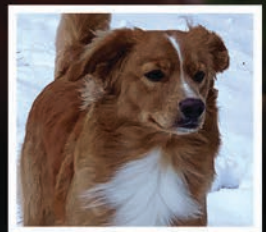
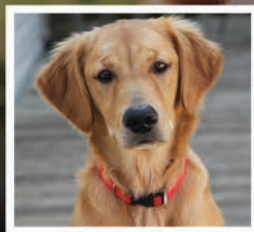


Third Edition

# The Dog

Its Behavior, Nutrition, and Health

*Linda P. Case*



WILEY Blackwell

**The Dog**



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Its Behavior, Nutrition, and Health

Third Edition

*Linda P. Case*

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**In memory of...**

*Our dogs and cats who are no longer with us in life, but who are forever in our hearts. We love and miss you all.*

**Dedicated to...**

*Our dogs (and cat, Pete), who continue to bring laughter, joy, and love to our lives.*



## Contents

**Preface** *xii*

**Acknowledgments** *xiv*

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

- 1 Man and Wolf: The Process of Domestication** *3*
  - The Dog's Phylogeny (Evolutionary History) *3*
  - The Dog's Taxonomy (Naming the Dog) *4*
  - The Process of Domestication *6*
  - In the Beginning: Man Meets Dog *7*
  - Changes of Domestication *9*
  - Conclusions *12*
  - Cited References *13*
  
- 2 Selective Breeding: The Creation of the Working Dog** *15*
  - Natural and Artificial Selection *15*
  - Working Breeds versus "Pure" Breeds *16*
  - Early Breeds: The Romans and Their Dogs *17*
  - Darwin's Influence *18*
  - Advent of Organized Dog Shows *18*
  - Spitz Breeds *19*
  - Mastiff Breeds *20*
  - Sight Hound Breeds *21*
  - Scent Hound Breeds *23*
  - Terrier Breeds *24*
  - Gundogs *26*
  - Livestock-Herding Breeds *28*
  - Livestock-Guarding Breeds *30*
  - Toy Breeds *31*
  - Dog Breed Registry Organizations *32*
  - Conclusions *33*
  - Cited References *33*
  
- 3 The Dog's Body: Structure, Movement, and Special Senses** *34*
  - The Dog's Structure *34*
  - The Dog's Movement *42*



	The Dog's Special Senses	44
	Recognizing the Normal Dog	49
	Conclusions	54
	Cited References	54
<b>4</b>	<b>Reproduction and Breeding Management</b>	<b>57</b>
	Reproductive Anatomy of the Female Dog	57
	Reproductive Anatomy of the Male	58
	The Female Estrous Cycle	60
	Detection of Ovulation in the Female	62
	Breeding Management	64
	Gestation	65
	Care of Newborn Puppies	67
	Reproductive Problems in the Female	69
	Reproductive Problems in the Male	71
	Neonatal Health Problems	71
	Conclusions	73
	Cited References	74
<b>5</b>	<b>Genetics and Breeding Programs</b>	<b>75</b>
	Basic Genetic Principles	75
	Selection of Breeding Animals	81
	Types of Breeding Systems	85
	Genetically Influenced Disorders in Dogs	88
	Genetic (DNA) Testing in Dogs	92
	Conclusions	92
	Cited References	92
<b>6</b>	<b>Sharing Our Lives with Dogs: Benefits and Responsibilities</b>	<b>94</b>
	The Human–Dog Bond	94
	Benefits of Sharing Our Lives with Dogs	99
	Dogs and Recreation	102
	Bonds That Fail: Dogs in Shelters and Rescue	104
	Selecting the Right Dog	106
	Conclusions	110
	Cited References	110
	Part 1 References and Recommended Reading	112
	Books	112
	Journal Articles	114
	<b>Part 2 Behavior: Communicating with Man's Best Friend</b>	<b>125</b>
<b>7</b>	<b>Developmental Behavior: Puppy to Adult</b>	<b>127</b>
	Neonatal Period (Birth–14 Days)	127
	Transition Period (14–21 Days)	128
	Primary Socialization (3–12 Weeks)	129
	Juvenile Period (Secondary Socialization) to Adulthood	132
	Conclusions	133
	Cited References	133

