Puppy Love: The Evolution of Hypersociability in Domestic Dogs

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Impressed in the soft sediment that forms the floor of the [Chauvet] cave are the clear impressions of a child's footprints. He or she, let us say he, was about eight years old. What he was doing that far back in the pitch-black cavern [26,000 years ago] we can only imagine.... Alongside the child's [footprints] is another, quite different, set of prints. Perfectly preserved in the limey sediment that covers the cave floor, ... are the tracks of a fully-grown wolf .... The footprints hint at a very close relationship, friendship even, between the boy and the wolf. Or was the animal that trotted comfortably at the boy's side no longer a wolf, but already on its way to becoming a dog? (Sykes, 2018, pp. 49-50)

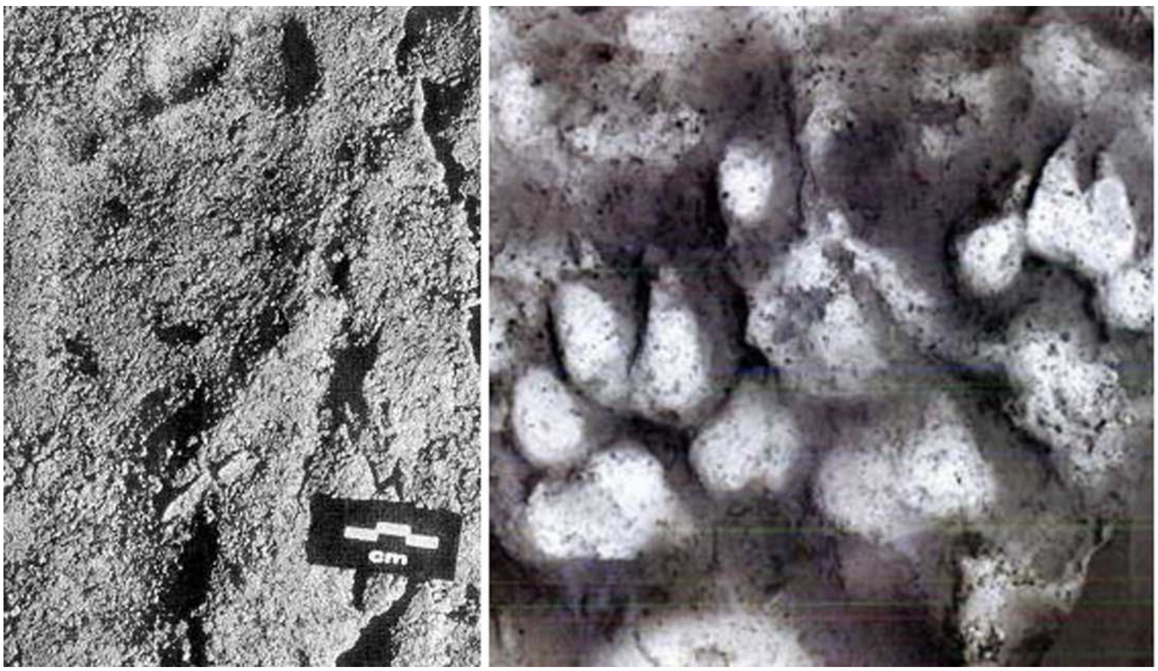

Figure 1. Fossilized footprints of child and canid in Chauvet Cave.

Dogs (Canis lupus familiaris) descended from an extinct population of ancient wolves that humans began to domesticate tens of thousands of years ago (Perri et al., 2021; Serpell, 2021). Domestication is an evolutionary process that occurs when a population of animals or plants depends on humans for survival and reproduction (Price, 1999; Wynne & Udell, 2020). Over many generations, domestication results in changes in physical, psychological, and behavioral traits. For example, large differences in body size have evolved across dog breeds (Speakman et al., 2003). the sizes range from about three pounds (e.g., the Chihuahua) to well over 200 pounds (e.g., the Saint Bernard).

