

# The Dog

Its Behavior, Nutrition,  
and Health

SECOND EDITION



Blackwell  
Publishing

*Linda P. Case*

Illustrated by Kerry Helms



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Illustrations by Kerry Helms

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**In memory of. . .**

Those who are no longer with us in life, but who are forever in our hearts—Fauna, Stepper, Roxie, Gusto, and Sparks. We love and miss you all.

**Dedicated to. . .**

Nike, Cadie, and Vinny Binny Vanilla Bean, who continue to bring laughter, joy, and love to our lives.





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# Preface

TODAY, about 40 percent of households in the United States share their homes with at least one dog, comprising a total of more than 61 million dogs. The multibillion dollar pet food industry and the more than seven billion dollars that pet guardians spend on veterinary care each year provide tangible evidence of the increasing importance that dogs have in our society. This devotion is further illustrated by the continued growth of the pet supply industry, which includes increasing numbers of pet “super-stores”, play-parks, training centers, and doggie day care centers in many communities. The bond that human caretakers have with their dogs and the many health benefits that are afforded by this bond have been the topic of numerous research studies in the past 30 years. The dog as a cherished companion and family member is here to stay, and many caretakers, students, and companion animal professionals are eager to learn more about man’s best friend, *Canis familiaris*.

*The Dog: Its Behavior, Nutrition and Health* is a comprehensive study of the domestic dog. This book is written for people who are either pursuing or are currently engaged in a profession or avocation that involves dogs. Dog trainers, breeders, kennel owners, veterinary technicians, veterinarians, and other companion animal professionals will find this book to be an indispensable resource. In addition, *The Dog: Its Behavior, Nutrition and Health* is an essential text for college students who are studying the physiology, care, behavior and nutrition of companion animals. The book is divided into four topical sections. Part 1, Man’s Best Friend: The Animal within the Companion, examines the origin of the relationship between humans and dogs and follows the development of the dog from the first stages of domestication through present day. This section also includes basic information about the dog’s physiology, structure, reproduction, and genetics. The status of the dog today and the importance of proper pet selection and responsible guardianship are discussed in the final chapter of this section. Part 2, Behavior: Communicating with Man’s Best Friend, examines the developmental behavior of the dog from birth to adulthood. Species-specific behavior patterns are examined, followed by a discussion of breed specific behaviors. Learning process and principles of training are the topic of Chapter 8. Basic tenets of learning are first reviewed, followed by an examination of successful training methodologies. Various training principles are compared and contrasted, and practical examples are provided throughout the chapter. The final chapter in this section identifies several common behavior problems and their solutions. Part 3 concerns Health and Disease: Taking Care and Keeping Fit. Infectious and non-infectious diseases and common internal and external parasitic diseases are included. Types of vaccines, procedures for their use, and new information regarding recommended vaccination

schedules are discussed. The final chapter in the section reviews emergency care and first aid procedures that are essential skills for all pet care professionals and dog caretakers. Part 4, Nutrition: Feeding for Health and Longevity, provides an overview of the dog's nutrient requirements and examines available pet foods and methods of feeding. Detailed instructions for feeding throughout the dog's life cycle and criteria for the selection of optimal pet foods are included. The final chapter of the book reviews common medical disorders that can be treated or managed through diet.

The first edition of this book was completed by the author in 1998 and was published by Iowa State University Press in 1999. In the six-plus years since its completion, numerous research studies and academic journal articles have been published on the topics of companion animal domestication, breeding, behavior, training, health care, and nutrition. All four sections and most chapters of this second edition have been updated with new information from recently published journal papers and books. These revisions will serve to provide college professors and companion animal professionals with the most up-to-date information possible in the field of companion animal science.

This new edition of *The Dog: Its Behavior, Nutrition and Health* offers the reader extensive information and technical depth in a readable and "user-friendly" format. The book is intended not only as a helpful resource, but also as an enjoyable and interesting exploration of the domestic dog, our relationship with him, and the best methods of caring for him. The knowledge gained can only strengthen the well-established and enduring bond that exists between dogs and their human caretakers in our culture today.