- 8 Understanding Normal Canine Behavior** 134
- The Social Nature of Wolves 134
  - The Social Nature of Dogs 135
  - The Concepts of Social Dominance and Submission 135
  - Communication Patterns 136
  - Aggression 144
  - Predatory Behavior 147
  - Breed Differences in Behavior 147
  - Conclusions 153
  - Cited References 153
- 9 Learning, Cognition, and Training Principles** 156
- Habituation and Sensitization 156
  - Classical Conditioning 157
  - Operant Conditioning (Instrumental Learning) 161
  - Social Learning 168
  - Social Cognition 171
  - Influences on Learning 175
  - Conclusions 176
  - Cited References 177
- 10 Manners Training and Prevention of Common Behavior Problems** 180
- Training Practices 180
  - Manners Training for Puppies and Adults 186
  - Prevention and Management of Common Behavior Problems 194
  - Conclusions 198
  - Cited References 199
  - Part 2 References and Recommended Reading 199
    - Books 199
    - Journal Articles 200
- Part 3 Health and Disease: Taking Care and Keeping Fit** 211
- 11 Infectious Diseases and Vaccination Programs** 213
- Viral Diseases 213
  - Bacterial Diseases 220
  - Fungal Infections 222
  - Vaccinations 224
  - Vaccination Schedules and Guidelines 230
  - Conclusions 231
  - Cited References 232
- 12 Common Noninfectious Disorders of Dogs** 234
- Canine Hip Dysplasia 234
  - Osteochondrosis 239
  - Juvenile Panosteitis (Wandering Lameness) 241
  - Gastric Dilatation Volvulus (Gastric Torsion, Bloat) 242
  - Hypothyroidism 243

- Cushing's Syndrome (Hyperadrenocorticism) 245
- Addison's Disease (Hypoadrenocorticism) 246
- Hot Spots (Acute Moist Dermatitis) 247
- Canine Atopic Disease (Atopy) 248
- Dental Problems 249
- Conclusions 251
- Cited References 252

**13 Internal Parasites 255**

- Canine Heartworm Disease 255
- Roundworms (Ascarids) 260
- Hookworms 264
- Whipworms 266
- Tapeworms (Cestodes) 267
- Coccidiosis 268
- Giardiasis 269
- Conclusions 269
- Cited References 270

**14 External Parasites 271**

- Fleas 271
- Mange Mites 277
- Ticks 279
- Conclusions 281
- Cited References 282

**15 First Aid Procedures for Dogs 283**

- Preparing a First Aid Kit 283
- Immediate Procedures 283
- Cardiac and Respiratory Arrest 285
- Shock 286
- Bleeding 286
- Choking 287
- Heatstroke 288
- Burns 288
- Insect Stings and Spider Bites 289
- Snake Bites 290
- Poisoning 290
- Conclusions 292
- Part 3 References and Recommended Reading 292
  - Books 292
  - Journal Articles 293