Evolutionary changes are caused primarily by selection. Selection occurs when individual differences in traits result in individual differences in reproductive success. For example, if larger dogs in a population have more pups, on average, than smaller dogs, and if the individual differences in body size are heritable, then over generations dogs in that population will become larger.

Domestication occurs because of two types of selection: natural and artificial (Price, 1999). Natural selection refers to the increased reproductive success of individuals because they express a trait that better adapts them to their environments. For example, the Tibetan Mastiff diverged from lowland dogs that followed nomadic humans migrating into the Himalayas. Low oxygen levels at these high altitudes cause severe tissue damage and eventual death in many dogs. The Tibetan Mastiff, however, can survive at these high altitudes because of the evolution through natural selection of biological changes that allow these dogs to use oxygen more efficiently (Miao et al., 2017).

Artificial selection refers to the increased reproductive success of individuals because they express a trait preferred by humans. In this case, humans control the reproduction of domesticated organisms and breed only those organisms that express a particular trait. For example, dog fanciers who raise show dogs choose only those dogs with particular physical and behavioral traits for breeding (Svartberg, 2006).

In order for evolutionary changes to occur through selection, trait differences must be heritable—they must be associated with differences in genes. Genes, as you will learn later in this paper, are the basic hereditary units. When selection occurs on trait differences, the frequencies of the associated genes change over generations.

The Beginnings of the Domestic Dog

Domestication of plants and animals began in earnest about 12,000 years ago with the rise of agricultural settlements (Serpell, 2021). The one exception was the domestication of ancient wolves, which began up to 25,000 years before that, at a time when humans were still living in nomadic hunting-gathering groups.

We do not know how or why humans began to domesticate ancient wolves. Canine researchers have proposed at least two possible ways that wolf domestication began. First, wolf packs may have followed nomadic bands of humans and scavenged their discarded food (Herbeck et al., 2022). Eventually, close contact with humans tamed the wolves and, at some point, humans socialized newborn cubs by hand-rearing them.

A second possibility is that nomadic humans captured wolf cubs and raised them as pets (Serpell, 2021). Humans tend to have a strong drive to nurture their young—a drive that sometimes extends to the young of other mammals. Paleolithic humans certainly encountered bands of wolf cubs when the dominant female wolf birthed her annual litter. And again, the handling of newborn cubs would have socialized them.

Regardless of how the domestication of wolves began, humans would have favored wolves that had traits they preferred. These favored wolves, therefore, would have been more reproductively successful. Assuming that these preferred traits were heritable, then over thousands of generations, significant physical, psychological, physiological, and behavioral changes would have occurred, thereby leading to the divergence of dogs from the ancestral wolf population.

Although these musings on the origins of the domestic dog seem reasonable, we probably can never confirm them because the events are buried in human prehistory. Researchers instead focus on identifying the time and place of dog origins by studying the:

- archaeological evidence—evidence of dog-wolf separation based on an analysis of fossilized remains
- genetic evidence—evidence of dog-wolf separation based on estimates of the number of genetic differences between them

Archaeological Research on Dog origins

Archaeologists have excavated the remains of many ancient canids looking for signs of the first domestic dogs. The first remains that are clearly those of a dog were found in Germany and are dated to about 15,000 years ago (Perri et al., 2021). Older sets of remains, however, are more difficult to identify as being dogs rather than wolves. For example, archaeologists cannot clearly identify canid remains found in Belgium and dated to about 35,000 years ago (Freedman & Wayne, 2017).

Ancient canid remains are difficult to identify for four reasons (Freedman & Wayne, 2017):

1. The traits used to identify the subspecies of fossil remains (e.g., tooth size, tooth position, skull size, and skull shape) overlapped in ancient times. In other words, the first dogs looked very similar to the wolves they evolved from.
2. Wolves and dogs lived in the same locations in ancient times. Archaeologists, therefore, cannot use location to decide if fossil remains are a wolf or dog.
3. The fossil record of dogs, wolves, and related species is patchy with many gaps over the millennia. This incomplete record makes it difficult to get a broad understanding of the history of dog evolution around the world and overtime.
4. The fossil remains most relevant to researchers are those from populations that have modern descendants (i.e., remains that are not from extinct populations). But archaeologists cannot easily determine if a particular set of remains belong to an ancient population with modern descendants.

