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"[Bradshaw] reveals a wealth of scholarly literature in biology, psychology, veterinary medicine, and zoology through detailed analyses and uses those findings to support and critique popular dog-training methods. Clear and charming black-and-white drawings illustrate key points. . . . Pet owners and those interested in the animal mind will learn from this balanced, well-referenced guide to the science of canine behavior."
—*Library Journal*

"Bradshaw . . . offers an alternative to conventional, dominance-based approaches to understanding dogs (Cesar Milan's methods, for example) in an informative . . . guide to how canine biology and psychology determine behavior. . . . His analysis of dogs' emotional landscape provides insight into typical misinterpretations—that dogs feel guilt, say, or that there is a 'pack mentality.' . . . His bailiwick is psychology, in the vein of Alexandra Horowitz's *Inside of a Dog*. . . . Bradshaw's book is useful to those looking to further their understanding of dog behavior and clarify common misconceptions."
—*Publishers Weekly*

"Every so often we are reintroduced to an old friend, and we may see them in a new light, reinvigorating a long standing relationship. John Bradshaw reintroduces us to mankind's oldest friend, the dog. He compiles and explains new information on the origin of dogs, their relationship with ancestral wolves and why we need to base our relationship with dogs on partnership and cooperation, not outmoded theories about dominance. Dogs and dog lovers alike will benefit from Bradshaw's insight."

—Stephen Zawistowski, PhD, CAAB, ASPCA Science Advisor

Dog Sense

HOW THE NEW SCIENCE OF
DOG BEHAVIOR CAN MAKE YOU A
BETTER FRIEND TO YOUR PET

John Bradshaw

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place and that time are currently shrouded in mystery—but what is certain is that the aberrant and atypical behavior of modern, captive wolves is highly unlikely to be of any value in understanding either the behavior of these ancestral wolves or that of domestic dogs. Rather than focusing exclusively on the grey wolf, we should regard the dog as a canid whose closest living relative happens to be a wolf. It is the possession of the canid toolkit that was vital to the successful domestication of the dog—a story whose roots are intimately entwined with those of our own.

CHAPTER 2

How Wolves Became Dogs

The story of the dog's domestication—its evolution from wolf to its own unique sub-species of canid—parallels that of our own emergence into civilization, from the hunter-gatherers of the Mesolithic through to the modern age. There were domestic dogs well before any other animal was domesticated, so arguably the dog is likely to be more altered relative to its ancestors than any other species of animal on earth. The process of domestication has stripped away much of the detail of the ancestral species, but dogs nonetheless retain some of the characteristics of the more ancient lineage that gave rise to jackal, coyote, and wolf alike. Dogs are somewhat like each one of these, but they are also unique, the only fully domesticated canid, and much of what makes them unique was introduced by that very process of domestication. The story of that domestication therefore makes an essential contribution to our understanding of what our dogs are—and what they are not.

Over the last decade we have learned a great deal about the domestication of the dog. The sequencing of the DNA of hundreds of individual dogs has forced a reappraisal of previous data regarding the process of domestication. While there are undoubtedly more surprises to come, the broad scope of how it happened as well as much of the detail are now fairly well established.

In addition, we have new perspectives on when and where the dog may have been domesticated. We can be reasonably sure that there were several, possibly many, attempts at domestication of the grey wolf, in

various parts of the world, but also that the products of some of those domestication events—in places other than North America—ultimately endured whereas others did not. The process of discovery is still ongoing; ancient bones and fossils that were formerly identified as unequivocally belonging to wolves are being reexamined, in case they might actually have come from early wolf-like dogs. The evidence has been clear enough, however, to place the separation between wolf and dog further back in their evolution, by thousands of years, giving more time for wolf and dog to diverge—an analysis that further undermines the idea that the behavior of the dog is simply a subset of that of the wolf.

While we are gaining a better understanding of the ways in which dogs are different from wolves, we are also learning more about how we, as humans, have helped to make the dog different. The domestication of dogs has been revealed as a complex process, more convoluted than that of any other animal, leading not only to radical changes in the shape and size of their physical bodies but also to an almost complete reorganization of their behavior. Furthermore, while humans have guided that process, it is only in the past century and a half, and only in the West, that we have taken control of it completely. For ten thousand years or more, as the purposes for which dogs were valued changed and proliferated, dogs have coexisted and coevolved with us. Essentially, they domesticated themselves as much as we domesticated them.

When was the dog domesticated? Until fifteen years ago, the answer was thought to be simple. The oldest remains of dogs found by archaeologists were carbon-dated to be no more than twelve thousand years old, fourteen thousand at most. This timeline placed the first dogs before the beginnings of agriculture about ten thousand years ago, and well before the domestication of any other animal. So the dog was, for this reason alone, considered a special case: the pioneer for all subsequent domestications, such as goats, sheep, cattle, and pigs. Because it was domesticated so early in the history of humans, there is little detailed evidence as to how wolves became dogs—a paucity of information that has left a great deal of room for speculation as to why and where this first occurred. Until fifteen years ago, however, at least the “when” seemed well established: No bones had been found that both unequivocally be-

longed to a dog and were more than fourteen thousand years old, so domestication must have occurred no earlier than about fifteen thousand years ago.

Then, in 1997, a team of scientists from the United States and Sweden made an astonishing claim: They had sequenced DNA from living dogs and wolves, and the findings indicated that domestication could have taken place more than a hundred thousand years earlier.¹ If this was true, it would mean that dogs were man’s companions not just at the birth of agriculture but right at the dawn of our own species—as soon as modern humans had emerged from Africa, where they had evolved, and encountered grey wolves (which do not occur in Africa) for the first time. This announcement triggered a minor epidemic of speculation about the possible coevolution of man and dog. Most archaeologists rejected the idea, pointing to the complete lack of dog remains that could be dated any earlier than fourteen thousand years ago. But there was nothing intrinsically wrong with the DNA data, even though its interpretation was still open to debate. Dogs, it seemed, joined us during our pre-agricultural origins.

Since 1997, there has been a steady flow of more detailed studies of dog and wolf DNA, and, as a result of these, our conclusions about the exact moment of the dog’s domestication have changed and are still changing today. DNA technology is relatively new, and while it may give unequivocal answers when used for “fingerprinting” (e.g., confirming the parentage of a particular puppy in a dispute over pedigrees), its use in reconstructing events long since passed is much more open to interpretation. Different types of DNA can give different answers; for example, the story told by the type contained in the nucleus of most mammals’ cells (the subcellular organelle where paternal and maternal DNA mix) is often different from that told by the type associated with other parts of the cell, such as the mitochondria (which contains only maternal DNA). As new analyses have appeared and been integrated into the picture, the estimate that dogs might have been domesticated more than a hundred thousand years ago has since been revised down considerably—to between fifteen thousand and twenty-five thousand years ago.

One reason for this drastic downward revision is that problems have been found in the method used to calculate how much time has elapsed

since two animals had a common ancestor. The DNA most commonly used for this purpose comes not from the nucleus but from the mitochondria (whose genetic content is abbreviated as mtDNA). Very occasionally, only once every few thousand years, mitochondrial DNA mutates, such that mother and daughter, who would otherwise have identical mtDNA, exhibit sequences that differ at just one location (this applies only to mothers—fathers do not pass on any mtDNA to their offspring, male or female). Unlike other kinds of mutation, these changes have no effect on the health or fecundity of the animal, and so are passed on “silently” down the generations, spreading throughout all the daughter’s descendants. By counting the number of differences between two individual animals’ mtDNA, scientists can estimate the amount of time the two individuals’ lineages have been diverging—and can thus form an idea of how long ago their most recent shared female ancestor lived. The bigger the number of distinct mutations, the older the two animals’ joint lineage must be.

Errors slip into this sort of mtDNA dating when scientists, having determined how many unshared genetic mutations exist between two individuals, attempt to figure out just how often these mutations may have occurred in both animals. The regularity of these mutations varies from one kind of animal to another. However, scientists know from the fossil record and from carbon dating that the dog’s ancestor, the wolf, diverged from the coyote about 1 million years ago. A simple comparison between the number of differences between dog and wolf, and the number between wolf and coyote, suggests that the dog and the wolf had been separated for about one-tenth of that time—in other words, for about a hundred thousand years. This calculation, however, relies on the mutations in mtDNA occurring at the same rate in domestic and wild animals. Since the 1997 study, it has become apparent that mtDNA mutations occur more frequently in domesticated animals than in wild ones. The same comparative method used in the 1997 study has consistently overestimated the time since domestication for virtually every animal to which it has been applied: For example, the DNA of the pig, probably first domesticated nine thousand years ago, suggests a domestication of sixty thousand to five hundred thousand years ago; and the horse, more than three hundred thousand years ago

instead of about six thousand. The mutation rate must therefore be faster during domestication than in the wild, speeding up the rate at which mtDNA changes from once every few thousand years to once every few hundred. Studies of other species suggest that this accelerated rate is a side effect of chronically high levels of stress hormones, caused by living in crowded conditions and in close proximity with man. Thus the estimate of a hundred thousand-plus years is highly likely to be an overestimate, perhaps by a factor of five or more, bringing the interval since the dog’s domestication down to a much more realistic twenty thousand years or so.

