

Dog Sense

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



John Bradshaw

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*To Alexis
(1970–1984), a Real Dog*



Ginger

Preface

The first dog I became attached to was one I never met. He was my grandfather's Cairn terrier, Ginger—typical long-legged Cairn of the early twentieth century, only a few generations removed from his working forebears. Ginger had died long before I was born, and I grew up in a pet-free household; stories about Ginger were, for a while, the nearest I came to having a dog of my own.

My grandfather, an architect, liked to walk. He walked to and from his office in the industrial city of Bradford and to and from the churches and mill buildings he specialized in; but especially he walked for recreation, whether in the Yorkshire moors or in the Lake District or in Snowdonia. Whenever he could

he took Ginger with him. The family maintained that Ginger, who was taller than he should have been for his breed, had acquired his longer-than-average legs through all this exercise. Actually, in the photograph I have of him he looks quite typical of his breed, and not unlike the Cairn chosen to play Toto in the 1939 movie *The Wizard of Oz*. It was not until much later on, when I became professionally interested in pedigree dogs, that I was struck by how much the breed had changed over the intervening decades, including becoming significantly shorter in the leg. I doubt many modern Cairns would enjoy the amount of exercise that my grandfather evidently relished, although Cairns today are less prone to inherited diseases than many other breeds are.

Ginger was a genuine Yorkshire “character,” and the family had a fund of stories about him, but what amazed me the most was the freedom he had been given, even though he lived within sight of the city center. Every lunchtime, when my grandfather was at work, Ginger was allowed to take himself for a walk around the neighborhood. Apparently he had a routine. First he would cross the road into Lister Park, where he would sniff lampposts, interact with other dogs, and, in summer, try to persuade the occupants of the park benches to part with one of their sandwiches. Then he would cross the tram tracks on Manningham Lane and amble to the rear of the fish and chip shop, where a scratch at the back door would usually elicit a handful of scraps of batter and some misshapen chips. Then he usually headed straight for home, which involved crossing a busy junction. Here, according to family legend, there was usually a policeman, directing the lunchtime traffic, *who would solemnly stop the cars to allow Ginger safe passage across*.

I’ve not been to Bradford for many years, but if other cities are anything to go by, Lister Park is probably now ringed with poop-bins, most of the dogs walked there are at the end of a leash, and the Bradford dogwardens are called out to catch any dog that routinely roams the park, let alone the nearby streets. The trams are long gone, of course, and traffic lights have replaced policemen on point duty, but I doubt that one of today’s body-armored community support officers would dare to stop a car to allow a small brown terrier to cross the road, even if he or she wanted to.

Seventy-odd years have passed since Ginger was allowed to roam the streets and charm his way into the affections of everyone he met, including the local law enforcement officers. During that same period, almost unnoticed, there have been enormous changes in society’s attitudes toward man’s best friend.

Such attitudes were still quite relaxed when I was growing up in 1970s’ Britain. My first dog, a Labrador/Jack Russell cross named Alexis, was also a roamer, although he was more interested in the opposite sex than in lunchtime snacks. Despite our best efforts to keep him in sight he would manage to get away once in a while, and so, unlike Ginger, he did end up in police kennels a few times (in those days the police in the UK still had responsibility for stray dogs). But no one seemed to mind much. Nowadays such tolerance of dogs and their ways is hard to find, especially in cities, and dog ownership is showing signs of retreating to its roots in the countryside. After many millennia in which the dog has been man’s closest animal companion, cats are taking over as the most popular pet in many countries, including the United States. Why is this happening?

First of all, dogs are expected to be much better controlled than they used to be. There has never been a shortage of experts telling owners how to take charge of their dogs. When I took on my second dog, a Labrador/Airedale terrier cross named Ivan, I was determined that he would be better behaved than Alexis. I decided I ought to find out something about training but was then shocked to discover the approach adopted by the trainers of the day, such as Barbara Woodhouse, who seemed to see the dog as something that needed to be dominated at all times. This simply didn’t make sense to me—the whole point of having dogs as pets was for them to become friends, not slaves. As I researched, I found that this approach to training had stemmed from the ideas of Colonel Konrad Most, a police officer and a pioneer

in dog training who, more than one hundred years ago, had decided that a man could control a dog only if the dog was convinced that the man was physically superior. He derived this idea from contemporary biologists' accounts of wild wolf packs, which at that time were considered to be controlled by one individual who ruled the others through fear. Biology, by then my profession, seemed to be at odds with my gut feeling as to how my relationship with my dogs ought to work.