Genetic Research on Dog Origins

Genes are biological units that change gradually over time as they pass from one generation to the next. These changes in the biological make-up of genes are the result of processes like mutation and selection. When two populations of organisms separate from each other and no longer interbreed, the changes in their genes occur independently. Over long periods of time, the two populations accumulate more and more genetic differences (Freedman et al., 2014). Geneticists use the number of genetic differences to estimate the amount of time since the two populations diverged. For example, the number of genetic differences between modern humans and chimpanzees suggest that the ancestral populations of these two species separated about six million years ago (Hughes et al, 2005).

Compared to the time since the divergence of the ancestors of humans and chimpanzees, the ancestors of dogs and wolves separated only “moments ago”: probably less than 40,000 years ago (Freedman & Wayne, 2017; Koch et al., 2019; Perri et al., 2021).

Calculations using the number of genetic differences between two populations provide estimates of the number of generations since they separated. These calculations are straightforward if the two populations have not interbred since they separated. If they have interbred, however, the estimates of time since their initial separation are less reliable.

Dogs and wolves are subspecies of each other (see Figure 2). Subspecies can interbreed and produce viable offspring that are fertile. Although the ancient wolf population that gave rise to the domestic dog is extinct, the grey wolf (*Canis lupus*) has existed in the same locations as dogs for tens of thousands of years (Freedman et al., 2014; Von Holdt et al., 2017). The two subspecies have interbred an unknown number of times. A known example of interbreeding occurred between ancient dogs and another wolf subspecies, the Tibetan Wolf (*Canis lupus laniger), about 20,000 years ago* (Miao et al., 2017; Ostrander et al., 2017; Signore et al., 2019). This event introduced genes into ancient dogs that led to the evolution of the modern Tibetan Mastiff.