In addition to comparing the dog’s DNA with that of the wolf, scientists can examine how much variation there is between different types of dog, as a way of determining how long they have been around. However, this procedure, too, superficially seems to suggest that dogs were domesticated much earlier than twenty thousand years ago. A recent analysis of the DNA that codes for the dog’s immune system has produced an estimate of several hundred thousand years since domestication—a figure even more unlikely than the hundred thousand years indicated by the mtDNA, since it predates the evolution of our own species. On the other hand, such an estimate assumes that mutation is the only source of variation and that all dogs are descended from a single pair of wolves. A similar degree of diversity could occur if, say, several wolves had been domesticated, each of which had distinctive DNA. But this is likely to be the case only if each of those wolves had lived in a different part of the world—a supposition that, in turn, implies several domestication events.

The apparent contradictions between the archaeological evidence and the DNA evidence can be reconciled if we posit not just one domestication event but several, in different parts of the world. It is now becoming possible to examine the DNA of fossilized dog teeth taken from Neolithic burial sites. While only a few dozen individuals have been sequenced so far, the results tend to confirm that wolves were indeed domesticated at several, possibly many, different locations.

Scientists have also begun to find proof for multiple domestications by looking at a different type of DNA, extracted from living dogs. The DNA that codes for the immune system is inherited from both parents, not just the mother, as mtDNA is. The much greater diversity in the

DNA for the immune system suggests that dogs have far more forefathers than foremothers; in other words, dogs overall seem to have many male wolf ancestors between them, but only a few female wolf ancestors. Thus the genetic material from the "extra" males must have been introduced after domestication had started. The early domestic dog bitches would presumably have been attractive to, and so occasionally mated by, wild male wolves. Moreover, their puppies would have been born in close proximity to humans. And provided that the genetic contribution of their wolf father did not make them too intractable, they could have survived to contribute to the dog genome. There is no reason why a mating between a male dog and a female wolf should not also produce puppies, but they would be born in the wild and, hence, would be more likely to contribute to the wolf's genome than to the dog's.

Thanks to recent scientific developments, we now know that the diversity of the modern dog's genome is not hopelessly incompatible with the archaeological evidence surrounding the dog's domestication. Nevertheless, there is still a discrepancy—possibly as large as five thousand to ten thousand years—between the most likely date suggested by the DNA (twenty thousand or more years ago) and the oldest date that most archaeologists will agree to (fourteen thousand years). The reason for this discrepancy probably lies in the type of evidence that archaeologists will accept as evidence for domestication. Human remains and the bones of wolves have been found together at sites going back a half-million years, long before modern humans evolved, but archaeologists do not accept these joint burials alone as signs of domestication. Rather, they look for evidence of domestication either in the remains of animals that are clearly distinguishable from wolves (e.g., those with a wider skull, a shorter muzzle, or smaller teeth) or in signs that the animals, even if otherwise indistinguishable from wolves, had a special place in human society—preferably both.

Probably the earliest well-established archaeological example of a dog that is both biologically distinct from wolves and specially connected to humans is the burial, about twelve thousand years ago in what is now northern Israel, of a human with one hand resting on the body of a puppy. Not only does the position of the puppy show that it had a close relationship with that person, but its teeth are also signifi-

cantly smaller than those of any wolf that lived nearby at that time, indicating that it must have come from domestic stock.

Neither the physical signs of domestication in this puppy, so distinct from its wild counterpart, nor the evident bond between the animal and its owner, can have arisen overnight. Rather, the puppy must have been preceded by many generations of dogs who made up the transition from wild wolf to domesticated pet. Such transitions may be virtually invisible to archaeology, but the subsequent rapid emergence of dogs all over the Old World is compatible with the idea that there was not one domestication but several. In the next two millennia after this twelve-thousand-year-old burial, other similar burials—either of humans and dogs together or of dogs on their own—occurred in various parts of Europe. These sites have been found in, among other places, the United Kingdom, suggesting that dogs had also spread quickly from their points of origin, which are thought to be far to the east. Scientists also believe that, at roughly the same time, humans were taking other domestic dogs, probably from another focus of domestication in East Asia, out of Siberia and into what is now Alaska. (At the time, both were part of a single landmass known as Beringia, which, depending on the period, stretched as far as 600 miles from north to south.) These dogs moved with one of the early waves of colonists down the west coast of North America and then into the interior: The earliest confirmed dog remains in the United States, in Danger Cave, Utah, are perhaps ten thousand years old. Meanwhile halfway across the world, humans took dogs with them as they moved into the farthest reaches of southeast Asia; the DNA of the eight hundred thousand street dogs found in Bali today shows that they are the descendants of dogs who arrived there overland, before Bali became an island twelve thousand years ago.

This rather rapid appearance, in the archaeological record, of dogs all over the globe can potentially be explained by many independent domestications taking place almost simultaneously—but it is also plausible that domestication of the dog did actually start much earlier than the archaeology indicates. The point at which archaeologists can be sure that the dog had already become a domesticated animal may actually reflect not the beginning of the transition from the wolf but, rather, the culmination of a fundamental change in the relationship between

man and dog, one that had already taken thousands of years to develop. This process could not be complete until the dog had become an integral part of human culture, and also until it no longer needed to maintain the physiognomy of the wolf, because many of its essential needs were being taken care of by its owner. Thus the five-thousand-year discrepancy between the date of domestication as shown by the archaeological record and that indicated by the dog's DNA can be explained by positing an extended period over which domestication took place gradually. These earliest dogs, or proto-dogs as they are sometimes called, would have been indistinguishable from wolves in terms of physical appearance, and they were probably treated in a strictly utilitarian way. For example, they may have been communal "property," as today's village dogs are, rather than having a single "owner."

To be sure, any pre-domestication theory that suggests several thousand years of coexistence between wolves and people before the transformation to domestic dogs must account for the lack of archaeological evidence over this period—say, from twenty thousand to fifteen thousand years ago. If dogs existed during this period, possibly even earlier, why are they absent from human burials for the whole of this period but then suddenly start appearing in burials, across the globe, over the course of "only" a couple of millennia? The archaeological record itself may hold the answer.

The earliest known dog burial is more than fourteen thousand years old. Located in Bonn-Oberkassel in Germany, it was discovered in a quarry in 1914 and seems to have consisted of a partial skeleton of a dog buried alongside two humans. Unfortunately the outbreak of World War I led to the loss of much of this material; yet a single piece of the dog's jaw remains, the arrangement of its teeth showing that it was clearly not from a wolf. Archaeological evidence indicates that, from then on, dog burials became almost commonplace. (Other kinds of animals were buried as well—but not nearly as often as dogs.)² Some dogs were buried alongside people; others had their own dedicated graveyards. In what is now the southeastern United States, dog burials were so common during the period between nine thousand and three thousand years ago that it is their relative infrequency from *later* burial

grounds that archaeologists feel they need to explain, rather than the other way around.

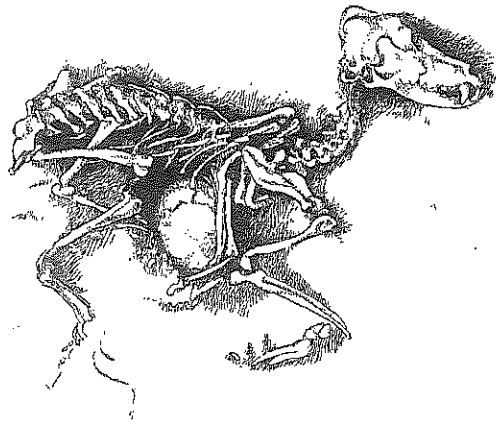
Mankind had been burying its dead for tens of thousands of years before dog burials began. Many ancient human graves contain animal remains; some may have come to be there accidentally, but many were obviously included deliberately, indicating a powerful emotional link between early humans and the animals they found around them. Consider this description of the contents of a grave, dug twenty-eight thousand years ago in Russia, that contained the remains of a boy, a girl, and a sixty-year-old man. Buried with them were thousands of pieces of deer's antlers, polar foxes' teeth, and mammoth ivory, which had probably been incorporated into necklaces or as decorations on their long-disintegrated clothes. Beside the boy was a sculpture of a mammoth, itself carved from mammoth ivory. In another grave nearby there was a small ivory sculpture of a horse (a hunted animal at this point, not domesticated). These people clearly had an important relationship with their local animals, one that included representing them in their art and possibly featuring them in religious rites. This relationship, however, seems to have been exclusively that of hunter and quarry.

The absence of dogs in known burial sites older than fourteen thousand years almost certainly means that dogs were, before then, rather rare. If the culture represented in this group grave in Russia had used dogs for hunting, it seems likely that there would also be evidence of dogs in this or similar graves—either bones or, as with the horse, some kind of representation. That there are no such traces indicates that the society from which these people came did not have domestic dogs. If they had, these dogs' remains would probably have been indistinguishable from those of wolves; but in fact there is no trace of any wolf-like animal, domestic or wild, in the Russian group grave, even though wild wolves would almost certainly have been in the vicinity. Indeed, very few graves hold traces of ancient wolves.

Unlike dog burials, which, as noted, were quite common after they first appeared in the archaeological record, wolf burials—whether alone or accompanying human burials—seem to have been extremely rare throughout ancient human history. (If common, they might have provided evidence for the early stages of domestication, when the bones of

proto-dogs would have been indistinguishable from those of wolves.) Wolf teeth do feature, alongside those of other predators, in many burials of humans, but their significance is usually unclear—and, in any case, many probably came from animals that were killed for their pelts. The close emotional relationship that hunter-gatherers evidently had with the animals they hunted seems not to have been extended to their competitors in the hunt, including wolves. Thus there is very little archaeological evidence indicating any kind of relationship between hunter-gatherer humans and wolves—either wild animals or those already on the path toward domestication—until dogs suddenly appear in burials some fourteen thousand years ago.