To my relief, this dilemma has resolved itself over the past decade. The wolf pack, always the touchstone for the interpretation of dog behavior, is now known to be a harmonious family group except when human intervention renders it dysfunctional. As a consequence, the most enlightened modern trainers have largely abandoned the use of punishment, relying on reward-based methods that have their roots in comparative psychology. Yet for some reason, old-school trainers continue to dominate the media—largely, I suspect, because their confrontational methods make for a more exciting spectacle.

While a more sympathetic understanding of dogs' minds is being applied to training, albeit patchily, their physical health has been progressively undermined. As more and more demands have been placed on the family dog in terms of hygiene, control, and behavior, the breeding of dogs who might be suited for this ever more demanding niche has been left in the hands of enthusiasts whose primary goal is to produce dogs that look good. Ginger, although he came from pedigree stock, was only ten or so generations away from Scottish and Irish rat-catchers of no particular breeding and, as a result, led a long and healthy life. Now, the Cairn terrier is in danger of becoming the victim of inbreeding for the show-ring, plagued by over a dozen hereditary complaints such as the exotically named but apparently excruciatingly painful Legg-Calvé-Perthes disease.

Biologists now know far more about what really makes dogs tick than they did even a decade ago, but this new understanding has been slow to percolate through to owners and, indeed, has not yet made enough of a difference to the lives of the dogs themselves. Having studied the behavior of dogs for over twenty years, as well as enjoying their company, I felt it was time that someone stood up for dogdom: not the caricature of the wolf in a dog suit, ready to dominate his unsuspecting owner at the first sign of weakness, not the trophy animal who collects rosettes and kudos for her breeder, but the real dog, the pet who just wants to be a member of the family and enjoy life.

Acknowledgments

I've spent the best part of thirty years studying dog behavior, first at the Waltham Centre for Pet Nutrition, then at the University of Southampton, and finally at the University of Bristol's Anthrozoology Institute. Some of what I've learned about dogs has come from direct observation, especially in the early days, but much has been informed by collaborations and discussions with many, many colleagues and graduate students. The original research described in this book owes much to them, though of course I take full responsibility for the interpretations presented here. In roughly chronological order, they are: Christopher Thorne, David Macdonald, Stephan Natynczuk, Benjamin Hart, Sarah Brown, Ian Robinson, Helen Norton, Stephen Wickens, Amanda Lea, Sarah Whitehead, Gwen Bailey, James Serpell, Rory Putman, Annie Nightingale, Claire Hoskin, Robert Hubrecht, Claire Guest, Deborah Wells, Elizabeth Kershaw, Ann McBride, Sarah Heath, Justine McPherson, David Appleby, Barbara Schöning, Emily Blackwell, Jolanda Pluijmakers, Theresa Barlow, Helen Almey, Elly Hiby, Sara Jackson, Elizabeth Paul, Nicky Robertson, Claire Cooke, Samantha Gaines, Anne Pullen, and Carri Westgarth—and many more too numerous to list. Two deserve a special mention: Nicola Rooney, who, in addition to producing consistently world-class research on dog behavior and welfare for the past dozen years, has been the social life and soul of my research group; and Rachel Casey—arguably the UK's leading veterinary behaviorist and unarguably an indefatigable champion of evidence-based dog training and behavioral therapy. My thanks also to the University of Bristol's School of Veterinary Medicine, and especially professors Christine Nicol and Mike Mendl, and Dr. David Main, for nurturing the Anthrozoology Institute and its research.

Our research has relied on the cooperation of literally thousands of volunteer dog owners and their dogs, to whom I express my gratitude. Also, much of our research would have been impossible without the facilities and cooperation offered by the UK's leading animal rehoming charities: Dogs Trust, the Blue Cross, and the RSPCA.

There are many other academics and dog experts I've met only briefly, but whose published work has been an enormous inspiration. Many I have been able to mention specifically in the endnotes. Like any branch of science, the systematic study of dog behavior embraces many approaches and opinions, and sometimes these can be expressed quite forcefully. Yet there is a crucial difference between canine science and canine folklore—scientists are ready to evaluate evidence gathered by others, and to change their opinions if these evaluations indicate that they should. Canine scientists are not in the business of peddling opinion as if it were fact; they contribute to a body of knowledge that, while never completely settled, continually gains strength from ongoing discussion among numerous experts. I am grateful to them all, even those whose views are now largely discredited or unfashionable. Science advances through the replacement of one hypothesis by another that better fits the data; without the first to act as a stimulus to creative thought, the second might never have been conceived.

Condensing all of this science into a book of reasonable length has not been easy, but my agent Patricia Walsh, and Lara Heimert, my editor at Basic Books, have taught me a great deal about how to aim for a wider audience than the academic community that I have mainly written for in the past.

