Lisa Valiev

As human populations increased and ancient civilizations emerged, dogs gradually lost their freedom to choose, and became part of an ownership society. As a result, the dogs' opportunities to influence our behavior diminished, but their evolutionary changes continued at an ever accelerating rate, because people began breeding dogs in isolated groups and deliberately changing them. This is how a new type of breed, which we may call cultured (or man-made) breeds, was created. Cultured breeds became further domesticated and more submissive, and easier to teach novel kinds of work. Their appearance also changed, becoming more diverse, because particular traits of

appearance, helping to distinguish breeds, became favored. Cultured breeds grew in popularity, replacing natural breeds, now forced to retreat to the fringes of civilized society; some of them still survive in regions remote from the densely populated, economically advanced centers of civilization.

Finally, from the late 19th century onward, breeding dogs for showing changed their role once more; the interactions between dogs and people during hunting and other work were largely eliminated, along with much of the emotional sharing that accompanies those activities. Dogs enjoy sharing all kinds of physical activities with humans, but many do not like dog shows; competition among dogs became replaced by competition among their owners. Dog breeders became hobby breeders, similar to breeders of other organisms, such as goldfish, snakes, rodents or ornamental plants. Hunting and other working breeds, inherited from the past, became the pedigreed pets of urbanites, and the old covenant of the wild was broken. Although some hunting and other physically capable working dogs are still bred and used for their original purpose, show and pet dogs are growing in popularity worldwide. They outnumber, pollute genetically and swamp not only the primitive aboriginal dogs, but also those dogs of cultured breeds still capable of high performance.

The history of the domesticated dog, with all its breeds, is negligibly short by comparison with the history of life on Earth. This may raise a question: Why concern ourselves with the evolution of dogs and dog breeds? Adaptive and ecologically meaningful changes of the genetic structure of natural populations are a part of evolutionary biology. They are micro-evolutionary phenomena. Although dogs live under human control, their adaptive changes associated with domestication, and their successful specialization for performing different jobs (or for extinction) are interesting and exciting subjects for micro-evolutionary studies.

The dog show culture, with its purebred dog concept, developed before the science of genetics became established. Even after geneticists had made important discoveries in natural populations, breeders of pedigreed dogs continued to ignore the observed facts of superior vitality of heterozygous individuals. A general obsession with competition at dog show contests overwhelmed common sense and empathy to dogs, which as a largely unintended result became genetically abused, sometimes to the extent of chronic pain, suffering and early death. The most vigorous dog is most likely a heterozygous dog, which can be found among naturally "mongrelized" actively working aboriginal dogs, which earn their keep by hunting, herding, sledding or guarding. Therefore, I will begin by reminding the dog loving public about the history and importance of discoveries made by studying the genetics of natural populations.

Natural populations

Essential to an understanding of evolution is the realization that hereditary material is passed on unchanged from one generation to the next; it is not modified by the life experiences of the individual who carries it. Gregor

Mendel discovered the basic laws of genetics by crossing pea varieties in a monastery garden, and published his "Versuche über Pflanzen-Hybriden" in 1866. This work remained unnoticed, however, for more than 30 years. In the meantime German zoologist August Weismann laid important groundwork for later understanding by insisting on the "continuity of the germ plasm" even though, at the time, a physical explanation for inheritance was not yet available. Mendel's work was rediscovered in 1900, by three researchers independently of one another, and in 1902 Sutton recognized that the behavior of the chromosomes, during reproduction, corresponded exactly to that of Mendel's "factors". That publication could be considered the foundation event of modern genetic science. In 1915 T. H. Morgan and colleagues published "The Mechanism of Mendelian Heredity" spelling out the mature chromosomal theory of heredity in detail. In the 1920s Sewall Wright, R.A. Fisher and J.B.S. Haldane founded the modern science of population genetics. These discoveries provided a solid physical basis for Darwin's theory of evolution, which then became the backbone of modern biology. Genes have all the properties necessary for explanation of the evolutionary process: they are particulate, constant, but can change as a result of mutations, do not blend or mix with each other, are passed unchanged from parents to offspring, reshuffle in each generation and interact in many peculiar ways, usually with a maximal beneficial effect in a heterozygous state. Genetics, systematics and the Darwinian theory of evolution thus merged, becoming one unifying biological science. The concepts of species and subspecies took their modern form.



Tuva Ovcharka - male Picture donated by Ilya Zakharov-Gezekhus

Now, a species is understood as a population, or a system of several genetically variable subpopulations, changing in time and space. Genetic diversity is a normal attribute of a natural population and results from a complex process, involving mutations, genetic recombination in meiosis and also genetic exchange among subpopulations by dispersal of individuals. Genetic diversity in every population is tested by natural selection, and beneficial genes and gene combinations are preferentially passed to

the next generation. Differences between natural populations can be described in terms of frequencies of alleles, causing morphological, behavioral and other kinds of variation, observable by different methods, such as chromosomes with different arrangements of genes, or variations in enzymes and other proteins. Recent progress in methods of DNA analysis is providing powerful tools for research and for making detailed comparisons to establish affinity between individuals and geographic populations.

Only a small part of the existing genetic variation is expressed in a form accessible to direct visual observation; most of it remains hidden, because it is expressed only in physiological or behavioral differences or in resistance to pathogens, etc., things which can be analyzed only under laboratory or experimental conditions. Many quantitative differences, such as body size, proportions of body parts, qualities of skin, feather or hair color, etc., are controlled by multiple genes, each with only a small effect on the phenotype. Much of the observable genetic diversity is called "neutral", because we have so far been unable to find any advantage or disadvantage of having certain alleles. Sometimes minor changes in a DNA sequence do not change the gene product at all.