**Part 4 Nutrition: Feeding for Health and Longevity 305**

**16 Nutrient Requirements of the Dog 307**

- Essential and Nonessential Nutrients 307
- Energy 307
- Water 311

Carbohydrates	312
Fat	315
Protein	317
Vitamins	319
Minerals	321
Digestion and Absorption in Dogs	322
Conclusions	324
Cited References	325
<b>17 Providing a Healthy Diet</b>	<b>327</b>
Types of Commercial Dog Food	327
Evaluation and Selection of an Appropriate Dog Food	332
The Pet Food Label	335
Conclusions	337
Cited References	337
<b>18 Feeding for Health Throughout Life</b>	<b>339</b>
Normal Feeding Behavior of the Dog	339
Feeding Regimens (Schedules)	340
What to Feed (Overview)	341
How Much to Feed?	342
Feeding during Growth	343
Feeding for Adult Maintenance	345
Feeding during Gestation and Lactation	345
Weaning Puppies	347
Feeding Senior Dogs	347
Feeding Working Dogs	349
General Feeding Guidelines	350
Dog Characteristics	350
Food Characteristics	351
Conclusions	352
Cited References	352
<b>19 Common Feeding Problems</b>	<b>354</b>
Overweight Conditions in Dogs	354
Food Allergies	359
Particular Foods to Avoid with Dogs	363
Conclusions	366
Cited References	366
Part 4 References and Recommended Reading	369
Books	369
Journal Articles	370
<b>Glossary</b>	<b>380</b>
<b>Index</b>	<b>385</b>

## 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 50 years. The dog as a cherished companion and family member is here to stay, and many dog owners, students, and canine 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 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 dogs. 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, in Chapter 7, including a discussion of breed specific behaviors. Learning process and principles of training are the topic of Chapter 9. Basic tenets of learning are first reviewed, followed by an examination of successful training methodologies with a focus on reward-based training methods. Practical examples are provided throughout the chapter. The final chapter in this section provides practical instruction for teaching basic manners to dogs and approaches for preventing common behavior problems. 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 owners. 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 feeding problems and their management and prevention.

The first edition of this book was completed by the author in 1998 and was published by Iowa State University Press in 1999. The second edition was published in 2005. In the years since the completion of the second edition, 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. Many of the chapters have also been restructured to emphasize new information and material. 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 as a species, our relationships with dogs, and the best methods of caring for them. 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**

## **Part 1**

### **Man's Best Friend**

The Animal within the Companion





# 1

## Man and Wolf

### The Process of Domestication

TODAY, almost 40 percent of households in the United States own at least one dog, comprising a total of more than 77 million dogs.<sup>1</sup> In the year 2020, pet owners spent more than 40 billion dollars on food for their animals, and about 30 billion dollars on veterinary care.<sup>2</sup> 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>3</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 gray 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, several 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 exist as 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 pounds and travels alone or in very small packs. For many years, there was scientific dispute over whether the red wolf (*Canis rufus*) should be classified as a separate species of wolf or as a subspecies. This question was finally put to rest in 2019 when a comprehensive study of red wolf genetics, anatomy, and behavior came to the conclusion that the red wolf is indeed a separate species (*Canis rufus*) and is currently protected under the Federal Endangered Species Act.<sup>4</sup>

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>5</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>6</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. Yet 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 *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

**Table 1.1** Taxonomy of the Dog.

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

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 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 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 can provide an estimate of a species' 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>6</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>7</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 readily establish and maintain social groups. In contrast, jackals are known to live and hunt alone, while coyotes hunt in pairs or, at the most, as a three-some. The typical wolf pack consists of closely related individuals who are each independent yet voluntarily function 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>8–11</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 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.

There have been two predominant theories that have attempted to explain the morphological and behavioral changes that occurred during domestication of the dog from the ancestral wolf. The first and earliest of these developed a model of the dog as a pedomorphic (or neotenized) wolf.<sup>12,13</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 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 characteristics 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 several 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 human caretakers. 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 and among individuals in both dominant and subordinate behaviors, in general, the display of dominant behaviors has been attenuated in the domestic dog.

A second, but related theory challenges the premise that pedomorphosis or neoteny can explain all 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>13-15</sup> This theory proposes that the dog can be viewed 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 several 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 now believed to have begun earlier than previously believed—some time between 32,000 and 18,000 years ago.<sup>16,17</sup> The process of domestication began when humans were still living a nomadic lifestyle, periodically moving their camps from place to place. Approximately 15,000 to 12,000 years ago, humans began to change from being completely

nomadic hunter-gatherers to living in semipermanent and permanent settlements. Although archeological (fossil) evidence of a domestic dog existing from this period is scant, there is 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>18</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, suggested that the dog was domesticated separately in the Old and New Worlds.<sup>19,20</sup> However, other studies support the theory that domestication occurred at one time only and earlier than previously believed, in northern Asia.<sup>21</sup> Regardless, it 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>22–24</sup> This hybridization has been 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 “tameable” 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 the dog as a campsite friend, and supposedly, this led to artificial selection and the eventual development of breeds.

