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(*The online version of this article appears in three parts. Click here to go to parts one and three.*)

Prehistoric Dog

THE standard myth about the origin of the dog is that man found him to be a useful companion and so took him in. Dogs were sentinels or shepherds or they helped in the hunt. The oldest archaeological evidence of dogs with a morphology distinct from that of wolves is from about 12,000 years ago in the Middle East, suggesting an evolution coinciding with the rise of the first agricultural settlements and permanent villages, and pre-dating the domestication of other animals, including sheep and goats, by a few thousand years.

The view that dogs came along at about the same time as human beings settled down is so widespread and so often repeated in standard texts that it is more than a bit surprising to find genetic evidence flatly contradicting it. The evidence comes from a study by Robert Wayne, an evolutionary biologist at the University of California at Los Angeles, who has applied the modern tools of genetic fingerprinting to dogs, coyotes, wolves, and jackals. He and his colleagues collected blood, tissue, or hair samples from 140 dogs of sixty-seven breeds and 162 wolves from three continents. To gauge how closely related these various canines were and when they might have diverged from a common ancestor, the scientists measured

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differences in their mitochondrial DNA. Mitochondria are like small cells within the cells of animals; they convert stored food into energy with the assistance of oxygen, and they also have the peculiarity -- much cherished by geneticists -- of reproducing asexually, independent of the rest of the cell. The regular DNA of an animal cell derives equally from both parents. Mitochondrial DNA, however, comes entirely from the mitochondrial DNA of the mother. In normal sexual reproduction genetic change from one generation to the next is very rapid, as the parental genes are mixed and remixed in new combinations. Mitochondrial DNA, in contrast, can change only by mutation, which takes place quite slowly -- at a rate of around one or two percent every 100,000 years.

That means that mitochondrial DNA can be used as an evolutionary chronometer. Wolves and coyotes differ by about six percent in their mitochondrial DNA, and, according to fossil evidence, separated from a common ancestor about a million years ago. Wolves and dogs differ by about one percent; using the wolf-coyote time scale, this suggests that they parted company about 135,000 years ago -- a lot earlier than the date implied by the first distinctly non-wolflike dog fossil.

Wayne's study also definitively laid to rest an assertion made by both Charles Darwin and Konrad Lorenz -- that more than one wild canid species had to have made an appearance in the dog's recent family tree, given the diversity of physical types and behaviors exhibited across the range of modern dog breeds. In fact, long sequences of dog mitochondrial DNA are similar or identical to those in gray wolves, and analysis of the highly variable markers in the regular DNA of dogs and wolves shows a considerable overlap there as well. Jackals and coyotes, though they can interbreed with dogs and produce fertile offspring, possess quite distinct groups of mitochondrial DNA sequences.

The evolutionary chronometer is a measure of ancient origins -- it cannot pick up divergence into separate breeding lines that has occurred in the past few hundred years. The most striking discovery Wayne's team made was that there is almost no correlation between a dog's breed and the mitochondrial DNA sequences it carries. In eight German shepherds the scientists found five distinct sequences; in six golden retrievers they found four. And the same sequences repeatedly showed up in many different, and apparently quite unrelated, breeds. The Mexican hairless, or Xolo, a breed known from historical and archaeological records to have existed more than 2,500 years ago in Aztec Mexico -- and which presumably

separated from Old World breeds some 12,000 years ago, when the Bering land bridge disappeared -- contained representatives of all the major mitochondrial DNA sequences found in dogs throughout the world. (The Xolo sequences also resembled those of Old World wolves much more closely than those of New World wolves.)

The point is, then, that if dogs were indeed domesticated more than 100,000 years ago, as Wayne's data suggest, there wasn't much selective breeding going on for most of those 100,000 years. Rather than diverging into separate lines, the dog gene pool remained a well-mixed soup in a bowl of global dimensions. There was considerable gene flow throughout the population, which would not have been the case had early human beings been trying to direct the breeding of their dogs or to develop special lines with certain selected characteristics. Wayne's study also suggests that for a long time the genetic difference between a dog and a wolf was too small to cause any striking morphological change that would show up in the fossil record.