Among the very few wolf burials that have been discovered, one is particularly odd and may provide evidence for the transition from wolf to dog. Russian archaeologists recently found, in a cemetery near Lake Baikal, what they identified as a wolf buried with a human skull between its paws. The burial probably dates from only about 7,500 years ago, by which time there may well have been dogs in this area. What is remarkable about this wolf is that it was not local; it appears to be a tundra wolf and, if so, must have traveled several thousand miles before ending its days in this grave. But what if the animal is not a wolf at all?



A wolf burial near Lake Baikal in Siberia; its limbs enfold a human skull.

Rather than a far-flung tundra wolf, the wolf buried near Lake Baikal is, I believe, more plausibly the descendant of a “socializable” tundra wolf that had been adopted, many generations before, as a pet. Under this interpretation, such a burial gives us a tantalizing glimpse of the process of domestication in action. Domestication is very unlikely to have involved a steady transition from one group of wolves to today’s dogs; on the contrary, it appears to have been a haphazard process in which several domestications occurred, in different places and at different times. The “wolf” in the grave may in fact be a proto-dog, the product of a late attempt at domestication in the frozen north, brought south, where it lived and died alongside its more “domesticated” cousins—the progeny of earlier domestications—who, by then, were recognizable as dogs.

Archaeologists have found a few other burials of “wolves” that may in fact be proto-dogs. For example, 8,500 years ago in what is now Serbia, a small type of domestic dog was used for food, as attested by the many broken leg-bones and skulls found in rubbish pits there. Another (larger) type of dog from the same area and at about the same time was buried unharmed in proper graves, implying a role that included companionship. Even more pertinent, however, is evidence—from the same location and period—of the remains of what appear to be wolves. These may have been wild, but it is also possible that they were a third type of dog, which, unlike the other two, had not changed much in appearance from its wild ancestor.

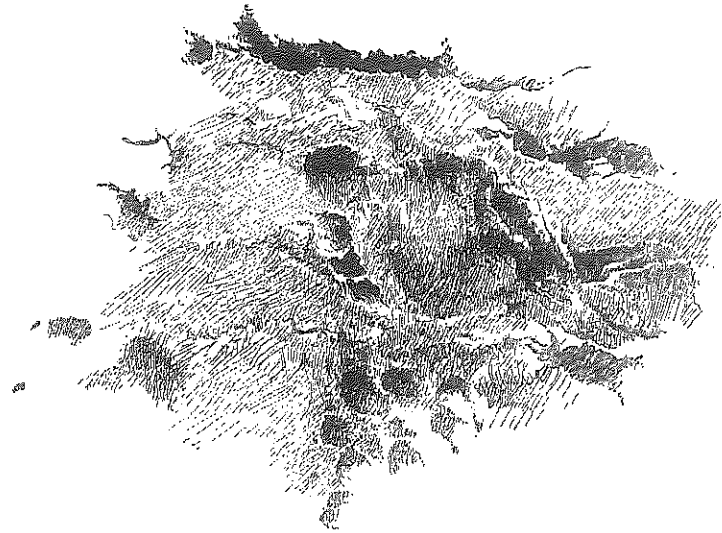
Few traces of proto-dogs have been found in human burials, but is there anything in the fossil record to support the idea of gradual and haphazard domestication? Until recently, archaeologists were reluctant to identify wolf skulls more than fourteen thousand years old as belonging to anything other than a wolf, so any proto-dogs that were found were not labeled as dogs. The earliest distinct dog skull, from Eliseevich, in the Russian plain, was excavated from the edge of a pile of mammoth skulls, and it, too, has been dated to about fourteen thousand years ago; roughly the size of a husky’s skull, it seems to have been buried accidentally rather than deliberately. However, three new skulls have recently been found that are intermediates between those of wolves and early dogs such as the Eliseevich dog. All three are very similar to today’s Central Asian shepherd dog (although of course skulls cannot tell us anything about the texture or color of the dog’s coat). The oldest of these skulls, from Goyet in

Belgium, is a staggering thirty-one thousand years old, more than twice the age of the oldest dog burial. The other two, from the Ukraine, are probably only about thirteen thousand years old, roughly contemporary with the first dog burials. The Goyet specimen is therefore something of an anomaly. Could it have been a direct ancestor of today's dogs? Or is it our only record of a very early domestication of the wolf—one that failed, hence the absence of any trace of dogs for the next seventeen thousand years?

There is one more small piece of evidence that suggests a relationship between man and dog going back more than twenty thousand years. Deep in the Chauvet cave in the Ardèche region of France, which is famous for its prehistoric art, a fifty-meter trail of footprints made by an eight- to ten-year-old boy, alongside those of a large canid, hints at a close relationship between the two. The footprints of the canid are intermediate between those of a dog and a wolf. Soot from the torch that the child was carrying date the event at twenty-six thousand years ago, making these probably the oldest human footprints in Europe. With a little imagination, one can picture a boy and his faithful (proto-)hound, venturing into the cave to view the spectacular representations of wild animals painted on its walls.

Evidence such as the foregoing is, ultimately, too flimsy to give us a firm idea of when or where domestication of the wolf began. Nevertheless, this process does appear to have been repeated several times, in several locations in Europe and Asia, over a period of many thousands of years, to the point where domestic dogs may already have been established in some parts of the world at the same time that wolves were being taken from the wild in others. Some of these attempts must have succeeded; others almost certainly failed, leaving no trace in today's dogs. The habit of burying dogs with humans seems, for some reason that is still unclear, to have been adopted only after domestication was well advanced; otherwise, there would be human graves from somewhere between twenty-five thousand and fifteen thousand years ago that contained the bones of proto-dogs, indistinguishable from those of wolves.

We can say for certain, however, that the earliest confirmed dogs—at fourteen thousand years ago—logically represent not the beginning of



Single footprints of a child and a canid in the Chauvet cave, in the Ardèche region of France

domestication but, rather, the end of its first phase, marking the point at which dogs became physically distinct from wolves. Before that, there must have been changes in the brains of wolves that made them suited to living with people but left little or no trace in their skulls for archaeologists to find today. The question still remains as to how long those changes took, how many of those first alliances between dogs and wolves failed, and how many wolves left their traces in the dogs of today.

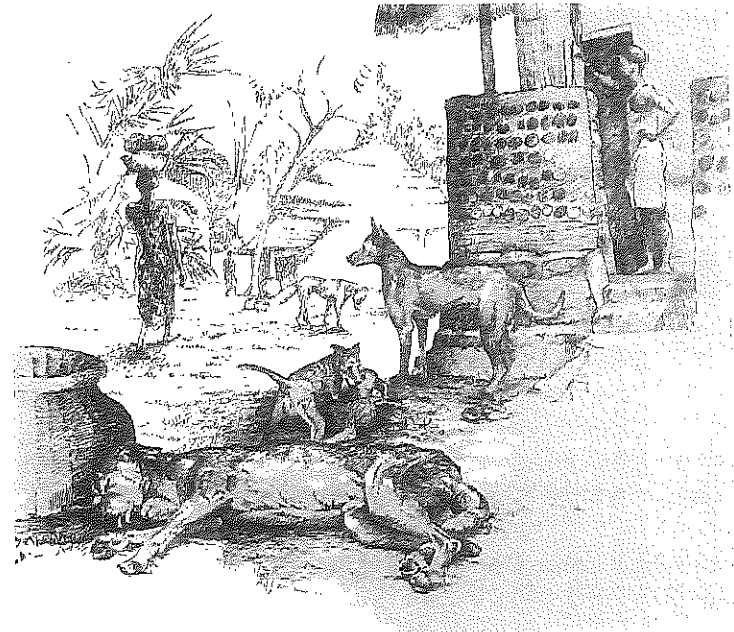
Since we can account for the diversity of dogs' DNA only by hypothesizing that individual domestications of wolves occurred in different parts of the world, these different "proto-dog" populations must initially have been isolated from one another, and probably remained so for thousands of years. As domestication progressed, however, these early dogs would eventually have become manageable enough to travel with people on large-scale migrations, thereby allowing individuals from one proto-dog population to meet up with, and begin interbreeding with, individuals from another. The resultant churning of the dog's gene pool probably started more than ten thousand years ago, such that even dog

remains old enough to be fossilized may have originated in wolf populations many hundreds or even thousands of miles away.

Thanks to this complicated timeline of domestication, the location of the original domestication events has proved impossible to pin down. The wolf itself is a highly mobile animal, even though it has not benefited from being transported around by man. Migrations of wolves, even since the dog was domesticated, have resulted in the incidence of almost identical DNA among individuals in regions as far apart as China and Saudi Arabia. Thus the DNA of modern wolves gives only very weak clues as to where domestication might have taken place.

Leaving the wolf to one side and approaching the locational problem from the opposite end, other biologists have recently analyzed the DNA of local "village dogs." The scientists' hope was that these dogs would turn out to be the direct descendants of the first wolves to be domesticated in the area, and the assumption was that, as dogs dependent on humans, they were much less likely than wolves to have traveled long distances since then.³ One recent study has suggested that, because the village dogs of southern China have the most varied DNA found so far, it was there that domestication must have occurred—but subsequent research has revealed that village dogs are almost as diverse in Namibia, where the nearest wild wolf is three thousand miles away.⁴ To have gotten that far, and to have become so widespread (there is little difference between the DNA of village dogs in Namibia and the DNA of those in Uganda), these dogs must have had considerable help from mankind; perhaps they accompanied humans on their various migrations around Africa. There also appears to have been a substantial amount of interbreeding between apparently localized village dog populations, resulting in a gradual trickling of greater diversity into their DNA—even in places as isolated as Namibia.