Although this scenario has been widely propagated and popularized, it has several flaws from an evolutionary perspective and 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>25</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 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>14</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 ancestral 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 tended 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.

These new subpopulations of wolf were also feeding themselves more through scavenging and less through hunting (predation). 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. Therefore, natural selection would begin to 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 as a new environmental niche presented itself and was exploited. The ancestral 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, nutrition, 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 modifications to size. Compared with the wolf, the domestic 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 the 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 some, but not all 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>26</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 development of dominance behavior patterns, and the active defense of territory (see Chapter 7). 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 certain types of behavioral problems (see Chapters 8 and 10). Other important changes in social behavior reflect adaptations to living in close proximity with humans. Dogs evolved a set of social behaviors that enhance their ability to both communicate and cooperate with human caretakers (see Chapters 8 and 9).<sup>27,28</sup>

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>29</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 Malamute 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 both other unrelated dogs and 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>5</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 and become more mobile and capable of wandering further from the den area, the onset of a “fear of the new” and of having a long flight distance has distinct survival value.

Domestic dogs demonstrate primary socialization and develop social bonds most intensely between 5 and 12 weeks of age. Frequent and positive interactions with human caretakers during this period have been shown to facilitate strong attachment behaviors and training at a later age. In contrast, puppies who are isolated from humans during the period of primary socialization have a greater tendency to become aloof or even timid toward humans. If no interactions occur between puppies and humans before 12–14 weeks of age, the formation of normal relationships may be compromised. By comparison, the wolf pup’s primary socialization period appears to be shorter in duration than that of the dog, and the manifestation of the fear imprint period is more intense. It has been hypothesized that this early and enhanced fear imprint period is the cause of the wolf’s inability to bond strongly to humans, even when raised in captivity.<sup>28,30</sup> It appears that although the socialization period starts at about the same time in dogs as in wolves, the fear reaction to new animals and situations is delayed in the puppy and is demonstrated far less intensely.

Even when wolf pups are raised in captivity and spend many hours with humans during the period of primary socialization (i.e., the period during which they will be forming primary social attachments), the bond or orientation that wolf pups develop toward humans is still very weak. Although they will passively accept handling by and interactions with human caretakers up until about 7 weeks of age, they begin to show a strong period of fear imprint between 6 and 8 weeks of age. Throughout their development, if the pups have access to a foster mother or to another adult wolf, they will demonstrate a strong social preference to the member of their own species, rather than to the human caretaker. This is in strong contrast to developmental behavior in puppies. The study cited previously reported that as soon as the Malamute puppies were mobile, they would readily abandon their foster mother on the approach of a human caretaker.<sup>29</sup> Moreover, by the time of weaning, the dog puppies were demonstrably more independent of their foster mother than were the wolf pups at the same age.

Of special interest is the greeting behavior of wolf pups compared to that of dog puppies. Wolf puppies typically demonstrate an intense and effusive “greeting frenzy” toward elder pack members. This greeting behavior is characterized by body postures and facial expressions that convey submission. Wolf pups consistently demonstrate this type of greeting toward their dam, sire, and other pack members. In contrast, puppies greet other dogs much less intensely and reserve most of their frenzied greeting responses for their human caretakers. This is another example of how domestication has shifted the dog’s primary social attachment from his conspecifics to that of another species, the human.<sup>27</sup> As wolf pups attain physical maturity, they begin to show normal agonistic behaviors, which include dominance displays and challenges to other pack members. The purpose of these behaviors is to establish a stable social hierarchy within the pack. There are natural selective pressures against overt intragroup aggression in social species that are predatory in nature. There are several reasons for this. First, any energy that is spent on altercations with other individuals within the social group is energy that could be better spent in the procurement of food through cooperative hunting. The wolf pack that spends large amounts of time fighting among themselves would be at a distinct disadvantage in terms of survival. Therefore, there is