Genes with definite effects on survival, fecundity, endurance, etc. are of major interest to evolutionary biologists, and have received the most scrutiny. Each gene may have a single effect on the phenotype with obvious impact on viability, but it may also have multiple effects on several different traits of the body, some of which may be either beneficial or deleterious depending on the environment. Moreover, the system becomes even more complicated because each gene acts not singly but in concert with other genes, and the same gene can be deleterious in one combination, and advantageous or neutral in other ones. This is how genetic diversity within a population serves as a buffer system against both environmental changes and the damaging effects of newly arisen mutations.

The detrimental effects of inbreeding were well known to people long before genetics emerged as a science, and incest has been avoided and outlawed in most human societies at many different times and places. We know that the almost universal occurrence in higher organisms of sexual rather than asexual reproduction is also an evolutionary adaptation, facilitating genetic recombination and so promoting faster adaptation to a changing environment. There are vast amounts of data confirming the competitive advantage of heterozygous individuals in wild populations. The superior fitness of heterozygous individuals can be observed in many different taxonomic groups and with different forms of genetic variation. This involves superior fecundity, better survival of the young, physical endurance, resistance to diseases and better survival under all kinds of stressful conditions. Even sexual selection favors heterozygous individuals. Thus, heterozygous males of some butterflies have the most symmetrical pattern, and are selected by females as carriers of "better genes". Perhaps this may be a principal function of the extravagant sexual displays of many animals with elaborate courtship behavior.

Cases with conspicuous color polymorphism represent an easily observable aspect of variation within a single population. Variation of color forms within one population is often maintained selectively in a form of balanced polymorphism, due to the superiority of heterozygous individuals. The balance of frequencies of series of different so-called co-dominant and recessive alleles within one population is maintained by their relative selective value in heterozygous states. Some of the alleles may be even deleterious, if occur in homozygous state, but still remain in the population due to their advantage in heterozygous combinations. Although balanced polymorphism has attracted the most attention by researchers, it is only one small aspect of the much broader variation in natural populations, which is also maintained by the beneficial effects of alleles paired in heterozygous combinations.

Comparisons of variation within species across an entire species distribution range showed interesting patterns. In a series of contiguous populations, isolation by space is incomplete and migration or dispersal of young (or seeds) is another powerful cause of genetic diversity. In the 1920s the Russian geneticist N. V. Vavilov studied variation in wild wheat and other plants. He observed the highest level of variation near the central and oldest parts of the species range. Similar facts were discovered in animals as well. A general rule is that a large geographic range, and a large number of breeding individuals, is better for creating and maintaining a higher genetic diversity.

Detailed descriptions of empirical data, theoretical discussions and bibliography on this topic can be found in *Selection in Natural Populations* by J.B. Mitton, Oxford University Press, 1997, and in *The Natural History of Inbreeding and Outbreeding. Theoretical and Empirical Perspectives* edited by N. W. Thornhill, The University of Chicago Press, 1993. There are more recent publications which repeatedly confirm that genetic variation and a high level of heterozygosity is a healthy attribute of natural populations.

The wolf, before its mass extermination, had an enormous geographic distribution range in Eurasia and North America. It was one of the most adaptable and individually variable species, forming numerous subspecies (races). It is not surprising that some of its south Asian populations conquered a new ecological niche and became a different species – the domesticated dog. Together with people, the dog expanded its geographic range farther to the south in Central and South America and in Australasia, including many islands and Australia, regions where wolves never existed. Most primitive Dingo-like aboriginal dogs continue to live both wild, feral, and with people. A few other aboriginal breeds became functionally specialized for performing specific jobs. In their home countries, however, all aboriginal dogs live and reproduce without pedigrees, relatively free, and their populations are therefore essentially natural. They are very variable within each population, and retain a high level of heterozygosity. Unlike primitive aboriginal dogs, dogs of cultured (pedigreed) breeds live and reproduce under strict control. Their breeds are effectively isolated from each other, selected for

maximal similarity of appearance and sometimes for peculiar recessive traits with special appeal to dog show fans. Thus a uniform appearance of each cultured breed is achieved by taking genetic shortcuts, especially inbreeding disguised under different terms, such as line breeding and close breeding, which ends with the fixation of valued recessive traits but unfortunately also with degenerative changes in the dogs' health and vitality.

The author wishes to thank John Burchard, Ph.D. for editing this article.

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In part 2: Primitive and aboriginal dogs, their appearance, reproductive biology, behavior, way of life selection.

Vladimir Beregovoy graduated from Perm State University as a biologist in 1960. He defended his dissertation in 1964 and was awarded a Degree of Candidate of Sciences from the Institute of Biology, Uralian Branch of Academy of Sciences of the USSR, where he worked as a zoologist. He taught at the Kuban State University, Krasnodar. During his work as a zoologist, he traveled to Ural, West Siberia, Volga River region, Kazakhstan and North Caucasus.

In 1979, Beregovoy immigrated with his family to Vienna, Austria and in 1980 to Oregon, USA. He worked on series of research projects in North Dakota State University and in 1989 accepted a position as Senior Agriculturist in the Department of Entomology, Oklahoma State University, where he worked until retirement in 2000.

From 1991 to 1996, he imported five West Siberian Laikas, three males and two females, as the foundation stock of this breed, newly introduced in North America. Currently, he is retired and lives with his wife, Emma, and their favorite Laikas on a small, 90-acre farm in Virginia.

Beregovoy has published several articles in popular magazines and two books: *Primitive Breeds-Perfect Dogs and Hunting Laika Breeds of Russia*. He is also the advisor and curator of the Primitive and Aboriginal Dog Society (PADS) as well as a member of the editorial board of the PADS Newsletter.