Despite all this considerable—and continuing—research, there are still no firm answers to the question of where the dog was domesticated. It must have happened in areas where wolves occurred naturally, yet North America has been ruled out, since the DNA of North American wolves is quite different from that of domestic dogs. This leaves most of Europe and Asia as possible locations. Beyond this consensus,



Village dogs

there is a great deal of conjecture, even disagreement, among the various researchers pursuing a definitive answer.⁵

The most likely scenario is that wolves were domesticated at several different locations, possibly across Asia, including the Middle East, although one or more additional European origins also seem plausible. Taken at face value, the archaeological evidence points to at least one early origin in the Fertile Crescent, and this is the preferred scenario of some of the DNA experts. However, one interpretation of the DNA points to the earliest domestication as occurring in South China, where far less archaeological investigation has taken place. Each of the teams of DNA experts has their own samples of dogs and wolves, and so far these have led them to different conclusions. Their accounts are not easy to reconcile at present, but the most likely conclusion is that there

was no single point of origin but, rather, that wolves entered human society at several far-flung locations across Asia and Europe. Some left few or no descendants; others prospered and eventually interbred as humans began to take dogs with them as they traveled.

Although we still do not know where, exactly, the dog originated, it is clear that our modern dogs do not trace their ancestry back to any one particular kind of wolf. Dogs are the result of a mixing of many different kinds of wolves from across Asia and Europe; the only wolf that is definitely missing from the recipe is the American timber wolf. Thus there is no wolf alive today that can act as the perfect model for understanding dogs and the way they behave. Moreover, the long period over which domestication occurred means that dogs have had the opportunity to change radically since they became separate from wolves, ten thousand or more generations ago. During the same period their environment, too, has undergone a considerable transformation.

The dog's evolution did not occur all at once, and the forces driving it have themselves altered over the dog's long period of coexistence with man. Indeed, over the same span of many thousands of years, we have changed almost as much as dogs have. The dog's history is bound up in our transition from hunter-gatherer to modern city-dweller, and its roles have changed during that time as well. Unlike that of some other species, the domestication of the dog has served more than just a single purpose. Dogs have fulfilled many functions within human society, and so the story of their domestication is necessarily complex: a series of steps without a coherent underlying plan, but each one significant to our understanding of the dogs we have today.

Unfortunately, the early stages of the dog's domestication occurred so long ago that we know little of how they occurred. Given that the dog was the first domestic animal of all, deliberate domestication seems far-fetched anyway—where, after all, would such a radical idea have come from? The most likely scenario is that associations between man and wolf appeared spontaneously, in several places, over thousands of years, long before the archaeological record shows any dogs that were distinct from wolves in appearance. Many of these associations would have died out, perhaps as environmental conditions or human customs changed.

Others—probably only a small minority—lasted long enough for the “village wolves” to turn themselves into the prototypes for domestic dogs. The “village wolf” would have looked so much like a wild wolf that the two would be indistinguishable in the archaeological record.

Despite the difficulties of understanding the process by which dogs became domesticated, we can gain some insight by studying the process in other animals, where the evidence is more detailed and better preserved because domestication occurred later. The history of the pig is one instructive example. Our modern domestic pigs are descended from the wild boar: While the archaeological record points to a single domestication in Turkey, the DNA indicates six other domestications, each independent of the next and stemming from a different population of boars. Did seven different civilizations each domesticate the pig independently of one other, or did one think of it first, after which the idea of domesticating pigs spread from one area to another, each turning to its local population of wild boars for the raw material? It turns out that this is the wrong question, because both alternatives are based on the concept that domestication is a deliberate and cumulative process.

The first few domestications appear, with the benefit of hindsight, to have been haphazard affairs, progressing in fits and starts and occasionally going into reverse. This scenario certainly applies to the domestic pig. More than two thousand years elapsed between the first pigs that were distinguishable from wild boars and the pigs that showed clear evidence of being farmed (e.g., a high adult female-to-male ratio, since culling of males when they are young maximizes productivity). That it took nearly a hundred generations of humans to accomplish a single domestication doesn't suggest much of a plan. Rather, the gradual changes in the bones of the pigs recovered during this period suggest that, initially, pigs were scavengers around human settlements, where they would also have served as a useful walking larder when hunting failed. They may also have been useful in cleaning up human wastes, including feces: The “pig-toilet” is still found in some parts of Goa (India) and China, and was probably once widespread throughout Asia.

The likely origins of the pig's domestication shed important light onto the process in general; domestication is almost certainly as much the agency of animals as of humans. In the case of the pig, every human

settlement near a population of wild boars was a potential source of domestication: Once the settlement had grown to a suitable size, a few boars with the right temperament to tolerate the proximity of humans moved in, exploited the new food source, and were themselves exploited as food. In many cases these arrangements would have died out temporarily, perhaps when food shortages resulted in the consumption of all the pigs in the village. But the whole cycle could easily have started again in better times, if there were still wild boars in the vicinity. Domestication could have followed much later, presumably when the conditions were right among the local people—for example, when their culture allowed for individual or family (rather than communal) ownership, which would protect the animals against slaughter when food was in short supply. The next stage would have been the evolution of husbandry methods such as enclosure to protect the captive pigs from predators, and the selective culling of the more belligerent males, reducing the risk of injury to their human captors.

Since there is no indication that the dog was initially domesticated as a food animal, the details of its story are likely to be different from those of the pig, but the transition from wild to domesticated was probably just as piecemeal and haphazard. If the pig took two thousand years to change from hanger-on to agricultural animal, most likely the dog took just as long, perhaps even longer. With no prior experience in domestication, humans are unlikely to have deliberately begun the process of domesticating wolves; a much more probable scenario is that the wolves themselves started the process. Indeed, I'm firmly of the opinion that the pioneers of the long road to today's dogs were wolves that were simply exploiting a new niche, a new concentration of food provided by man, as humans began to live in villages rather than being constantly on the move. These wolves then evolved to fit our new lifestyle, which would have demanded capabilities very different from hunting on the open range.

Living near human settlements would have required a tolerance of the proximity of humans that no modern wolf can manage, and probably few ancient wolves could have either—but humans would almost certainly have aided in selecting for this trait. Initially, those wolves that were suited to scavenging from man would have prospered and produced

offspring, whereas those wolves that were unsuited either did not or left to rejoin their wild cousins. It is difficult to imagine how hunter-gatherer humans could have actively intervened in this process; selecting which male would breed with which female, for instance, would have been unlikely at such a tenuous stage. However, humans probably did intervene, in a much less deliberate way—one that nevertheless speeded up the separation between village and wild wolves.

Humans must have at least tolerated the wolves that were gravitating to their settlements, because otherwise such a transition could never have taken place. There must have been times, of course, when having a large well-armed carnivore hanging around would have been dangerous. The very young and the infirm would have been at particular risk from an animal, perhaps only a few generations removed from a wild hunter, that had run out of food to scavenge. Any wolf that threatened to injure a human must have been driven away or even killed; only wolves that posed no apparent threat would have been allowed to remain in the village for very long.

The domestication-by-scavenging hypothesis is a start, but it cannot be the whole story, for it seems unlikely that wolves would have been able to survive entirely on the by-products of early human settlements. Modern village dogs can get most of their food by scavenging, but then they are much smaller than wolves are, and modern villages are a lot bigger, and more productive, than hunter-gatherer villages must have been. The scavenger theory depends, critically, on whether hunter-gatherers regularly produced enough surplus food to make scavenging worthwhile. Wolves are large and require a great deal of energy—about two thousand calories a day, equivalent to two-and-a-half pounds of meat. It seems unlikely that, twenty thousand years ago, any human settlement would have produced that much surplus meat day after day. It must be remembered, however, that wolves are not strictly carnivorous; they are perfectly capable of subsisting on a diet of plant material supplemented with the occasional bone or scraps of meat. They may even have contributed to village hygiene by performing the same function as today's toilet pig; however unsavory this idea may seem to us today, it would explain the unfortunate penchant that some modern dogs have for eating feces.⁶ Whether or not the village wolves exploited this insalubrious source

of calories, however, it is hard to imagine that several wolves, even a pair, could do well enough—and survive for long enough to produce offspring—by relying entirely on scavenging. Indeed, it seems illogical that any animal would give up hunting, a way of life for which it had evolved over millions of years, for the uncertainties of scavenging from a species that was not yet as skillful at obtaining meat as it was.

Thus scavenging, while a plausible contributor, isn't nearly sufficient by itself to account for a transition from hanger-on to domestication. Scavenging around hunter-gatherer encampments is unlikely to have provided a reliable source of food even for small wolves, and I thus strongly suspect that there must have been some deliberate feeding by the hunter-gatherers themselves. Of course, such behavior on the part of humans requires explanation: Why would humans give up their own resources to animals that served no clear purpose within the community?