I've been amazed and delighted by how my old friend Alan Peters' drawings have brought my descriptions of dogs and canids to life. He's not only a wonderful artist but also a skillful gundog trainer (and falconer) and so was able to bring to the task a lifetime's experience of how dogs move and interact.

Finally, to my family. My wife, Nicky, has been an unwavering source of support throughout all the years of my academic career, and especially during the year or so it's taken me to write this book—

cannot thank her enough. Thanks also to my brother Jeremy for giving me the encouragement to start the book in the first place. Netty, Emma, and Pete, thank you for refreshing my brain with music; Tom and J likewise but with microbrews, Rioja, and cricket.

Introduction

The dog has been our faithful companion for tens of thousands of years. Today, dogs live alongside humans all across the globe, often as an integral part of our families. To many people, a world without dogs is unthinkable.

And yet dogs today unwittingly find themselves on the verge of a crisis, struggling to keep up with the ever-increasing pace of change in human society. Until just over a hundred years ago, most dogs worked for their living. Each of the breeds or types had become well suited, over thousands of years and corresponding number of generations, to the task for which they were bred. First and foremost, dogs were tools. Their agility, quick thinking, keen senses, and unparalleled ability to communicate with humans suited them to an extraordinary diversity of tasks—hunting, herding, guarding, and many others, each an important component of the economy. In short, dogs had to earn their keep; apart from the few lapdogs who were the playthings of the very rich, the company that dogs provided would have been incidental, rewarding, but not their *raison d'être*. Then, a few dozen generations ago, everything began to change—and these changes are still gathering pace today.

Indeed, an ever-increasing proportion of dogs are never expected to work at all; their sole function is to be family pets. Although many working types have successfully adapted, others were and still are poorly suited to this new role, so it is perhaps surprising that none of the breeds that are most popular as family pets have been specifically and exclusively designed as such. Thus far, dogs have done their best to adjust to the many changes and restrictions we have imposed upon them—in particular, our expectation that they will be companionable when we need them to be and unobtrusive when we don't. However, the cracks inherent in this compromise are beginning to widen. As human society continues to change and the planet becomes ever more crowded, there are signs that the popularity of dogs as pets has peaked and that their adaptation to yet another lifestyle may be a struggle—especially in urban environments. After all, dogs, as living beings, cannot be reengineered every decade or so as if they were computers or cars. In the past, when dogs' functions were mostly rural, it was accepted that they were intrinsically messy and needed to be managed on their own terms. Today, by contrast, many pet dogs live in circumscribed, urban environments and are expected to be simultaneously better behaved than the average human child and more self-reliant as adults. As if these new obligations were not enough, many dogs still manifest the adaptations that suited them for their original functions—traits that we now demand they cast away as if they had never existed. The collie who herds sheep is the shepherd's best friend; the pet collie who tries to herd children and chases bicycles is an owner's nightmare. The new, unrealistic standards to which many humans hold their dogs have arisen from one of several fundamental misconceptions about what dogs are and what they have been designed to do. We must come to better understand their needs and the nature of their niche in human society if their niche is not to diminish.

Our rapidly changing expectations are not the only challenge that dogs face today. The ways in which we now control their reproduction also represent a major challenge to their well-being. For much of human history, dogs were bred to suit the roles that humankind assigned to them—but whether their task was herding, retrieving, guarding, or hauling, dogs' stability and functionality were considered far more important than their type or appearance. In the late nineteenth century, however, dogs were grouped into self-contained breeds, reproductively isolated from one another, and each assigned a single ideal appearance, or "standard," by breed societies. For many dogs this rigid categorization has not worked out well; rather, it has worked against their need to adapt into their new primary role as companions. Each

breeder strives not to breed the perfect pet but to produce the perfect-looking dog who will succeed in the show-ring. These winning dogs are considered prized stock and make a hugely disproportionate genetic contribution to the next generation—resulting in “pure” breeds whose idealized appearance belies their deteriorated health. In the 1950s, most breeds still had a healthy range of genetic variation; by 2000, on some twenty to twenty-five generations later, many had been inbred to the point where hundreds of genetically based deformities, diseases, and disadvantages had emerged, potentially compromising the welfare of every purebred dog. In the UK, the growing rift between dog breeders and those concerned with dogs’ welfare finally became public in 2008, resulting in the withdrawal of the humane charities—and subsequently that of BBC Television, the event’s broadcaster—from Crufts, the country’s national dog show. While such protests are a start, the dogs themselves will not feel any benefit until the problems brought about by excessive inbreeding have been reversed and dogs are bred with their health and role in society, not their looks, in mind.