Even if the step from wolf to dog was a small one, it apparently didn't happen very often. Wayne found that the dog mitochondrial DNA sequences fell into four major groups. If there had been a continual influx of new wolf blood into the dog population (that is, if the dog had been reinvented again and again from wild populations at different times), such distinct grouping would not have occurred. Wayne's conclusion is that the earliest dogs "must have been integrated somehow into human society" to keep them genetically isolated from the surrounding population of wild wolves, and also that the domestication of dogs from wild populations must have been "a rare event" -- something that happened only a few times in history.

That it happened at a time when "humans were barely human," as Gregory Acland -- a veterinarian who works with Aguirre at Cornell's Center for Canine Genetics and Reproduction -- puts it, raises an interesting possibility. It suggests that early man may not have sought to domesticate dogs at all. Rather, proto-dog found it in his interest to hang around people, and somehow persuaded them not to throw rocks at him or eat him.

That is a teleological statement, of course; if this scenario is correct, there was no conscious intent on the part of the dogs. But there was arguably little or no conscious intent on the part of the people, either. The wonder and beauty of natural selection is that it is creative; it crafts solutions that

for all intents and purposes seem to reflect intelligence -- "unthinking" intelligence, as the philosopher Daniel Dennett aptly put it. The evolutionarily correct way to state all this is that human beings, with their campfires and garbage heaps and hunting practices, but above all with their social interactions, represented an ecological niche ripe for exploitation by wolves. Or at least by those wolves that through some chance modification in their genetic makeup were able to exploit that niche and then prospered to pass on those traits to their offspring. Although wolves today are the most widespread wild land mammal in the world -- with a range that extends from North America to Europe to Asia, encompassing everything from semi-desert to tundra to subtropical forest -- their total population probably numbers no more than 150,000. In the United States there are about 50 million owned dogs and millions more unowned -- eloquent evolutionary testimony to the wisdom of mooching off people rather than fighting it out in the wild.

Dogs and Determinism

WHAT is so exploitable about human society? And how do dogs manage to exploit it? We are, as the animal behaviorist John S. Kennedy called us, "compulsive" anthropomorphizers -- always on the lookout for behaviors that mimic, even superficially, human social phenomena such as loyalty, betrayal, reciprocity. These are useful things to look out for when one is a group-dwelling animal whose survival is threatened less by ravenous wild beasts than by back-stabbing fellow group dwellers. Our cognitive ability to ascribe motives to others is a large part of what makes us human. But it truly is compulsive. Human beings do it so instinctively that they are forever ascribing malignant or benignant motives even to inanimate forces such as the weather, volcanoes, and internal-combustion engines. Our very cleverness is the start of our undoing when we're up against an evolutionary sharpshooter like the dog. We are primed to seize on what are, in truth, fundamental, programmed behaviors in dogs and read into them extravagant tales of love and fidelity. Often dogs need do no more than be their simple selves to amaze and beguile us.

From the archives:

"Homer's Seeing Eye Dog," by William Matthews (November, 1988)
A poem from the point of view of Homer's dog.

Take the protectiveness that dog owners almost universally impute to their pets. "Protectiveness" is almost certainly nothing of the kind; it is not a sign of a dog's loyalty to and concern for us but an example of what behaviorists call "facilitated aggression." Rather than protecting us, the dog feels protected *by* us; he is emboldened to react to any threat that appears on his radar screen. Such behavior is

observed regularly in wolves: aggression by a dominant member of the pack toward another wolf will trigger an attack by other members.