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**Linda P. Case**  
**Mahomet, Illinois**



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Part 1      **Man's Best Friend: The Animal  
within the Companion**



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# 1

## Man and Wolf: The Process of Domestication

TODAY, more than one-third of households in the United States own at least one dog, comprising a total of more than 61 million dogs.<sup>1</sup> In the year 2001, pet owners spent more than 8 billion dollars on food for their animals, and dog owners alone spend more than 10 billion dollars on veterinary care. It is undeniable that the dog is a valued and important member of our society. Unlike any other nonhuman species, the dog has become fully integrated into our lives, and it appears that he is here to stay. So what exactly was it that brought man and dog together so many years ago? And more important, what characteristics of these two very different species enabled them to forge the strong and ongoing partnership that is still so important to us today?

### The Dog's Phylogeny (Evolutionary History)

The dog, like the cat, is a member of the order Carnivora, which includes a diverse group of animals that are all predatory in nature. Carnivores are so named because of their enlarged carnassial teeth. These include the enlarged upper fourth premolar and the lower first molar on each side of the mouth. These adaptations make the teeth efficient at shearing and tearing prey. All carnivores also have small, sharp incisors for holding prey, and they often have elongated canine teeth for stabbing and tearing.

During the time when dinosaurs dominated the earth, a group of animals called the miacids were evolving. The Miacidae family included a very diverse group of predatory mammals, many of whom were small, tree-dwelling animals. This group existed about 62 million years ago and formed the ancestral family for all members of the order Carnivora. The miacids all walked on the palms/soles of their feet (plantigrade), were long bodied and slim, and were the first animals with carnassial teeth—an indication of their predatory nature.

Over time, a group called the viveravines branched off from the miacids. The viveravines are now known to be the oldest ancestor of the domestic cat. A second branch that evolved from the miacids was the miacines. Animals in this group were the ancestors of all extant canid species, as well as the bear, raccoon, and weasel. The miacines existed about 60 million years ago and eventually gave rise to *Hesperocyon* (meaning western dog), who is designated as the oldest member of the Canidae family. Remains of *Hesperocyon* have been found in South Dakota, Nebraska, Colorado, and Wyoming and are estimated to have existed about 36–38 million years ago. Interestingly, current evidence indicates that the Canidae family evolved completely in North

America and did not migrate into Eurasia until much later in its development. *Hesperocyon* was a digitigrade mammal (walking on its toes) and was long bodied and long legged, obviously adapted for speed. Its dentition (including the presence of carnassial teeth) and body structure showed it to be an agile predator. By the end of the Oligocene period, about 23 million years ago, *Hesperocyon* had evolved into *Leptocyon*. *Leptocyon* is thought to be the most recent common ancestor of all of today's canids, although there is some controversy over this mammal's eventual fate.<sup>2</sup> Some accounts claim that *Leptocyon* gave rise to *Tomarctus*, who became the wolf's and our dog's primary ancestor. Other records depict *Tomarctus* and *Leptocyon* as two separate branches of *Hesperocyon*. Regardless, it appears that *Leptocyon*, and probably *Tomarctus*, gave rise to the dominant group of canids in North America, who were destined to become all of our modern-day canid species.

### The Dog's Taxonomy (Naming the Dog)

Today, the domestic dog is classified as a member of the Canidae family (Table 1.1). This family also includes the wolf, coyote, dingo, fox, jackal, and Cape hunting dog. The dog's genus is *Canis*, and its species is *familiaris*. Other members of *Canis* are the coyote (*Canis latrans*), two species of wolf (the grey or timber wolf, *Canis lupus*, and the red wolf, *Canis rufus*), and four species of jackal. The extreme regional variations that are observed in wolves all represent varieties (subspecies) of *Canis lupus*, rather than separate species. Twenty to thirty subspecies have been identified, a number of which have become extinct in the last century. The genetic plasticity of the wolf as a species is illustrated by the great variation in physical and behavioral attributes in various subspecies. For example, Alaskan timber wolves (*Canis lupus pambasileus*) typically weigh more than 100 pounds at maturity and live in well-organized packs consisting of an average of five to eight adults. In contrast, the small Asian wolf (*Canis lupus pallipes*) weighs only about 45–50 lbs and travels alone or in very small packs. There is much dispute over whether or not the red wolf (*Canis rufus*) should continue to be classified as a separate species of wolf or be classified as a subspecies.