Ultimately, people will have to change their attitudes if the dog’s lot is to improve. So far, however, neither the experts nor the average owner have had their preconceived notions challenged by the wealth of new science that is emerging about dogs. Much of the public debate thus far, whether about the merits of outbreeding versus inbreeding or the effectiveness of training methods, has amounted to little more than the statement and restatement of entrenched opinions. This is where scientific understanding becomes essential, for it can tell us what dogs are *really* like and what their needs *really* amount to.

Science is an essential tool for understanding dogs, but the contributions of canine science to dog welfare have, unfortunately, been somewhat mixed. Canine science, which originated in the 1950s, set out to provide a rational perspective on what it’s like to be a dog—a perspective ostensibly more objective than the traditional human-centered or anthropomorphic view of their natures. Despite the attempt at detachment, however, canine scientists have occasionally misunderstood—and even given others the license to cause injury to—the very animals whose nature they have endeavored to reveal.

Science has, unwittingly, done the most damage to dogs by applying the comparative zoology approach to studies of dog behavior. Comparative zoology is a well-established and generally valuable way of understanding the behavior and adaptations of one species through comparisons with those of another. Species that are closely related but have different lifestyles can often be better understood through comparative zoology, because differences in the way they look and behave mirror those changes in lifestyle; so, too, can those species that have come to have similar lives but are genetically unrelated. This method has been highly successful in helping to disentangle the mechanisms of evolution in general, especially now that similarities and differences in behavior can be compared with differences between each species’ DNA, so as to pinpoint the genetic basis of behavior.

Yet although the applications of comparative zoology are usually benign, it has done considerable harm to dogs, as one expert after another has interpreted their behavior as if they were, under the surface, little altered from that of their ancestor, the wolf. Wolves, which have generally been portrayed as vicious animals, constantly striving for dominance over every other member of their own kind, have been held up as the only credible model for understanding the behavior of dogs.¹ This supposition leads inevitably to the misconception that every dog is constantly trying to control its owner—unless its owner is relentless in keeping it in check. The conflation of dog and wolf behavior is still widely promoted in books and television programs, but recent research on both dogs and wolves has shown not only that it is simply unfounded but also that dogs who do come into conflict with their owners are usually motivated by anxiety, not a surfeit of ambition. Since this fundamental misunderstanding has crept into almost every theory of dog behavior, it will be the first to be addressed in this book.

Despite the misapplication of comparative zoology, more recent scientific discoveries could, if applied

properly, benefit dogs considerably. Although canine science went into eclipse in the 1970s and '80s, the 1990s saw the field's resurgence, which has continued to the present day. After nearly fifty years almost total neglect, this extraordinary uplift in scientific interest in the domestic dog has been driven partly by the increasing role that dogs play in detecting substances such as explosives, drugs, and other illicit substances (which they still sniff out more effectively than any machine) and the attendant realization that humans need to better understand how dogs perform these tasks. It has also been due to the shift in attention from the chimpanzee to the domestic dog on the part of a few primatologists who have attempted to gain fresh insights into the way that animal and human minds work. A further contribution has come from veterinarians and other clinicians who wish to improve the therapies available for treating dogs with behavioral disorders. Finally, it should not be forgotten that many biologists are dog lovers too. Once the professional stigma of working on so-called artificial animals has been overcome, such scientists are often keen to apply their skills to improving dogs' lives.

By further pulling back the curtain on dogs' inner lives, the new school of canine science has the potential to provide everyday dog owners with new ways of thinking about—and relating to—their pets. Thanks to the efforts of this new community of scientists, we now have a vastly improved understanding of how dogs' minds work—specifically, how dogs gather and interpret information about the world around them, and how they react emotionally to varying situations. Some of this research has revealed startling differences between dogs and people, suggesting that it is both desirable and possible for dog owners to “think dog” rather than simply assuming that whatever they themselves are sensing and feeling their dog must be sensing and feeling too.

Although the new science about dog behavior has the potential to put the dog's role in human society back on track, little of the research has been made available outside of obscure academic texts until now. In this book, I attempt to translate for the general readers—and dog lovers—the exciting new developments in canine science. Doing so requires me to overturn a great deal of conventional wisdom about dogs and how we should interact with them. In the first half of the book, I show that the most up-to-date account of the dog's origins, while confirming that the wolf is indeed the dog's only ancestor, reveals a very different image of dog's nature than seemed to be the case only two decades ago. Dogs may be constructed from wolf DNA, but this does not mean that they are compelled to behave or think like wolves; indeed, domestication has changed dogs' minds and behaviors to the point where such comparisons can be a hindrance, rather than an aid, to any genuine understanding of our pets.