Or consider the countless stories about dogs that have "saved" people. In fact dogs have no particular instinct to save people and no particular understanding that that is what they are doing even when they do it. Search-and-rescue dogs are trained by exploiting the instinct to retrieve thrown objects. They are trained to fetch. And they are trained to fetch *one* toy only. Once they master that, they are ready for the next step: A person takes the toy and hides; the dog is encouraged to find -- well, his toy. When he finds the "victim," the dog is rewarded by getting his toy. At actual disaster scenes trainers get someone to go and hide with the dog's toy several times a day, so that the dog can score a few successes and not become frustrated.

This takes nothing away from dogs' amazing sense of smell or trainability or utility to humankind in such situations. It does say that what is going on here may be simpler than we are ready to believe. As Gregory Acland points out, "All you're doing is taking a behavior that's there and subverting it." Other "rescuing" behavior in dogs is an even simpler matter. Newfoundlands and other water retrievers will bring anything they can out of the water. Often Newfoundland owners cannot swim with their dogs, because the dogs keep pulling them to shore.

The degree to which seemingly complex behaviors are rigidly and genetically programmed is quite frightening at times -- frightening for what it suggests about motivation and free will, at least. Pregnant dogs will often pick up stuffed animals and try to "nurse" them. A cardinal in the wild was once observed feeding goldfish for several weeks; a fish would rise to the surface of the pond and open its mouth, and the cardinal would stuff it full of regurgitated insects. That, of course, is what birds do to feed their young, and apparently all it takes to trigger that behavior is the sight of a gaping mouth.

An early part of Elaine Ostrander's work in the Dog Genome Project was an attempt to locate genes responsible for such complex canine instincts as herding behavior in border collies and the affinity for water in Newfoundlands. The grandpuppies of crosses between border collies and Newfies showed a rich assortment of the two behaviors, enough to make it clear that they were under genetic control -- but also enough to show that perhaps a dozen or more genes were involved, and that to accomplish any sort of mapping of those genes, one would need to start with

several hundred dogs.

A former postdoctoral research fellow with Ostrander, Melissa Fleming, has developed an assay that attempts to quantify certain innate breed-specific behavioral differences. Fleming found, for example, that border collies would stare at a moving remote-controlled toy car for the duration of a 120-second test. Newfoundlands, in contrast, not only would fail to stare at the car but would not even react to it unless it ran directly into them.

Other studies have turned up some remarkably narrow and distinctive behavioral lineages that further demonstrate the extent to which canine behavior is genetically determined. Certain strains of Siberian huskies and pointers have developed a strongly inherited shyness or aversion to human beings; when kept under identical conditions in identical kennels, the shy dogs will stay back (or, in the case of the pointers, actually freeze and quiver when people approach), while the normal dogs come up to be petted. Breeders have succeeded in producing lines of bloodhounds that bark or do not bark while trailing a scent; of Dalmatians that do or do not take up the proper "coaching" position, trotting under the front axle of a carriage, very close to the heels of the horses; and even of miniature poodles that do or do not "shake hands."

There is probably no "deflecting aggression," or submission, gene, but much of what enables dogs to get away with everything up to and sometimes even including murder in human society is an innate part of wolf social behavior. Dogs are social animals, and so are we. Dog society consists of a strong dominance hierarchy in which submission to and appeasement of higher-ranking animals is necessary to survival. Dominance hierarchies avoid violence for the most part, but the threat of violence is ever present. Thus reading social cues adeptly, down to such details of body language as a flick of the ear or the angle of a tail, is the most basic of canine instincts. "That's what dogs do for a living," Gregory Acland says. "They figure out what's expected of them in a social situation and do it."

Even people who are very bad animal trainers can usually make themselves understood to dogs. If you shout at a dog, it cringes. Does this mean the dog feels sorry for peeing on your Oriental rug? The fact is that it doesn't matter, as far as the dog is concerned, whether he feels sorry or not. The cringe is a successful technique for deflecting aggression. Millions of years of wolf evolution have selected such behaviors because they are socially effective; thousands of years of dog evolution have fine-tuned such behaviors so

that they are socially effective on people. Just as we are genetically programmed to seek signs of love and loyalty, dogs are genetically programmed to exploit this foible of ours.

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