If humans encouraged wolves to stick around by deliberately feeding them, then part of the motivation behind this might possibly lie in the apparently universal human trait of keeping animals as pets. Pet-keeping is not just a modern phenomenon; it is widely practiced among contemporary hunter-gatherer societies and was probably a feature of many pre-agricultural societies as well. In contemporary contexts, these "pets" are usually obtained as very young animals from the wild, perhaps when a nest or den is discovered by the hunters, and are brought back to the village and hand-reared by women and children. As they grow, some of these animals will escape back into the wild; others will become too large or boisterous for comfort and will be driven out, or even killed and eaten. It is apparently rare for the "pets" to breed successfully within the village, so each generation has to be newly obtained from the wild. These are therefore not really pets in the usual sense of the word, but the hunter-gatherers lavish on them the same level of care when they are young as do the owners of a new kitten or puppy in the developed world.

Modern hunter-gatherers have remarkably varied pet-keeping tastes. In some of today's hunter-gatherer societies, such as the Penan of Borneo and the Huaorani of the Amazon rainforest, there seems to be no particular preference for one animal over another. Virtually any young bird or mammal of manageable size may be adopted, such that at any

given time there may be dozens of different species within a single village—parrots, toucans, wild ducks, racoons, small deer, assorted rodents, opossums, and monkeys. Other societies may attach particular importance to one particular species. For example, the Guaja of Amazonia are a matriarchal society, in which all the women keep monkeys as pets; the head woman will have several, while adolescent girls will usually look after just one. They treat their monkeys at least as well as, possibly even better than, their own children. The newly collected infant monkeys are suckled at the breast, constantly fed choice tidbits, and carried everywhere—the matriarch will usually have two or three draped over her head and shoulders as a sort of living robe of office. In other such cultures—for example, Polynesia, Melanesia, and the Americas—it is dogs who are treated in this way, including the nursing of puppies alongside human infants.

Thanks to contemporary evidence, the most direct of which comes from the indigenous Aboriginal peoples of Australia, we can guess that our ancestors found puppies just as appealing as we do today. There are no grey wolves or other canids in Australia; in their place are dingoes, which are actually the descendents of dogs that reverted to the wild several thousand years ago. Aboriginals were hunter-gatherer-cultivators until recently; they had no domesticated animals but do have a long tradition of taking dingo puppies from the wild and keeping them as pets. Some were collected from litters found accidentally, during hunting trips; others were taken deliberately, as part of religious ceremonies. These puppies were highly valued and well cared for, but as they grew into adults they became a nuisance, stealing food and becoming overboisterous, and were usually driven away soon after they had become sexually mature. Thus a separate population of domesticated dingoes never emerged—and yet the tradition continues to this day.

The persistence of the dingo-keeping tradition in Australia suggests that, in the absence of (or sometimes in spite of) practical considerations, humans will keep puppies purely for their cuteness. Dingoes are clearly a drain on human resources, not an asset. Originally, scientists speculated that Aboriginal Australians kept dingoes to serve as hunting companions, but in fact dingoes interfere with hunting, to the point that Aboriginals bring home more meat if they leave their dingoes

behind. Furthermore, dingoes often outnumber the human inhabitants of a village and accordingly have to compete for food; their scavenging can be so intense that they have to be deliberately excluded from meal times. Nevertheless, the habit of taming large numbers of these animals has persisted for hundreds, probably thousands of years, so they must have some redeeming features in the eyes of their hosts. Indeed, dingoes feature more in the Aboriginals' art and spiritual narratives than any other animal, with the possible exception of snakes. Although respect for dingoes of all ages has long been encapsulated in Aboriginal culture, the habit of keeping young dingoes must surely have started as an exaggerated susceptibility to the cuteness of puppies.

It thus seems entirely possible that, in one or two locations, perhaps twenty thousand years ago, there were hunter-gatherer groups in which wolf cubs taken from the wild came to have a social significance similar to that of contemporary hunter-gatherer's pets. The feeding and care of the young wolves, so difficult to account for if their parents had been merely scavengers, would instead have been performed by the villagers, initially for their own enjoyment and subsequently to gain social esteem—much as, for example, the keeping of monkeys as pets brings status to women of the Guaja. Additionally, the intimate relationship between the cub and its carer would have enabled the cub to become socialized to people as well as to its own kind—provided, of course, that it had the capacity to do both.

There is one very important way in which the dog is different from other hunter-gatherer pets. Whereas the dog eventually became domesticated, these other "pets"—from rodents to parrots to monkeys—are really just tame animals, many of whom have been raised in isolation from their own kind and probably would not know how to breed even if given the opportunity. Hence the need for these "pets" to be continually replenished from young born in the wild. The wolf, however, became domesticated because it stayed near humans by choice, forming a reciprocal relationship. For domestication to begin, a wolf would need to be raised by humans from a cub, and then stay in (or return to, but that seems unlikely) the village to produce its own first young. (Village habitation would be necessary only for the females; the cubs could just

as well be fathered by wild wolves, but it would be essential for the females to be completely tame so that the cubs could be born in the village.)

In fact, by comparing today's wolves and dogs, we can see that dogs have adapted to human presence in a remarkable way. Perhaps the most striking difference between dogs and wolves today, apart from their appearance, is the ease with which domestic dog puppies adopt a dual identity, something today's wolf cubs seem incapable of. This capacity for the dog to adopt a dual identity—part human and part wolf—is essential in accounting for the transition from primitive pet to truly domesticated animal. Perhaps it is the key attribute that singled out the grey wolf, from all the other possible candidates among the canids, for successful domestication. Perhaps its unique transformation to domestic animal has little to do with its ability to form packs or to communicate by body language (neither of which, as we have already seen, are traits unique to the grey wolf). Perhaps the grey wolf was simply able to form social bonds with humans, whereas other canids were not.

It is entirely possible that some accident of genetics—some sort of mutation—gave a few wolves the ability to socialize to two species simultaneously, to direct their social behavior to mankind *and* to other wolves, while their sexual preferences remained steadfastly directed at their own species. Until man came along, this hereditary change would have been of no advantage (or disadvantage) to the wolves that carried it. But as hunter-gatherer societies in places where there were also wolves developed to the point where the "pet"-keeping habit became established, those local wolves with the altered socialization mechanism would have been pre-adapted for coexistence with mankind. On the one hand, then, societies that serendipitously happened to adopt wolves in the locations where their socialization mechanisms had been altered were presented with animals that could breed successfully within a man-made environment.⁷ On the other hand, societies that fixed on canids such as the golden jackal as their prototype pet of choice could tame them as individuals but could never succeed in breeding them, because their socialization mechanisms were still suited only to their original wild lifestyle.

What evidence is there for the existence of these special, easily socialized wolves? Simple: It is all around us, in the form of modern dogs.

They are the only living descendants of the socializable wolves that, I suspect, existed twenty thousand years ago. Modern wolves are, of course, quite different from the earlier wolves I'm describing; today's grey wolves are very difficult to tame, let alone socialize to people. Even tame wolves do not seem to form specific attachments to individual humans. Modern wolves, however, are not the descendants of the wolves that became dogs.

Today's dogs are, if my hypothesis is correct, the descendants of a small fraction of the original wolf population, products of a mutation that separated these wolves from the majority of their species by allowing them to socialize with both humans and other wolves. While this small fraction of wolves went on to live among humans and eventually turned into dogs, most wolves could never follow this path, because they displayed a natural wariness of man. In essence, what I am suggesting is that this ability to socialize to humans is not, as it is usually assumed, a *consequence* of domestication. Instead, I conceive it as the crucial, if accidental, pre-adaptation that opened the door to domestication in the first place.

The key difference between a dog and a wolf is not what it looks like but how it behaves, and especially how it behaves toward people. DNA and bones cannot tell us how these early dogs behaved or what their everyday interactions with people were actually like. Domestication affects outward appearance, for sure, but at the very earliest stages this is incidental. What defines an animal such as a dog is what goes on under the skin—specifically, how the behavior of its ancestors has been altered to enable it to live comfortably in man-made environments.

Although we know a great deal about the behavior of today's American timber wolves and an increasing amount about the relict wolf populations of Europe, this information gives us little insight into the behavior of the first domestic dogs. Modern wolves are only very distantly related to the domestic dog, and they have been under intensive selection pressure, especially over the past few hundred years, from those who wished to exterminate them. It is therefore unsurprising that today's wolves are very difficult to socialize, and that tame wolves tend to remain unpredictable and potentially aggressive toward people throughout their

lives. By persecuting wolves, we have selected those individuals that are naturally wary of us; it is therefore very difficult to derive any knowledge about early dogs from what we know about contemporary wolves. Moreover, we cannot even replicate domestication, by taking wolves out of the wild and selectively breeding them to become more like dogs. Since the wolves that were the direct ancestor of domestic dogs are, in their original form, extinct, that would be impossible.

One recent modification of a canid is widely held to provide pointers as to how wolves might have changed into dogs. This is the silver fox, a color variety of the wild red fox that is bred in fur-farms. Silver foxes are usually kept in cages and are barely tame, let alone domesticated, but in the 1950s a group of Russian scientists began to breed them selectively, using only the tamest individuals in each generation.⁸ At first, few of the foxes could be handled, even by a person offering a tasty food treat. After a few generations of breeding only from individuals that would tolerate handling, however, some individuals emerged that would actively seek contact from people. Indeed, after thirty-five generations, most of the foxes were behaving in a remarkably dog-like way—wagging their tails, whimpering to attract attention, sniffing and licking their handlers' hands and faces. Some were even taken home as pets by the staff, who reported that these animals could be as obedient and loyal as domestic dogs. The geneticists' objective of producing a fox that was easier to handle seemed to have improved its welfare too. Freed from the relentless fear and anxiety of having to encounter an alien species (us!) every day of their lives, the new "tame" farm-foxes exhibit levels of stress hormones four times lower than those in the original "wild" version. A similar reduction in reactivity, and susceptibility to stress, is evident when dogs are compared with wolves—a reduction traceable to changes in the hypothalamus, a part of the brain that is, among several functions, concerned with emotional reactivity. Such changes are probably a direct consequence of selection for tameness, so in this respect the tame farm-foxes may well be similar to the wolves that adapted to living near, and scavenging from, human settlements.