The new science of dog behavior has dramatic implications for humans—and for our choice of the best and most humane ways to train our dogs. A word of caution here, though: This book is not a training manual. Rather, its purpose is to show where modern ideas about dog training have come from, so that owners themselves can effectively evaluate whether the training manuals or trainers they have chosen really know what they are talking about.

After revising the story of the dog's origins, I will explore what might loosely be referred to as dog “brainpower.” Scientists have recently turned their attention to the kinds of beliefs that owners have about their dogs' emotional and intellectual capabilities, and their findings are demonstrating how accurate—but also how mistaken—these beliefs can be. It's an integral aspect of human nature to attribute feelings not just to animals but also to inanimate objects—to speak, for example, of “an angry sky” or “the cruel sea”—and yet, until a few decades ago, it was anybody's guess as to what emotions different animals might have. Many scientists, moreover, used to regard emotions as simply too subjective to be accessible to serious study. While animal intelligence has been studied for more than a hundred years, hardly anyone considered dogs worthy of study until perhaps the end of the twentieth century. Since then, research has significantly changed the ways in which we think about dogs' minds. The new canine science reveals the

dogs are both smarter and dumber than we think they are. For example, they have an almost uncanny ability to guess what humans are about to do, because of their extreme sensitivity to our body language, but they are also trapped in the moment, incapable of projecting the consequences of their actions backward or forward in time. If owners were able to appreciate their dogs' intelligence and emotional life for what it actually is, rather than for what they imagine it to be, then dogs would not just be better understood—they'd be better treated as well.

Just as canine science can inform human attitudes about dogs' minds, it can also tell us how dogs experience and interpret the world around them. Physically speaking, a dog and his or her owner live in the same house, visit the same park together for exercise, travel in the same car, meet the same friends and acquaintances. However, the types of information arriving at the dog's brain and the owner's brain in each of those situations are profoundly different. We are visual creatures; dogs primarily rely on their sense of smell. We refer to high-pitched noises that we can't hear (e.g., the squeaking of bats) as "ultrasound," but dogs would, if they could, scoff at our inability to hear such sounds, which they pick up perfectly. To fully appreciate our dogs' world, we need science to tell us what they can and can't detect, what they find pleasant and what they would object to if they could. For example, I don't suppose your dog has ever been bothered by the colors you've picked out to decorate your house, but his or her delicate nose would very likely be insulted by the odor of the drying paint.

Although our lack of understanding of dogs' nature often compromises their well-being, it pales in insignificance beside the problems we have generated for pedigree dogs through excessive inbreeding. Rigid breed standards encourage breeders to eliminate all traits that don't fit the "perfect" type. In theory, this should allow breeders to select for traits that would create healthy and well-adjusted, if rather uniform, animals—but in practice it has led to the appearance of an extensive range of inherited defects that compromise the welfare of large numbers of dogs in many, many breeds. Science, thankfully, can help us to get dog breeding back on track. While it is beyond the scope of this book to provide a detailed manual of canine genetics, the penultimate chapter addresses the underlying principles that breeders should follow, emphasizing what it is about pedigree breeding that directly affects dogs' well-being.

In the final chapters of the book, I look at how science can help dogs to adjust to twenty-first-century life. Currently, most of the attention given to dogs' breeding has focused on endowing them with superficial, rather than practical, traits. Many pet dogs are essentially breeders' rejects, deemed unlikely to reach the perfection demanded by the breed standard; puppies who look as though they're never going to become champions in the show-ring are the ones who become pets. Surely the needs of the pet dog deserve more attention than that? As dog owners and dog lovers, we need to think constructively about how to breed dogs whose primary purpose is not to herd sheep, retrieve game, or win prizes at dog shows, but, rather, to be rewarding, obedient, healthy, happy family pets.

In writing this book, I have tried to promote a greater understanding and appreciation of the special place that dogs hold in human society. If these aims can be achieved, they should go a long way toward sustaining and reinforcing our relationship with our beloved companions as the next decades unfold.

CHAPTER 1

Where Dogs Came From

“The wolf in your living room”—a powerful image that reminds dog owners that their trusted companion is, under the skin, an animal, not a person. Dogs are indeed wolves, at least as far as their DNA is concerned; the two animals share 99.96 percent of their genes. Following the same logic, you might just as well say that wolves are dogs—but, surprisingly, no one does. Wolves are generally portrayed as wild, ancestral, and primeval, whereas dogs tend to be cast in the role of the wolf’s artificial, controlled, and subservient derivatives. Yet dogs, in terms of sheer numbers, are far more successful in the modern world than wolves are. So, what do we gain from knowing that wolves and dogs share a common ancestor? Many books, articles, and TV programs about dog behavior have claimed that understanding the wolf is the key to understanding the domestic dog. I disagree. My view is that the key to understanding the domestic dog is, first and foremost, to understand the domestic dog, and it’s a view I share with an increasing number of scientists worldwide. By analyzing the dog as its own animal rather than as a lesser version of the wolf, we have the opportunity to understand it—and refine our dealings with it—as never before.