**TABLE 1.1** Taxonomy of the Dog

Phyla	Animalia
Class	Mammalia
Order	Carnivora
Family	Canidae
Genus	<i>Canis</i>
Species	<i>familiaris</i>

There is similar dispute regarding the domestic dog. The immediate common wild ancestor of *Canis familiaris* continues to be the subject of some debate. At one time, it was believed that the dog was descended from the interbreeding of ancestral wolves, coyotes, jackals, and possibly other wild canids.<sup>3</sup> During the 1940s, the Nobel prize-winning ethologist Konrad Lorenz wrote that some breeds of dogs were descended from the golden jackal, whereas others, those that he called “lupus” breeds, were directly descended from the wolf.<sup>4</sup> This theory has been largely discarded, however. During the 1970s, wolf and dog expert Michael Fox developed a “missing link” theory. He believed that the dog is descended from a now-extinct, European, dingo-like dog. However, little fossil evidence of this ancestor has been found. Another theory suggests that our present-day domestic dog arose from a type of semiwild dog similar to the Australian dingo (classified as either *Canis lupus dingo* or as *Canis familiaris dingo*) and the New Guinea singing dog (classified as *Canis familiaris hallstromi*).

Current behavioral, morphological, and molecular biological (genetics) evidence supports the theory that today’s gray wolf, *Canis lupus*, is the domestic dog’s closest relative. Although it is often stated that the wild wolf is our domestic dog’s immediate wild ancestor, in evolutionary terms this is impossible. More correctly, the present-day wolf and the present-day dog share their most recent ancestor, which was probably very wolflike in appearance and behavior. This distinction is important because the wolf that is extant today has been evolving for the same period of time that today’s domestic dog has been evolving. Therefore, the present-day wolf is actually the present-day domestic dog’s closest relative.

Overall, the most compelling evidence in recent years about how to accurately classify the domestic dog comes from relatively new methods of analyzing genetic information. Mitochondrial DNA (mDNA) is genetic material that is passed from mothers to their offspring (in the ovum), with no genetic recombination. Analysis of mDNA allows the reconstruction of matrilineal histories and also can provide an estimate of evolutionary history. These studies have shown that although there are morphological and behavioral differences between wolves and dogs, from a genetic standpoint, the domestic dog is virtually identical to the other members of the *Canis* genus. In fact, there are greater mitochondrial DNA differences between some breeds of dogs than are found between dogs and wolves! This knowledge, coupled with the fact that dogs, wolves, coyotes, and jackals are still reproductively interfertile, provides strong evidence that there is very little phylogenetic distance between these groups of canids.

Both dogs and wolves have 39 pairs of chromosomes (78 total), as is true for the four species of jackal and the coyote. Because of this very close genetic relatedness, some argue that the domestic dog should not be classified as a new species but, rather, as a subspecies of wolf (i.e., *Canis lupus familiaris*).<sup>5</sup> Conversely, another criterion for species classification is adaptation to different ecological niches. Some biologists and ecologists, although accepting the close genetic relationship between the dog and the wolf, maintain that because dogs, wolves, coyotes, and jackals all adapted to occupy and thrive in

very different ecological niches, they should each represent a separate species.<sup>6</sup>

Additional evidence for the dog's close relationship to the wolf lies in the existence of physical, genetic, and behavioral similarities between the two species. One of the most basic is the social nature of dogs and wolves. Both species establish social groups. In contrast, jackals are known to live and hunt alone, while coyotes hunt in pairs or, at the most, as a threesome. The typical wolf pack consists of closely related individuals who are each independent yet voluntarily work together to obtain food, raise young, and protect the pack from other predators. For the wolf, this means survival in a harsh environment in which food is scarce and the primary food source is often large ungulates (hooved mammals). Hunting such large prey would be impossible for one wolf hunting alone. As individuals, both dogs and wolves seek out contact and interactions with conspecifics (other pack members), and social activity is an important component of their daily life. Common examples include the elaborate greeting rituals, play, and exploratory behaviors of both species.