The most interesting finding of the Siberian fox experiment was that the farm-foxes became easier to tame because the period before they became frightened of new experiences was effectively lengthened.

Most young mammals go through a period of their lives in which they are naturally inquisitive and trusting. And it's usually during this stage that they're still being looked after by their parents, who are on hand to make sure that these characteristics don't get them into trouble. As they get older and more independent, the offspring become much more suspicious of anything unusual and much more likely to run away after an initial inspection. In the farm-foxes, selection for tameness corresponded with an extension of this "trusting" phase, which ends when wild foxes are about six weeks old but lasts for about nine weeks in the "tame" variety. That extra three weeks is enough to allow regular handling to take effect, producing a fox that trusts, rather than fears, the people who look after it.

Another finding of the Siberian experiment has been used to posit the effect of domestication upon canids' appearance, though this is largely unsubstantiated. The appearance of some of the tame foxes produced in the experiment is different from that of the wild variety; a few, though by no means all, of the tame foxes have unusual dog-like features, such as curly tails, floppy ears, and white patches on their coats. Some authorities have claimed that such features are part and parcel of domestication, that selection for tameness inevitably brings with it all these changes in appearance. Unfortunately the data don't support this idea. True, more "tame" foxes have floppy ears than do the "wild" ones, but they are still in a tiny minority—fewer than a quarter of 1 percent. Fewer than one in ten of the tame foxes have a curly tail. Fewer than 15 percent have a white "star" on their forehead. Exactly how these changes became slightly more common in the "tame" foxes is still something of a mystery, but they are still rare, and probably tell us little or nothing about domestication.

While the Siberian experiment produced tame foxes, there is a significant difference between these foxes and domestic dogs in terms of the extent to which they are—or, it seems, can be—"domesticated." In dogs, the process of acclimatizing to humans does not disrupt normal social relations with other dogs. By contrast, when the foxes develop a relationship with humans they seem to lose interest in socializing with other foxes. Red foxes—the same species as the farm-fox—are rather sociable animals, often living in groups of four to six animals. Yet the

tame farm-foxes are solitary animals—as devoted as dogs but as independent as cats. This contrasts with both the domestic dog (and the domestic cat), whose social relationships can and indeed normally do develop simultaneously with humans and with members of their own species (and perhaps other species as well).

Thus if the tame foxes can tell us anything useful about the dog, it is that tameness, while a useful first step, is not the same thing as full domestication. Tameness permits the replacement of one set of social responses—directed at members of the same species—with another—directed at humans. Dogs, by contrast, need to retain both, in order to continue functioning as members of their own species while simultaneously establishing and maintaining relationships with their human owners. Nothing in the farm-fox experiment sheds any light on how this capacity might have come about during the domestication of the dog.

The farm-fox experiment does show that selection for tameness can be extremely rapid—indeed, it seems to be fast enough to suggest a plausible first stage in the domestication of the wolf. The key difference between the two animals is, of course, that the foxes were a captive, isolated population that was deliberately selected for tameness. The wolves that were sufficiently tolerant of humans, on the other hand, selected themselves to be the ancestors of domestic dogs: Those that were easily tamed could start breeding in the proximity of humans; those that could not rejoined the wild population. The appearance of dog-like behavior in the tame foxes, such as licking of humans' faces and hands, and whimpering, also supports the idea that the dog's social repertoire is drawn not from that of the wolf exclusively but, rather, from an ancestral palette of possibilities inherited from the canids as a whole.

The farm-foxes tell us that natural variation in tameness within a species can be sufficient, in at least one of the canids, to produce individuals that could be the ancestors of a domestic animal. This experiment thus provides us with a model for the initial separation between wild wolves and those that were naturally tame enough to live alongside people. The resources that the naturally tame wolves were able to obtain from humans must have been sufficient to allow them to adopt a new way of breeding. Instead of hiding them away in a den, the intrinsically "tame" mother wolves must somehow have allowed their cubs

access to humans, so that taming, and selection for tameness in subsequent generations, could proceed further. Underlying the onset of tameness are changes in the production of and reactivity to stress hormones, alterations that are evident from tame farm-fox and dog alike. However, the farm-foxes tell us nothing about the way that dogs gained the capacity to sustain social relationships simultaneously with their own species and with humans. Nor do they tell us anything about how dogs achieved their remarkable diversity of shapes and sizes—and yet this very diversity permits another, very different approach to understanding the subsequent phases in the domestication of the dog, once tameable wolves had begun their association with mankind.

Instead of comparing dogs with wolves, or trying to reconstruct the domestication process, we can find important information about how dogs came to be by examining the differences between breeds and types of modern dogs. The ways in which they differ from one another can provide clues as to how those changes in appearance might have come about. Since different-sized dogs appeared very early in the history of domestication, at least ten thousand years ago, it's possible that the processes that led to the diversification in body shape are the very same as those that permitted domestication to proceed beyond tameness. And since many of the differences between breeds and types of dogs are known to arise through alterations in the rates at which the body and behavior develop in early life (alterations that are reflected both in the outward appearance of the dog and in the way its behavior is organized), the emergence of these superficial differences is thus arguably the most important underlying process that has produced today's dogs.

Dogs come in so many shapes and sizes that they have long been a puzzle to zoologists, but in fact many of the changes can be accounted for by a common biological mechanism, the technical term for which is *neoteny*. Roughly speaking, this refers to the phenomenon whereby growth in some parts of the body stops while other parts continue to grow at the normal rate. If the whole skeleton stops growing earlier than usual but the internal organs continue to mature, then the result is a smaller-than-usual animal that is still capable of reproducing. Thus, for

example, the skeleton of an adult Lhasa apso is similar to that of a Great Dane puppy, but the Great Dane will continue to grow for many more months before it becomes sexually mature. If the growth of the skeleton is altered selectively, then the end result is a change in shape as well as a reduction in size. Thus the skull of an adult Pekinese has essentially the same proportions as that of a wolf fetus but its body is more dog-like. In "toy" dogs, the growth of the whole skeleton stops at what would be, for a wolf, a very early stage. In flat-faced dogs, the growth of parts of the skull is slowed to maintain the proportions of that of a fetal wolf.

We are now coming to understand even more about the physiology that underlies these differences in canid appearance. It turns out that the skull and skeleton of the wolf change shape dramatically between their genesis in the fetus and their final form in the adult, under the control of various hormones. Much of the size variation in today's dogs probably comes about through changes in the growth stages during which these hormones are produced, how much is produced, and how effective they are at doing their job. Thanks to all the work that is going on to unravel the canine genome, it should soon be possible to identify how these changes work.

The very same principle of selective arrested development that governs dogs' growth can be used to explain how domestication molded the dog's behavior. For example, dogs continue to play even when they are adults, unlike most animals. Because the behavior of juvenile wolves is more flexible than that of the adults, the dog has been likened to a wolf that has never grown up, except in the important sense that it becomes sexually mature and so can reproduce. Its behavioral development has, in a sense, been arrested. The farm-fox story sheds important light on this process by telling us that tameable wolves probably differed from untameable wolves in having a delayed period of social learning at the beginning of their lives, such that tolerance of human contact had time to develop. Dogs, for their part, are like tameable wolves in which development of behavior has been slowed down further still, to the point that it becomes arrested at the (wolf's) juvenile stage, where behavior is more flexible and can therefore be adapted much more easily to the requirements of humans. Some simple resetting of the dials that control

the development of brains and behavior can, in theory, account for much of the transition from wild wolf to tame, from tame to domestic, and then to the diversification of dogs into types of different sizes and shapes.

One further difference between dogs and wolves can be accounted for by a selective change in the development of the two animals: Dogs become sexually mature somewhat *earlier* than wolves do. Dogs are also fertile throughout the year, unlike wolves, which are sexually active only in the winter, leading up to the birth of the cubs in the spring. Both of these differences are likely to be consequences of the transition from the wild, with its seasonal but predictable food supply, to early human societies where food was more plentiful on average but also more unpredictable; proto-dogs that could breed any time after their first birthdays would have out-competed those that waited, as wolves do, until their second winter.

For the same reason that they need to be much more opportunistic in grasping opportunities for breeding, dogs are also much less choosy than wolves in their choice of sexual partners. This is evident from the Y-chromosome (paternal) DNA of today's dogs, which is much more diverse than their mitochondrial (maternal) DNA. Because wolves pair-bond, males and females are about equally likely to contribute to the DNA of the next generation. Given the promiscuous tendencies of male dogs, some males can potentially sire over a hundred litters in their lifetime, while many others leave no offspring at all. Bitches are constrained by the fact that they can produce only one litter per year. Moreover, the variability in male reproductive success appears to have been set up well before the creation of the modern breeds in the nineteenth century, suggesting that male promiscuity is an ancient, not a recent, trait of dogs.