To be sure, it’s undeniable that dogs share many of their basic characteristics with other members of the Dog family (the Canidae) of which the wolf is a part. Dogs evolved from canids, and they owe such qualities as their basic anatomy, their refined sense of smell, their ability to retrieve, and their capacity to form lasting social bonds to this evolution. To some extent, then, comparing dogs to their wild ancestors can be illuminating—but when the wolf is taken as the only available point of reference, our understanding of dogs suffers.

At the most fundamental level, dogs are distinguished by the fact that, unlike wolves or other canids, they have adapted to live alongside human beings, the result of the process of domestication. As dogs have been altered by domestication, many of the subtleties and sophistications of wolf behavior appear to have been stripped away, leaving an animal that is still recognizably a canid but no longer a wolf. Domestication has altered the dog considerably, more than any other species. It’s self-evident that dogs come in a wide range of shapes and sizes; indeed, there’s more size variation among domestic dogs than in the whole of the rest of the Dog family put together. Yet this is by no means the only profound effect of domestication. Perhaps the most important one, for both us and our dogs, is their ability to bond with and understand us, to an extent that no other animal can match. Understanding what has happened during domestication is therefore a key element in understanding the dog.

To understand the domestic dog fully, we need to look beyond the process of domestication—beyond even the wolf—to examine the dog’s entire history. We need to know where the dog came from and what all its ancestors were like—not just its closest living relative, the wolf. Of course, it is ultimately impossible for us to know precisely how the domestic dog’s ancestors behaved, whether we are examining its immediate forebears (wolves that lived more than ten thousand years ago) or its most distant ancestors (social canids, the precursors of the wolf, in the Pliocene era several million years ago). They are all extinct. We can, however, get some idea of how they might have behaved by examining the range of behavior that is characteristic of today’s social canids. Indeed, a detailed examination of the behavior of those species would not only shed light onto the dog’s earliest ancestors but also help

work out why it was that, apart from the wolf, none of the canids were successfully and permanently domesticated.

DNA analysis leaves no doubt that the dog is descended only (or at least almost entirely) from the grey wolf, *Canis lupus*. The first comprehensive sequencing of the maternal DNA of dogs, wolves, coyotes and jackals, published in 1997, produced no evidence that dogs had ancestors in any species other than the grey wolf.¹ None of the dozens of investigations performed since then have contradicted this, however, there is still a relative lack of data on paternal DNA, which is more difficult to analyze, so it is still possible that a few types of dog could claim descent from other canids through their paternal line.

Genetically, dogs and wolves have a great deal in common—but the mere fact that two species have considerable overlap in their DNA doesn't mean that their behavior will be the same. Indeed, many animals with similar DNA are drastically different from one another, especially in terms of behavior. We know this thanks to the DNA “revolution,” which has led to the sequencing of the genomes of humans, canines, felines, and an increasing number of other species. Many of these sequences exhibit a remarkable degree of similarity. For example, your DNA and your dog's are identical for about 25 percent of the length, which is perhaps not surprising given that you are both mammals; roughly the same 25 percent is also found in mice. The other 75 percent accounts for why dogs, mice, and people look—and behave—very differently from one another.

Species that are much more closely related to one another than we are to dogs can share almost the entire DNA sequences, and it's tempting to assume that they must therefore be restricted to the same range of behavior. But DNA doesn't control behavior directly; rather, it specifies the structure of proteins and other constituents of cells, such that a tiny change in DNA can lead to a huge change in behavior. For example, there is no “blueprint” for the brain; each nerve cell in the brain emerges out of interactions between thousands of DNA sequences. A change in one “letter” in those sequences could have a tremendous effect on the way the brain functions, or none at all—we simply don't know enough yet about how DNA and behavior interact. Take two closely related apes: the chimpanzee and the bonobo. Common chimps share 99.6 percent of their DNA with bonobos, and yet the social behavior of these two kinds of great ape couldn't be more different. Common chimps are omnivorous, often hunting other kinds of monkey, and their social groups are based on coalitions between males, who are highly aggressive toward outsiders and may even murder them if they get the chance. Bonobos, on the other hand, are vegetarians, live in societies centered on groups of related females, rarely show aggression, and have never been seen to murder in the wild. Genetically almost identical, the two species are vastly different in behavior.