A second important similarity between the domestic dog and the wolf involves methods of communication. Natural selection has resulted in the establishment of complex communication patterns in all species that are required to work cooperatively for survival. In wolves, primary communication patterns involve body postures, facial expressions, and vocalizations. The domestic dog has inherited some of these communication tools in their complete form, differing little from their expression in *Canis lupus*. Other patterns have been modified through domestication, but vestigial portions are still observed. The wolf and the dog exhibit similar postures that signal aggression, dominance, submission and fear. However, the level of stimulus that is necessary to evoke these expressions, along with their intensity and completeness, have been modified significantly through domestication. The development of different breeds of dogs for specific purposes has further exaggerated or attenuated both physical and behavioral characteristics of the wolf (see Chapter 2). Finally, recent studies comparing dogs with socialized wolves have shown that dogs are significantly better at responding to various types of human social cues, such as gesturing, pointing, and gazing, compared with wolves.<sup>7</sup> The ability to engage in this type of social communication and learning appears to be an important aspect of domestication in the dog (see Chapter 7 for a more complete discussion).

## **The Process of Domestication**

Domestication of a species occurs when the breeding and containment of large groups of animals are under the control of humans. Over a period of many generations, this results in the development of a group of animals who are genetically distinct from members of the original species. Although members of domesticated species can often still mate and produce viable offspring



with members of the progenitor species, the domestication process still involves changes in genetically determined morphology and behavior. The process of domestication can be contrasted to “taming,” which refers to simply decreasing fear of humans in an individual animal. A tame animal is merely a wild animal who has been habituated to his human caretakers. Such an animal usually easily reverts back to the wild state, most often when sexual maturity occurs. In contrast, domestication must be viewed as a process that affects an entire subgroup of a species over many generations and that involves the geographic, reproductive, and behavioral isolation of the selected group from its wild population.

At present, there are two predominant theories that attempt to explain the morphological and behavioral changes that occurred during domestication of the dog from the ancestral wolf. The first of these develops a model of the dog as a pedomorphic (or neotenized) wolf.<sup>8,9</sup> Pedomorphosis refers to the retention of juvenile body shapes (morphology) and features into maturity and occurs as a result of changes in the onset, rate, or completion of development in the individual. These changes may affect the individual as a whole (i.e., final body size), or they may be restricted to certain body structures. The term *neoteny* is commonly used to describe the persistence of physical or behavioral infantile characteristics into adulthood. However, neoteny is actually one of several forms of pedomorphosis and refers to a reduced rate of development. Regardless of the terminology that is used, a pedomorphic (neotogenic) animal remains permanently immature with respect to the characteristic in question. Physical attributes that are commonly observed in domestic species that are pedomorphic include decreased body size, altered jaw size and strength, decreased number and size of teeth, development of a prominent forehead, shortened limbs, and diminished secondary sexual characteristics in males.

Neotenized behavioral characteristics are of equal significance in the domestic dog. An examination of the normal wolf pup demonstrates a number of behavior patterns that have been selected to persist into adulthood in the domesticated dog. Wolf pups are highly curious about their environments and will readily explore and investigate new animals and objects without showing the characteristic wariness that is seen in adult wolves. It is only after a certain age that wolf pups begin to show fear of unfamiliar stimuli. This is called *xenophobia* or *neophobia*, meaning fear of the foreign or fear of the new, respectively. Xenophobia has survival value for any species that is living in a harsh environment. However, this trait is not desirable in a domesticated animal. Adaptability to new environments is a key characteristic in domesticated species. For example, an adult dog who is fearful of new situations, people, or animals is not well adapted to living and working with man. Therefore, the selection for dogs with a puppylike trust of new stimuli was of distinct advantage. Moreover, once the evolving dog began to live near human settlements there was less selective pressure to maintain xenophobia, as the wolf's normal predators were less of a threat and, more important, animals who were less nervous would have more opportunities to feed.

A second important neotenized characteristic that is seen in the dog is the presence of enhanced and easily elicited subordinate behavior patterns. Wolf pups are naturally subordinate to elder members of their pack and are also more sociable with animals of other species. However, as pups mature into adult wolves, subordinate behaviors are not as readily elicited, and a collection of dominant behavior patterns develop that are necessary and vital for the adult wolf's integration into the pack. In the domestic dog, both dominant and subordinate behavior patterns are present, but there is an intensification of subordinate behaviors in the adult dog, compared with the expression of these behaviors in the wolf. Although there are great variations between breeds in both dominant and subordinate behaviors, in general, the display of dominant behaviors has been attenuated.