direct selective pressure to minimize the amount of energy that is expended settling disputes within a pack. Second, social animals that are predators have the capability to inflict severe injury and death on other animals. Thus, aggression between pack members could result in injury or death, given the power of their defense mechanisms. If injured by another pack member during a dispute, a hurt wolf would not be able to hunt efficiently and may even attract other predators to the pack because of the presence of blood and its weakened state. Therefore, to prevent the problems associated with agonistic behavior toward others of the pack, evolution produced a set of highly predictable and ritualized dominance and submissive displays, along with a social order within the pack that defined the respective roles of dominant and subordinate animals of decreasing social rank. These displays allow the resolution of conflict and other types of interactions within the pack to occur without the danger of inflicting injury to pack members.

Although the dog has inherited many of these ritualized body postures, facial expressions, and vocalizations, two important and opposing pressures of the domestication process have distinctly modified the wolf's behavior patterns. During domestication, the natural selective pressure against aggression between pack members was unintentionally relaxed. This occurred because, during the period of self-domestication, evolving dogs no longer lived as large, cooperatively hunting groups but, rather, lived semisolitary lives as scavengers. This meant that the selective pressure for the survival of an entire pack was no longer present. In addition, as dogs eventually became completely domesticated and incorporated into human social groups, they no longer needed to function as a working unit with other dogs. Later still, in some areas of the world, dogs were selectively bred for guarding behavior and protectiveness. This selective pressure potentially increased the intensity of aggressive responses and decreased the level of stimulus needed to trigger the agonistic behavior.

The end result of these pressures was actually an increase in the expression of interdog aggression. The repercussions of this can be seen in some of the highly aggressive breeds of dogs that exist today (see Chapter 2). In direct contrast, a second selective force was at work during domestication. The selection for infantile behaviors, including the evolution of a more naturally subordinate animal, functioned to decrease aggressive behaviors. The final result of these pressures was the creation of a dog that is naturally more subordinate (and less dominant) than wolves. However, when aggressive behaviors toward other dogs (or humans) are displayed, they may be of higher intensity, and it may take a lower stimulus level to elicit them.

A final important behavioral change that has occurred during domestication is the alteration of normal predatory behavior. The wolf is a predatory animal that hunts cooperatively with a group to kill prey that is much larger than itself. The complete sequence of predatory behavior includes finding, stalking, chasing, catching, killing, dissecting, and ingesting prey. This sequence of activity both is diminished in intensity in the dog and is terminated before its end (i.e., prey kill and dissection are absent or severely diminished in most breeds). In all dogs, predatory behavior is diminished in intensity because of a lack of selective pressure as the dog evolved as a commensally living scavenger. In addition, certain parts of the predatory sequence were exaggerated, and others suppressed when particular breeds were developed to accomplish specific working functions (see Chapter 2).

## Conclusions

Human initial association with *Canis lupus* began over 18,000 years ago and resulted in very specific morphological, developmental, and behavioral changes. These changes eventually produced *Canis familiaris*, the dog as we know it today. Once the dog was domesticated, selective

breeding in different areas of the world, in widely different climates, and for a variety of functions resulted in the development of distinct breeds. An examination of the history of selective breeding and the development of different breeds provides valuable information about individual pets that live with us today.