Like bonobos and chimpanzees, dogs and grey wolves share most of their DNA—but there seems little reason to presume that, based on this fact, they must inevitably share the same social systems as well. In fact, domestication appears to have dissolved away much of the detail of wolf-specific behavior in dogs, leaving them with a behavioral repertoire that has much in common with that of slightly more distant related species, such as the coyote *Canis latrans*, and even some more distant relatives in the same family, such as the golden jackal *Canis aureus*.

Even to early biologists, the differences between dogs' behavior and that of wolves were obvious. Many of these differences are manifested socially: Dogs, for instance, are clearly not pack animals (although they do occasionally form groups), and they are much more adept than wolves at forming relationships with people. Over the years, many eminent biologists, including Nobel Prize winner Konrad Lorenz and even Charles Darwin himself, have been struck by the flexibility of the dog's behavior as well

as by the enormous size difference between the smallest and largest breeds. Both suggested that domestic dogs must be some kind of hybrid between two or even several of the canids. Lorenz, in his charming book *Man Meets Dog*, was convinced that wolves were far too independent in nature to explain the indiscriminate friendliness shown by many dogs, and proposed that most of the breeds that had originated in Europe were predominantly jackal in origin. He later retracted this idea, having realized that there was no evidence for spontaneous crossbreeding between dogs and jackals (as readily happens between dogs and wolves) and that the details of jackal behavior didn't fit that of the dogs (the jackal's howl, for example, is nothing like any dog's).

Despite these scientists' best efforts to determine why dogs are so different from wolves in their behavior, the puzzle was not resolved and remains largely unanswered to this day. Yet perhaps some clues can be gathered if we look further back in evolutionary time, thinking of our domestic dog as a product not of one species, the grey wolf, but of a whole family, the Canidae (also referred to as the Dog family, noted above, but hereafter referred to as canids to avoid confusion with the domestic dog). Many of the canid species have sophisticated social lives, which—when they overlap with those of dogs—can potentially shed light on the origins of dog behavior; coyotes, for instance, are much more promiscuous than wolves, a characteristic shared with dogs. Although the behavioral traits of other canids are not as well understood or well publicized as those of the grey wolf, they nevertheless have a great deal to tell about when—and how—dog behavior may have originated.

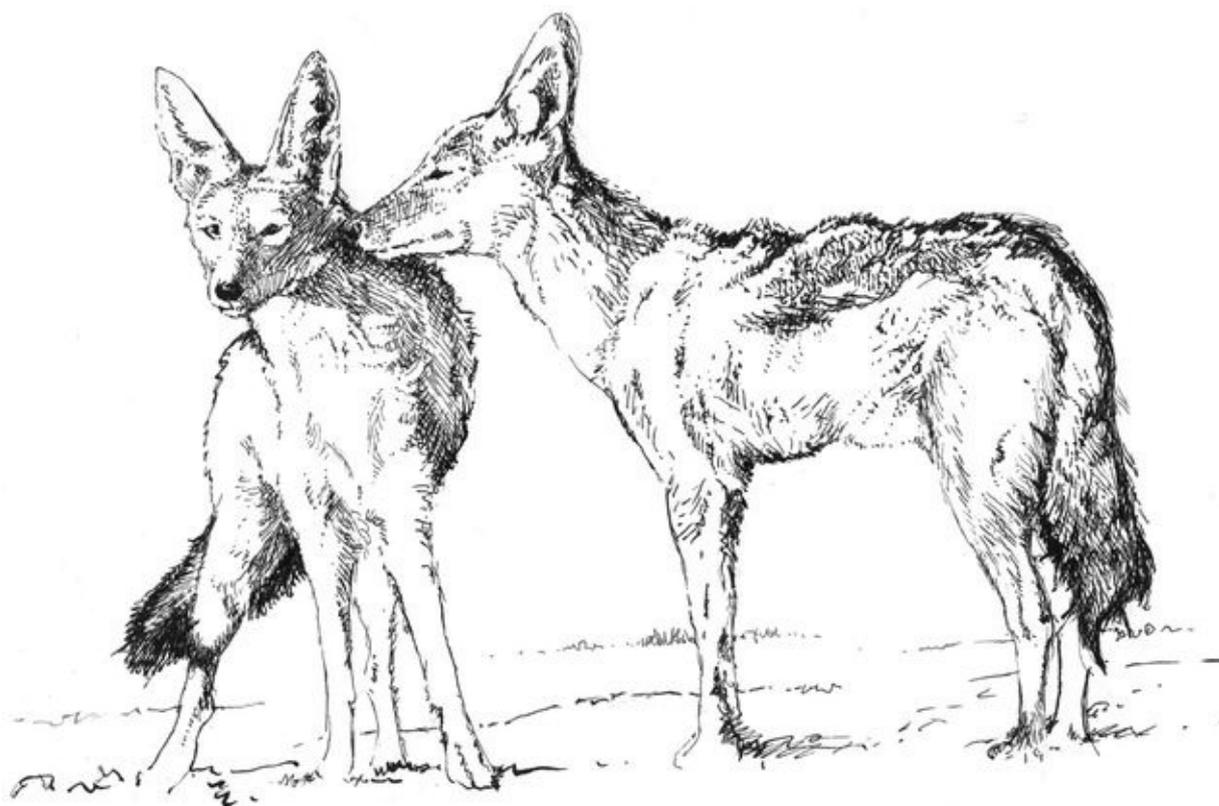
Tracing the canids back to their origins reveals that their social intelligence was likely one of the earliest traits that set dogs' ancient ancestors apart. Canids probably first evolved some 6 million years ago in North America, where they eventually replaced another type of dog-like mammal, the borophagine. This was a large, hyena-like animal that specialized in scavenging and had massive bone-crushing jaws to match. The original canids, which probably looked more like foxes than dogs, must have been little Davids to the cumbersome borophagine Goliaths, outcompeting them in speed, cunning, and intelligence, and ultimately helping to drive them to extinction. If we then fast-forward a mere 1.5 million years, we find that the surviving canids had spread all over the world and split into several types, one of which was the ancestor of today's dogs, wolves, and jackals—collectively referred to as *Canis*.² Subsequent further diversification produced three strands of evolution, any one of which could potentially have culminated in a domestic animal, for there is nothing in the behavior of any of the canid lineages that suggest that they could not have produced an animal that was suitable for domestication. Indeed, it is likely that at least two of the three did produce domestic animals and entirely possible that the wolf was not the only species in its lineage to be domesticated.