A second, related theory challenges the premise that pedomorphosis or neoteny can explain all of the morphological and behavioral changes that have occurred in the dog. The "mesomorphic remodeling theory" proposes that there are traits present in the domestic dog that are not to be found in either wolf pups or wolf adults.<sup>10-12</sup> This theory proposes that the dog may be looked on more as being arrested at some point during its adolescence or metamorphic period, rather than being strictly neotenic. The mesomorphic period refers to a period during which the young animal is rapidly changing into an adult form. In mammals such as the dog this period is typically referred to as the period of adolescence or the juvenile period. The various stages of life through which an individual progresses (i.e., fertilized egg, fetus, neonate, infant, juvenile, and adult) can be viewed as specialized stages in which the animal is behaviorally and morphologically adapted to the environment in which it exists at that time. Behaviors that are present in the infant slowly recede to give way to behaviors that are adaptive for the juvenile, and so on. In wolves, the mesomorphic juvenile exhibits some characteristics of the pup (which are decreasing with time), some traits of the adults (which are increasing with time), and some traits that are present only in the juvenile stage.

An interesting and important aspect of the mesomorphic period is that it represents a period of behavioral flexibility or plasticity. Proponents of this model believe that the mesomorphic period represents a period in which a multitude of new and different behaviors can evolve, and also a period in which the animal is highly responsive to learning. This theory maintains that a better model to use for the domesticated dog is one in which the dog represents a wolf whose development has been arrested or halted during the highly unstable mesomorphic period. The juvenile period in the wolf is relatively long in duration, and there are a number of changes that occur during this period. It is theorized that natural or artificial selection for traits that occur during different points of the juvenile period may be one source of the wide variation in size, morphology, and behavior seen in different breeds of domestic dog. This hypothesis of metamorphic remodeling is relatively new but, although it has not yet been thoroughly tested or examined by behaviorists, does represent another possible explanation for many of the behaviors and structural differences that are seen in the domesticated dog.

## In the Beginning: Man Meets Dog

Domestication of the dog is believed to have begun late in the Mesolithic period, 12,000–15,000 years ago, as humans were changing from being completely nomadic hunter-gatherers to living in semipermanent settlements. Although archeological (fossil) evidence of a domestic dog existing from this period of time is very scant, there is some evidence that a dog or “proto-dog” was living in close proximity to some human settlements about 12,000–14,000 years ago. By the Neolithic period, when agriculture was becoming the predominant way of life, the dog was fully domesticated, and various types of working dogs were beginning to emerge.<sup>13</sup>

Fossil evidence has shown that the dog was distributed across both Eurasia and the Americas before transoceanic travel during the fifteenth century. For some time, this fact, along with morphological data, seemed to show that the dog was domesticated separately in the Old and New worlds. However, a set of recent studies supports the theory that domestication occurred at one time only, in Eurasia, from the Old World gray wolf.<sup>14</sup> It now appears that when the first humans traveled to the New World across the Bering Strait approximately 12,000–14,000 years ago, they brought the newly domesticated (or semidomesticated) dog with them. Subsequently, semidomestic dogs, wolves, and coyotes appear to have occasionally interbred (hybridized), and some of their offspring were successfully integrated back into wild populations.<sup>15–17</sup> This hybridization is an influencing factor in the wide variations in size and body conformation observed in the domestic dog.

Traditionally, the theory that has been used to explain the evolution of the wild wolf into the domestic dog rested on the assumption that human hunters of the Mesolithic period coexisted with wild wolves and often competed for the same prey species. As humans began to recognize the superior hunting abilities of wolves (this theory states), they capitalized on these abilities by capturing, raising, and taming individual wolf pups, who were then used as hunting aids. Over time, artificial selection for individuals who were more naturally “tamable” and trainable, along with the isolation of this new group of canids from the wild population, led to genetic alterations in structure and behavior. As time went on, humans began to recognize other advantages to keeping this predatory species as a campsite friend, and supposedly, this led to artificial selection and the development of breeds.