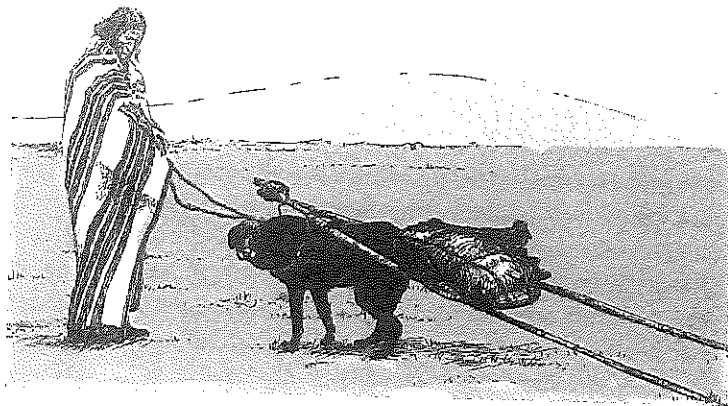
The promiscuity of the male dog must have been one of the factors that helped man, first accidentally but then increasingly deliberately, to impose his own selection pressures on the species. Some of these choices might have been simply fanciful, such as a preference for a particular coat color or an especially "cute" face—qualities of no particular consequence for the process of domestication. Other aspects of human behavior—such as taking special care of the offspring of a bitch prized

for her trainability and loyalty—might have pushed the process of domestication along.

At the early stages of domestication, certainly up to the point that dogs became physically distinct from wolves, human intervention in breeding is unlikely to have been a conscious process and, indeed, may have been haphazard, as it remains to this day in village dogs. The archaeological record indicates that dogs may have disappeared entirely from some societies, only to be replaced hundreds of years later by immigrants from elsewhere. Other societies may have rejected dogs even when they were available: Although Japan was first colonized by mankind about eighteen thousand years ago, there is no record of dogs in the region until about ten thousand years ago—presumably Japan's new inhabitants considered the dogs available in ancient China unsuitable, for some now impenetrable reason.

Despite the almost certain lack of early selective pressures from humans, over the course of several thousand years wolves must have made some kind of faltering progress toward becoming an animal that had many of the behavioral characteristics of today's dogs, even if it still looked much like a wolf. Certain physical changes, however, would likely have begun to occur during this time. Dependence on man for what was probably a rather erratic supply of food would have favored a reduction in body size. As dogs were transported into warmer climates, those with shorter, paler coats would have out-competed those with the wolf's long, darker fur, producing a conformation that survives in village dogs to this day.

Many of the other conformations that we see in today's dogs are also ancient. By ten thousand years ago, dog-keeping and therefore dogs themselves had spread throughout much of Europe, Asia, Africa, and the Americas; soon after this, and in many parts of the world, recognizably distinct types of dog appear. Over the next couple of thousand years, dogs diversified rapidly, so that by the time representational art became commonplace some five thousand years ago, there were already dogs for many purposes. Long-limbed, long-nosed sighthounds, superficially similar to the modern saluki or greyhound, were used for hunting.⁹ Heavy, large-headed mastiff types were used for guarding and general intimidation. Hounds were developed that hunted mainly by



Native American dog travois

scents, suited to finding and following large game in thick cover. Subsequently, larger dogs were found to be useful as pack animals, either carrying loads on their backs or—as widely practiced by some Native Americans—pulling a travois. Small terrier-like dogs were used for keeping rats and mice at bay and for hunting animals that go to ground, such as rabbits and badgers. Lap dogs, similar to today's Maltese dog, are first recorded from Rome more than two thousand years ago, but there were probably already lap dogs in China by this time, probably among the ancestors of today's Pekingese and pug. The arrival of lap dogs completed the process of generating the dog's remarkable variation in size; any that became smaller, or larger, would probably not have been biologically viable in the days before veterinary care. Lap dogs were also the first dogs bred solely for companionship, though for many centuries these through-and-through pets would have been rare compared to dogs kept for more utilitarian purposes.

We can be reasonably sure that there was a deliberate element in the breeding of all these dogs, over at least the last five thousand years, by the simple expedient of allowing bitches to mate only with chosen males of similar type. Some males were evidently favored over others: Molecular biologists have found much more variety in the mitochon-

drial (maternal) DNA of dogs than in the Y-chromosome (paternal) DNA, indicating that during the entire history of the dog, far fewer males than females have left surviving offspring. Favored males must therefore have been prized and taken to mate with many bitches, much as happens today within pedigree breeds. The choice of male must sometimes have been based on body conformation (e.g., in dogs bred for food), but mainly it would have been based on whatever kind of behavior was desired in the puppies, whether suitability for herding, hunting ability, or guarding.

Dogs were almost certainly being bred deliberately as of five thousand years ago, and matings based on the dogs' own preferences would have kept the dog population diverse. Dog-keeping would have been much more chaotic than it is today, so many matings would also have been unplanned—and if the resulting offspring turned out to be useful, they would have been retained. Taboos against raising puppies that were not “purebred” would have been rare, unlike the situation today. Thus without any deliberate planning, a healthy level of genetic variation was maintained within types, as well as between. Transfer of dogs from one location to another by traders would have ensured that most local populations were not reproductively or genetically isolated from one another, maintaining diversity at the local as well as global levels. In the absence of veterinary knowledge, natural selection would have continued as a major force directing the development of dogs in general; the rates of both reproduction and mortality would have been much higher than they are today, at least in the West. Dogs who were prone to disease or infirmity, or carried other disadvantages, such as difficulty in whelping, would have left few offspring, and their lineages would eventually have died out.

As the modern world developed, so did the degree of deliberate breeding, for purposes that were increasingly diverse and narrow in definition. For example, further specialization within the existing range of sizes and shapes occurred in medieval Europe, where the importance of hunting to the new aristocracy led to the breeding of many specialist kinds of hound, each with its own local variations—deerhounds, wolfhounds, boarhounds, foxhounds, otterhounds, bloodhounds, greyhounds,



Medieval dogs

and spaniels, to name but a few, although these are not necessarily the direct ancestors of the breeds that bear the same names today.

The mtDNA of some modern breeds shows that their identity extends back in an unbroken line at least five hundred years, and possibly much longer. Some of these ancient breeds are oriental, including the shar-pei, Shiba Inu, chow chow, and Akita. Others, including the Afghan hound and saluki, have Middle Eastern origins. A third group (malamute and husky) are Arctic dogs, while an African breed, the basenji (recently confirmed from its Y-chromosome DNA as both unique and ancient), forms the fourth. Some of the North Scandinavian breeds, such as the Norwegian elkhound, have probably been derived from interbreeding wolves with dogs, several hundred and possibly as many as a few thousand years ago.

Speciality breeds may have originally had other uses besides the standard ones, such as tracking and hunting. Several types of dog, such as the chow chow and the fat Polynesian types, were developed specifi-

cally for food; others, such as the Manchurian long-haired types, were probably bred for their fur as well. Breeding dogs is not a particularly efficient way to obtain nourishment or something to wear, so we have to presume that there was always some social significance attached to these uses: Dog meat may have been prized as a delicacy, and dog fur may have carried a higher social cachet than the hide of hunted animals such as gazelle.

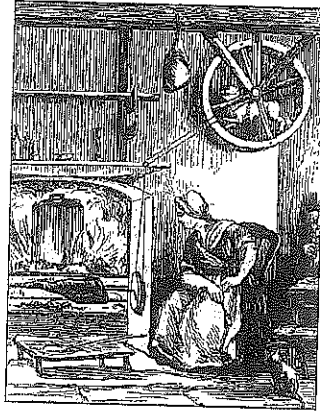
Whatever one may think of such uses for dogs, they are a testament to the dog's extreme adaptability to the twists and turns of human civilization. Dogs have been adapted, or have adapted themselves, to all kinds of roles, in a way unmatched by any other domestic animal, and such flexibility must lie at the heart of the enduring power of the human-canine relationship. Although today most dogs are valued primarily for their companionship, at least in the West, we must also remember that historically many dogs were kept first and foremost because they were useful. Some of these functions must have come and gone in just a few centuries; just a footnote to the dog's association with man, they are now almost forgotten (see the box titled "The Turnspete"). Others—such as hunting, shepherding, and guarding—persist today.

European breeding restrictions were comparatively lax at first and developed relatively late. The fact that the few genetically isolated "ancient" breeds come from such far-flung locations (and none from Europe) suggests that they are relics of dogs that were carried, by human migration, out of Asia and southeastern Europe and subsequently not interbred with more recent migrants, the most notable of which would have been the diverse types of dog developed in Europe in the Middle Ages and subsequently spread by colonialism. Such genetic isolation indicates a greater degree of human intervention in reproduction than for many other types of dog, although it is not possible to tell how much of this would have been achieved by selecting purebred partners for mating and how much by culling or simple neglect of accidentally crossbred puppies. By contrast, the DNA of modern dogs indicates that crossbreeding between different types of dog was commonplace in Europe and America. While much of this crossbreeding was probably accidental, historical records also indicate some deliberate breeding of unlikely combinations of types, just to see whether some useful new type might emerge.

The Turnspete

The sole purpose of this British "breed" of dog was to run in a mousewheel-like contraption, which, through a system of belts and pulleys, slowly turned a joint of meat roasting over an open fire. This apparatus was first mentioned in the mid-sixteenth century and had disappeared by the mid-nineteenth, replaced by more efficient ways of roasting meat without burning it. Actually, purely mechanical methods of turning spits had become available in the seventeenth century—Leonardo da Vinci had sketched one—so the continued use of dogs for this purpose for a further two hundred years may reflect not a strictly utilitarian consideration but a preference on the part of the British to use dogs wherever they could. The dogs were certainly given names—Fuddle, one of the turnspit dogs at the Popinjay Inn in Norwich, even had a poem written in his honor. On Sundays, it was apparently the custom to take them to church, where they would act as foot-warmers on cold winter days. Incidentally, there is no evidence that the Turnspete was ever a specific breed in the modern sense of a closed gene pool; short-legged and stocky, turnspit dogs were probably selected from a variety of terriers, including, according to one record, badger-hunting dogs. However, the one surviving specimen, a stuffed dog displayed at Abergavenny Museum in Wales, is more reminiscent of a dachshund.