The first evolutionary break within the *Canis* genus occurred in North America, and eventually (about 10 million years ago) gave rise to today's coyote, still confined to that continent. Another group emerged in South America, where they live to this day, and are classified as *Dusicyon* rather than *Canis*. Rather misleadingly, they are collectively known as South American foxes, though they are only distantly related to the much better known red fox of hunting fame. The other six species of *Canis* all evolved in the Old World, most likely in Eurasia, although some possibly in Africa. Four of these are jackals, although one of these, the Simien jackal, is sometimes confusingly referred to as the Ethiopian wolf; they include the golden jackal that Lorenz thought might have been the origin of some breeds of dog. The other is the grey wolf *Canis lupus*, the ancestor of our domestic dogs. Of the Eurasian canids, only the grey wolf reached North America, migrating across the Bering land bridge a hundred thousand years ago during one of the

periods when Alaska was joined to Asia.

Many of these species superficially seem to be potential candidates for domestication, thanks to a number of social tools that they share with the domestic dog. All can, when conditions are favorable, live in family groups or “packs.” All seem able to adapt their lifestyle—specifically, whether they live alone or in small or large groups—to the circumstances they find themselves in.³ (Nowadays, the most important such “circumstance” for all wild canids is often our own species’ activities, whether direct persecution or incidental provision of food at garbage dumps.) The current consensus is that the canid genome is rather like a Swiss Army knife,⁴ a social toolkit that has remained resistant to evolutionary change and can be used to cope with a wide variety of circumstances, ranging from solitary living when times are hard to complex societies when food is plentiful and persecution is at a minimum. The success of the domestic dog in adapting so well to life with humans can therefore be seen not as a specific set of changes that began only with the grey wolf but, rather, as a new use for this ancient canid social toolkit—one that allowed the dog to socialize not just with other members of the same species but also with members of ours.

While we are now certain that the grey wolf is the domestic dog’s one and only direct ancestor, the dog shares its earlier ancestors with many other still-living relatives, each of whom may offer us a new perspective on these ancient forebears. The dog’s lineage, after all, goes back much further than that of the grey wolf—specifically, to canids that are now extinct but were themselves the ancestors of all of today’s living canids. Each of the latter has something to tell us about the ways that canids can adapt to different circumstances—that is, construct their social groups—and therefore each provides a different set of clues as to what the canid “toolkit” may have looked like as it emerged some 5 million years ago. Although all of these canids carry the same “toolkit,” the fact that none apart from the wolf has been successfully domesticated will also need to be accounted for.



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