Although this scenario has been widely propagated and popularized, it has several flaws from an evolutionary perspective, and in recent years it has been challenged by evolutionary biologists. Given what is currently known about the behavior of wild wolves, the likelihood of prehistoric humans intentionally capturing, taming, and training a wild wolf to hunt, and then repeating this often enough to control breeding of the (still) wild wolves in captivity, is virtually nonexistent. Wild wolves are extremely shy and nervous animals and have a highly structured and ritualized system of social hierarchy. Even when pups are socialized to human caretakers from birth, they continue to be wary of any person who is not well-known to them and are highly resistant to human control and training.<sup>18</sup> As adults, socialized wolves still resist control

by human caretakers, retain their need for a strict social hierarchy, and pose a significant threat, even to humans to whom they are socialized. Therefore, the scenario presented above, in which humans who were living as hunter/gatherers during the Mesolithic period took the time and trouble (not to mention risked their lives) to force individual wolves into captivity is untenable.

An alternate, more reasonable theory suggests that the early domestication of the dog was a result of natural selection, leading eventually to self-domestication.<sup>6</sup> This theory posits that as humans settled into semipermanent villages at the end of the last Ice Age, these settlements provided a new environmental niche into which wolves could adapt. Specifically, these new villages provided a steady supply of food in the form of surplus human food, spoiled foods, and human wastes. In addition, the outskirts of human settlements provided relative safety from other predator species and the potential for new nesting sites. Although the popular mythology surrounding wolves depicts them as efficient predators, wolves are also highly opportunistic scavengers. They are capable of consuming and thriving on a varied omnivorous diet. Therefore, as a species, the wolf was already well adapted to feed at these newly formed “dump sites,” which contained a wide variety of food types. It is quite possible that humans of that period tolerated or, more likely, just ignored the presence of the wild wolves around their settlements. This type of relationship is called *commensalism*—a form of symbiosis in which one species obtains benefit while the other is not harmed but receives no benefit.

As stated previously, wild wolves are very shy and nervous and have a highly sensitive and well-developed flight response. In the early stages of this self-selection process, most wolves would have had a tendency to run away whenever humans appeared or an unfamiliar situation developed. Natural selection in this new environment would favor wolves who were more tolerant of humans and who had less inclination to flee. The rules of natural selection tell us that the less timid animals would have more opportunity to feed because they would stay longer and flee less often than more timid animals. Feeding longer would lead to enhanced survival and greater opportunities to breed. The frequency of nontimid behaviors would gradually increase in this new population of animals.

Because the waste sites associated with human villages contained food that was, in general, of lower quality and was less energy dense than the prey species of wolves, natural selection would also favor individuals who were smaller in overall size and who had smaller teeth and weaker jaws. In addition, selective pressure for social hierarchies and strict pack order would relax as pack behavior was replaced primarily by semisolitary scavenging behaviors. As this proto-dog became more adapted to eating and reproducing in the presence of humans, the population as a whole became “naturally” tame and developed a set of behavior patterns that differed significantly from those of the wild wolf.

Today, the relevance of this domestication theory is that the evolutionary tree of the wild wolf and the dog split about 14,000 years ago as a new environmental niche presented itself and was exploited. The wild wolf, *Canis lupus*, remained a pack-living predator, while the dog evolved specialized

adaptations to live in close proximity to humans and their newly developed permanent settlements. Therefore, in every aspect, including size, structure, and behavior, the domestic dog should be considered a distant cousin of the wild wolf of today, rather than as a “wolf in dog’s clothing” (more about this in Part 2).

## Changes of Domestication

Several distinct and important physical changes occurred to *Canis lupus* as it became adapted to living in close proximity to humans. As stated previously, there were significant changes in size. Compared with the wolf, the dog has a smaller jaw and smaller and fewer teeth. Even the largest St. Bernard has smaller teeth and less jaw strength than an adult wolf. In most breeds, the shape of the mandible is more curved than that of the wolf, and the angle between the facial region and cranium is greater, resulting in a pronounced stop. Other modifications to the mandible include alterations in length to produce the brachycephalic (shortened muzzle) breeds and doliocephalic (elongated muzzle) breeds. The dog’s ears, tail, and coat type became diversified. The pendulous ears of breeds such as the Cocker Spaniel and Beagle are probably examples of neoteny and may have come about through artificial selection. Although wolf pups’ ears often fold, all adult wolves have an erect (or prick) ear. In contrast, the erect ear has been retained in many breeds, such as the German Shepherd and the Siberian Husky.