## Cited References

- 1 American Veterinary Medical Association. *U.S. Pet Ownership and Demographics Sourcebook*, 2017–2018 edition, AVMA, Schaumburg, IL. (2019)
- 2 American Pet Products Association Pet Industry Market Size, Trends & Ownership Statistics; 2020. [https://www.americanpetproducts.org/press\\_industrytrends.asp](https://www.americanpetproducts.org/press_industrytrends.asp) (accessed on June, 2022).
- 3 Wayne, R.K. **Phylogenetic relationships of canids to other carnivores**. In: *Miller's Anatomy of the Dog*, 3rd edition (H.E. Evans, editor), W.B. Saunders Company, Philadelphia, PA, pp. 15–21. (1993)
- 4 National Academies of Sciences, Engineering, and Medicine. *Evaluating the Taxonomic Status of the Mexican Gray Wolf and the Red Wolf*, The National Academies Press, Washington, DC. <https://doi.org/10.17226/25351>. (2019)
- 5 Fiennes, R. and Fiennes, A. *The Natural History of Dogs*, The Natural History Press, Garden City, NY. (1970)
- 6 Lorenz, K. *Man Meets Dog*, first printed in 1953. Kodansha International. (1994)
- 7 Fox, M.W. *The Dog: Its Domestication and Behavior*, Garland STPM Press, New York. (1978)
- 8 Miklosi, A., Kubinyi, E., Topal, J., et al. **A simple reason for a big difference: wolves do not look back at humans, but dogs do**. *Current Biology*, 13:763–766. (2003)
- 9 Call, J., Brauer, J., Kaminski, J., and Tomasello, M. **Domestic dogs (*Canis familiaris*) are sensitive to the attentional state of humans**. *Journal of Comparative Psychology*, 117:257–263. (2003)
- 10 Gacsi, M., Miklosi, A., Varga, O., Topal, J., and Csanyi, V. **Are readers of our face readers of our minds? Dogs (*Canis familiaris*) show situation-dependent recognition of human's attention**. *Animal Cognition*, 7:144–153. (2004)
- 11 Schünemann, B., Keller, J., Rakoczy, H., et al. **Dogs distinguish human intentional and unintentional action**. *Scientific Reports*, 11:14967. <https://doi.org/10.1038/s41598-021-94374-3>. (2021)
- 12 Schenkel, R. **Submission: its features and functions in the wolf and dog**. *American Zoologist*, 7:319–330. (1967)
- 13 Kretschmer, K.R. and Fox, M.W. **Effects of domestication on animal behaviour**. *Veterinary Record*, 96:102–108. (1975)
- 14 Coppinger, R.P. and Schnieder, R. **Evolution of working dog behavior**. In: *The Domestic Dog: Its Evolution, Behavior and Interactions with People* (J.A. Serpell, editor), Cambridge University Press, Cambridge. 42–66. (1995)
- 15 Coppinger, R.P. and Smith, C.K. **A model for understanding the evolution of mammalian behavior**. In: *Current Mammalogy*, Volume 2 (H. Genoways, editor), Plenum Press, New York, pp. 33–74. (1989)
- 16 Freedman, A.H., et al. **Genomic sequencing highlights the dynamic early history of dogs**. *PLOS Genetics*, 10:e1004016. (2014)
- 17 Larsen, G., et al. **Rethinking dog domestication by integrating ge-netics, archeology and biogeography**. *Proceedings of the National Academy of Sciences*, 109:8878–8883. (2012)