Modern sensibilities would be offended by such a use of dogs today. Imagine how frustrated these dogs must have felt, endlessly running nowhere while the tantalizing aroma of roasting meat was all around them. Yet their continued use even when mechanical substitutes had become available could be explained by an affectionate attitude toward these dogged little workers, rather than simply a reluctance to embrace new technology. And don't we still give running-wheels to caged mice, hamsters, and gerbils on the grounds that they "need exercise"?



Aside from the few "ancient" breeds, crossbreeding of dogs continued apace in Europe and North America until the middle of the nineteenth century. The idea that a dog should be mated only with other identical dogs is a comparatively new one, dating back only about 150 years in Europe, the same notion then spreading rapidly to other countries. Nowadays, if a dog is to be registered as a particular breed, his or her parents, grandparents, and so on for many generations must also have been registered as the same breed—a restriction known as the "breed barrier." Although many mongrels and crossbred dogs continue to be born in the West, they are much less likely than pedigree dogs are to find homes and leave offspring of their own.

Pedigree breeding is the third phase of the transition from wolf to modern dog, each phase having been abetted by a different selective pressure. The first was the initial selection for tameness, from wolves that were already pre-adapted to scavenging from man. As we have seen, this process must have been essentially passive: The wolves that could tolerate interaction with man gradually isolated themselves reproductively from their wild cousins and became proto-dogs. In the second phase, deliberate selection by man for specific functions began to become a factor, through attempted isolation of one type of dog from another. However, this was rarely, and then only locally, the factor controlling which dogs had descendants and which did not, given that deliberate selection occurred as isolated exceptions against a background of some deliberate (and much accidental) interbreeding. By contrast, the third and most recent phase of the transition from wolf to dog has seen an explosion of deliberate selection: Dogs are mated with other, virtually identical dogs in an attempt to create "ideal" breeds—most of which are cherished for their appearance, not their functionality.

Domestication has been a long and complex process, and despite the self-evident differences between types of dog, every dog alive today is a product of this transition. What was once another one of the wild social canids—the grey wolf—has been altered radically, to the point that it has become its own unique animal. In the course of this change, the dog has shed many of its wolf-like attributes, so much so that there

is no reason to presume that the characteristics that define today's dogs are derived specifically from wolves; most of these are either products of domestication or general features of canids that predate the evolution of the grey wolf.

Whatever the selective pressures governing them, many of the characteristics that separate domestic dogs from the wild canids can be ascribed to changes in the rates at which the body and behavior mature. As noted earlier, dogs are in many respects similar to juvenile canids; although they grow into adults in the narrow sense that they become capable of reproducing, they remain immature in many other respects—a sort of arrested development that neatly accounts for the way they depend on their human owners for the whole of their lives.

Thus despite the differences between breeds, dogs are recognizably dogs—and not just so far as we humans are concerned. Dogs evidently recognize other dogs as such, even when the disparity in size and shape between them makes it seem implausible that they could. Dogs of all breeds, or almost all, must therefore retain some common social repertoire, enabling them both to recognize one another as dogs and to engage in at least rudimentary communication. The question, then, is to what extent are the dog's social capabilities a product of domestication, and what has been inherited directly from the wolf—or possibly from even further back in the canids' evolutionary history?

CHAPTER 3

Why Dogs Were—Unfortunately— Turned Back into Wolves

Today's dogs are clearly not wolves on the outside, but their behavior is often interpreted as if they were still wolves on the inside. Indeed, now that we know for sure that the wolf is the dog's only ancestor, it seems impossible to avoid such comparisons. The idea that dogs retain most of the wolf's essential character is not only out-of-date but also reflects some deep-seated misconceptions about wolf behavior that science is only now beginning to overturn. Despite these holes in the dog-wolf theory, however, it is still widely used to inform dog training, with unfortunate consequences for dog and owner alike.

For over fifty years, the concept of dog as a wolf dressed up in a cute package dominated dog training and management, with results that were—to say the least—mixed. Some bits of advice that logically flowed from this misconception are harmless, but others, if applied rigorously, can damage the bond between dog and owner. Moreover, equating dogs with wolves allows trainers and owners to justify physical punishment of the dog, by the mistaken analogy that wolf parents achieve control of their offspring through aggression.

The concept that dog behavior is little changed from that of wolves also does not jibe with the self-evident friendliness of the large majority of dogs. Most dogs love meeting other dogs, and most love people. This may seem a blindingly obvious statement, but from a biologist's perspective it's one that demands explanation. After all, neighboring cats often

6. See Dr. David Mech's illuminating article on the new conception of wolf biology at <http://www.npwr.usgs.gov/resource/mammals/alstat/alpst.htm> (accessed on August 25, 2010).

7. There is some controversy about just how many kinds of wolf occur in the wild in North America today, but only the grey wolf is sufficiently widespread for its social behavior to have been studied. The number of types of grey wolf on the American continent is constantly being reappraised; there may be five (Northwestern, Plains, Eastern, Mexican, and Arctic), but I've referred to the first two generically as the "timber" wolf. A sixth, the red wolf, is often considered a separate species. Although it is sometimes called the "Texas" red wolf, in the early part of the last century its range centered on North Carolina. Some people maintain that it is a unique and endangered animal, and a great deal of effort is being put into captive breeding and conservation. Bear in mind, however, that the red wolf looks suspiciously like a mixture between a grey wolf and a coyote—and its DNA appears to back the idea that it is a hybrid. Wolves and coyotes can mate and produce offspring, certainly in zoos and probably also in the wild; the Eastern or Algonquin wolf that occurs in Ontario and Quebec is probably such a hybrid, although it has also been posited as a third true species of wolf. To further confuse the picture, the DNA of red wolves suggests that they may have hybridized with coyotes for a second time in the nineteenth century, as changing agriculture and ranching practices began to favor coyotes over wolves in the southeastern United States. And given that many apparently purebred coyotes also contain wolf (as well as domestic dog) DNA, interbreeding between wolves and coyotes appears to have been going on for thousands of years—leading to the coining of the tongue-in-cheek term "*Canis soupus*" to describe coyote, eastern wolf, and red wolf alike.

8. As is most likely the story for the domestic cat; see *Science* 296 (April 5, 2002): 15 for a summary of my research group's study into this.

Chapter 2

1. The members of this international team, led by Carles Vilà at the University of California in Los Angeles, published their findings in volume 276 of the journal *Science* (June 13, 1997, pp. 1687–1689).

2. With the notable exception of the Egyptians, who mummified a wide range of animals, including vast numbers of domestic cats.

3. Indeed, such long-distance commutes were rare until comparatively recently, when European dogs were introduced as part of colonialization. However, it turns out that in most areas, pet dogs who escape, as well as hybrids between pets and local dogs, tend not to prosper; evidently they are less effec-

tive than local street dogs at exploiting local conditions. The DNA of many local populations is thus largely preserved in its original form.

4. See Peter Savolainen, Ya-ping Zhang, Jing Luo, Joakim Lundeberg, and Thomas Leitner, "Genetic evidence for an East Asian origin of domestic dogs," *Science* 298 (November 22, 2002): 1610–1613; and Adam Boyko et al., "Complex population structure in African village dogs and its implications for inferring dog domestication history," *Proceedings of the National Academy of Sciences* (August 19, 2009): 13903–13908.

5. See, for example, Nicholas Wade, "New Finding Puts Origins of Dogs in Middle East," *New York Times*, March 18, 2010.

6. More gruesome still is the Zoroastrian practice of allowing dogs, regarded as sacred animals, to dispose of human corpses.

7. This scenario, conveniently, would also explain why the mitochondrial DNA sequences of dogs and wolves appear to have diverged at an unfeasibly early date. The divergence would have to predate the genetic changes that split the "normal" wolves from the "socializable" wolves, because today there are no survivors of the latter, apart from the few that changed into dogs. Matings between "socializable" females and "normal" males might well have continued for many millennia after the split, but would be undetectable in the (maternally inherited) mtDNA of modern dogs.

8. Ludmilla Trut, "Early canid domestication: The farm-fox experiment," *American Scientist* 87 (1999): 160–169.

9. A few anthropologists have toyed with the rather romantic notion of man-wolf coevolution, suggesting that wolves taught us how to hunt in groups, even how to form complex societies. However, it seems highly unlikely that any two-legged human could ever have "adopted" the wolf's lifestyle. The wolves would have outrun him before he had time to blink. When he finally caught up with them after they had made their kill, why would they have let him share it with them? The primitive spears and knives that he had at his disposal would hardly have been adequate to drive off a pack of hungry wolves. Moreover, depictions of men hunting with dogs do not feature in cave paintings until five thousand to six thousand years ago, almost halfway through the history of domestic dogs as revealed by the archaeological record. It is certainly true that wolves feature prominently in the symbolism of recent hunter-gatherer societies, but myths do not recapitulate origins; indeed, they merely invent a framework for explaining the uncontrollable.

Chapter 3

1. Here I am indebted to biologist Dr. Sunil Kumar Pal and his colleagues, who have been studying the urban feral dogs of West Bengal for over ten years.