In addition, entire body size has been reduced in most dogs. Extreme examples are the toy breeds, such as the Papillon and the Italian Greyhound. In others, giantism has resulted in extremely large animals, such as the Great Dane and St. Bernard.

Most domesticated species demonstrate high fertility and early sexual maturity compared with their wild ancestors.<sup>19</sup> The wolf has only one estrous cycle per year, usually in the spring. Female dogs, in contrast, are not seasonal breeders and have approximately two estrous cycles per year. The male wolf only produces sperm seasonally, whereas the male dog is fertile throughout the year. Dogs also reach puberty at an earlier age, attaining sexual maturity at age 6–9 months. In contrast, wolves do not become sexually active until they are at least 2 years old.

Interestingly, the attainment of social maturity in the domestic dog still occurs at a later date, generally at about 18–24 months. Social maturity is conveyed by the development of strong social bonds, the onset of dominance relationships, and the active defense of territory (see Chapter 7). If the dog is of a dominant nature, certain types of aggression may arise as well. Domestication appears to have resulted in an uncoupling of sexual maturity and social maturity in the dog’s development. Although these two changes occur around the same time in wolves (2 years), social maturity occurs substantially later than sexual maturity in the dog. This dichotomy has important significance when one is dealing with behavioral problems associated with dominance hierarchies in the dog (see Chapters 8 and 10).

The physical and the behavioral development of wolf and dog puppies also show important differences. Compared with dogs, wolf pups develop physically much more quickly during the early weeks of life. Important information was gathered in a study that compared growth and development of a group of wolf pups to a group of Alaskan Malamute puppies.<sup>20</sup> Both groups were raised by the same foster wolf mother and socialized to humans. It was found that the wolf pups developed coordination and locomotor skills more rapidly than did the Malamute puppies. For example, at the age of 3 weeks, the wolf pups were capable of climbing out of a whelping pen with 16-inch sides. At the same age, even though they were of comparable size, the Malamutes pups were unable to traverse a 6-inch barrier. At 6 weeks of age, motor performance was tested in each group. The wolf pups' coordination was almost equivalent to that of small adult dogs. Again, in contrast, the Malamute pups still showed the uncoordinated, rolling gait of a neonate. Interestingly, by 10 weeks of age, these differences had disappeared. When retested for locomotor skills, the wolf pups and the Malamute pups showed very similar performances. It is possible that domestication has resulted in decreased selection for early coordination because the survival value of this trait is lessened in a protected environment.

All domestic dogs exhibit varying degrees of neotenus or juvenile behavior. Whining is a good example. Whining is commonly observed in wolf pups but rarely in adult wolves. The dog, in contrast, continues to exhibit whining into adulthood and often uses this verbal pattern as an important communication tool with human caretakers. Play behaviors in dogs are a second example. Although adult wolves do exhibit play behaviors, playfulness in general is more exaggerated and more easily evoked (i.e., lower response threshold) in dogs than in wolves. The natural subordinate attitude of puppies and the demonstration of passive and active submission are probably some of the most important behavioral traits that have been intensified in the domestic dog. The prolonged display of subordinate behavior into adulthood and a decreased tendency toward dominant challenges as sexual and social maturity is achieved are traits that have allowed the dog to live in close proximity and to bond closely with human caretakers. It has been hypothesized that both the young puppy's need for maternal care and its natural subordination to adult pack members are neotenized traits.<sup>4</sup> The need for maternal care manifests as an elevated propensity to bond to caretakers, whereas enhanced subordination facilitates acceptance of a leader and, subsequently, ease of training.

It appears that the primary socialization period in pups occurs for a longer span of time in dogs than in wolves (see Chapter 7). In canid species, socialization periods represent an age during which social bonds are easily and strongly established. During the early weeks of this period, pups readily approach and investigate novel stimuli such as new sights, new smells, and other animals. However, near the end of this period, pups become progressively fearful of new experiences (neophobic). The adaptive significance of this behavior for wolves is that it facilitates appropriate bonding to the dam, littermates, and other pack members early in life. However, as the pups grow