- 18 Davis, S.J. and Valls, F.R. **Evidence for domestication of the dog 12,000 years ago in the natufian of Israel.** *Nature*, 276:608–610. (1978)
- 19 Frantz, L.A., et al. **Genomic and archaeological evidence suggest a dual origin of domestic dogs.** *Science*, 352:1228–1231. (2016)
- 20 Leonard, J.A., Wayne, R.K., Wheeler, J., et al. **Ancient DNA evidence for Old World origin of New World dogs.** *Science*, 298:1613–1616. (2002)
- 21 Perri, A.R., Feuerborn, T.R., Frantz, A.F., et al. **Dog domestication and the dual dispersal of people and dogs into the Americas.** *Proceedings of the National Academy of Sciences*, February 118(6):e2010083118. <https://doi.org/10.1073/pnas.2010083118>. (2021)
- 22 Lehman, N., Eisenhauer, A., Hansen, K., Mech, L.D., Peterson, R.O., Gogan, P.J., and Wayne, R.K. **Introgression of coyote mtDNA into sympatric North American gray world populations.** *Evolution*, 45:104–109. (1991)
- 23 Adams, J.R., Leonard, J.A., and Waits, L.P. **Widespread occurrence of a domestic dog mitochondrial DNA haplotype in southeastern US coyotes.** *Molecular Ecology*, 12:541–546. (2003)
- 24 Tsuda, K., Kikkawa, Y., Yonekawa, H., and Tanabe, Y. **Extensive interbreeding occurred among multiple matriarchal ancestors during the domestication of dogs: evidence from inter- and intraspecies polymorphisms in the D-loop region of mitochondrial DNA between dogs and wolves.** *Genes and Genetic Systems*, 72:229–238. (1997)
- 25 Klinghammer, E. and Goodmann, P. **Socialization and management of wolves in captivity.** In: *Man and Wolf* (H.F. Dordrecht, editor), Dr. W. Junk Publishers, The Hague, The Netherlands. 87–94. (1987)
- 26 Zeuner, F.E. *A History of Domesticated Animals*, Harper and Row, New York. (1963)
- 27 Hare, B. **The domestication of social cognition in dogs.** *Science*, 298:1634–1646. (2002)
- 28 Range, F. and Viarney, Z. **Tracking the evolutionary origins of dog-human cooperation: the “canine cooperation hypothesis”.** *Frontiers in Psychology*, 5:1582. (2015)
- 29 Frank, H. and Frank, M.G. **On the effects of domestication on canine social development and behavior.** *Applied Animal Ethology*, 8:507–525. (1982)
- 30 Fox, M.W. *Behaviour of Wolves, Dogs and Related Canids*, Harper and Row, New York. (1971)

## 2

### Selective Breeding

#### The Creation of the Working Dog

AS HUMAN POPULATIONS increased and humans spread across the world, changes in the climate and habitats started to place different demands on our canine companions and working partners. Different types of dogs evolved through natural selection to cohabitate alongside human settlements in different environments. These natural breeds of dogs developed with little or no intervention from humans during the first part of the Neolithic period. It is estimated that intentional selective breeding of dogs began between 3,000 and 5,000 years ago. For example, around 2900 B.C., dogs resembling today's greyhound were depicted on paintings and pottery in Egypt and Western Asia. Selective breeding of dogs for specific working abilities flourished during the Middle Ages. However, most of the extreme alterations in form and function of the dog and the intensive line breeding and inbreeding of purebred dogs have occurred only within the last 150–200 years.

### Natural and Artificial Selection

A current theory of domestication of the dog suggests that natural selection was primarily responsible for the major changes associated with domestication. The exploitation of a new and consistent food source (human waste sites associated with Mesolithic villages) led to gradual changes in the wolf's morphology and behavior. Over time, natural selection for smaller, less pack-oriented, and less nervous individuals led to the creation of “village dogs,” the ancestors of our present-day domestic dogs.<sup>1</sup> This new population of animals existed commensally with humans for thousands of years and became the progenitor population of dogs eventually selected for further taming, training, and eventually, selective breeding (artificial selection). Evidence supporting this scenario can be found in studies of village or free-ranging dogs. Free-ranging dogs continue to exist in numerous countries around the world, including Mexico, Italy, Nepal, Japan, many African countries, and India. They survive almost entirely by scavenging and occasionally augment their diet by begging and hunting small animals. In India, the history of free-ranging dogs is well-documented, extending back to the ninth century B.C. and representing more than 1,000 generations of dogs. Although these dogs live in close proximity to humans, they are not house pets in the traditional Western sense.<sup>2,3</sup>

A theory of self-domestication for the dog is more congruous with historical evidence and is also more defensible than the premise that humans directly tamed and domesticated the wolf. The successful integration of a puppy taken from a population of smaller, less nervous, and more tame