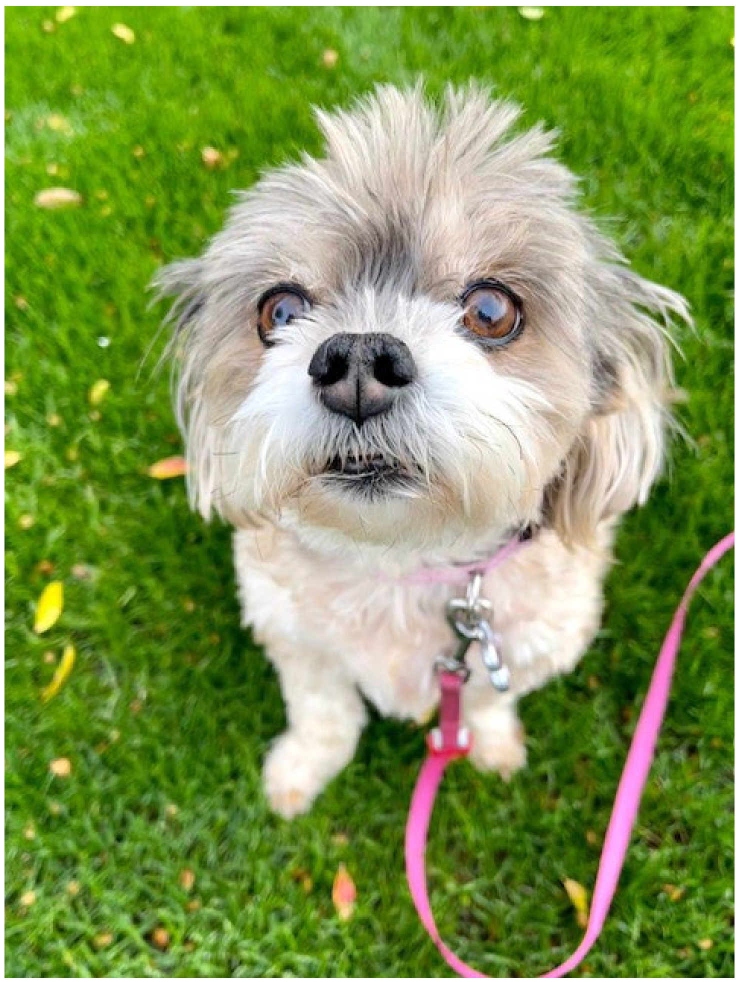

Figure2. Canis lupus familiaris, a subspecies of the grey wolf

Mutations are the ultimate source of genetic change in a population. A mutation is a random change in a gene caused by radiation, toxins, errors in gene replication, etc. The number of genetic differences between two populations due to mutations is used to estimate the amount of time since they separated. In order to make these calculations, geneticists must have a good idea of the number of mutations that occur over time. This number is compared to the actual number to estimate the amount of time that has passed since divergence. But mutations occur rarely, which makes it difficult to estimate the average number that occur each generation. Because of this difficulty, estimates of mutation rates vary widely. When these variable mutation rates are used to estimate the time since divergence of dogs and wolves, the result is a broad range of estimates (e.g., 16,000 to 64,000 years ago; Koch et al., 2019). This difficulty is yet another reason why no agreement exists regarding the specific time since the separation of dogs and wolves.

What Can We Conclude About Dog Origins?

Because of the limitations of the archaeological and genetic evidence, canine researchers are uncertain about exactly when and where dogs first separated from wolves. But they probably all would agree with the following generalization: *dogs diverged from a now-extinct population of wolves in Eurasia sometime between 15,000 and 35,000 years ago* (Freedman & Wayne, 2017).

Canine researchers continue to look for ways to more precisely determine the time and place of dog-wolf separation. A recent study tried to provide better answers to questions about dog origins by including in their calculations the timing of human migrations from Eurasia to North America (Perri et al., 2021). These researchers first established the following:

- The wolf population that gave rise to modern dogs diverged from other wolf populations sometime after 40,000 years ago.
- Dog domestication began sometime after 35,000 years ago.
- Humans migrated with their dogs from Asia, across the Bering Land Bridge (Beringia), to North America during the last ice age (about 15,000 years ago).

Perri et al. (2021) argued that the migration patterns of these ancient humans could be used to place limits on the timing of domestication events. In both humans and dogs, they identified genetic variants linked to specific periods of time in Siberia, Beringia, and North America. Based on their analysis, they concluded that dogs emerged in Siberia by 23,000 years ago. Then, by about 15,000 years ago, dogs had migrated with humans westward to Europe and eastward to North America.

How and Why Do Dogs Differ from Wolves?

You have learned that dogs evolved from wolves very recently. The recent divergence explains the physical and behavioral similarities between wolves and mongrel dogs (i.e., dogs not intentionally bred for specific breed-characteristic traits). But obvious differences between the subspecies also exist. Perhaps the most obvious difference can be summarized as: dogs make great pets, wolves do not.

Clive Wynne (2019), (a dog researcher at Arizona State University) provided an excellent example of this difference in a description of his visit to the *Wolf Science Center* at the Veterinary University of Vienna, Austria. At the Center, dogs and wolves are socialized to humans and raised in similar circumstances beginning at birth. They have daily interactions with humans but live in large enclosures with other members of their subspecies.

> As the wolves heard us approach, many, but not all of them, got up, stretched, and wandered over to the fence. Those in our party who were familiar to the wolves petted them through the wire. …. [They] pushed forward to be petted, but they kept their interest in visitors well in check.... Then, we walked farther back into the grounds to where the dogs were living. Even

> before we arrived at their enclosure, the dogs ran toward us, barking, yapping excitedly, and wagging their tails strenuously.... [Soon] there was a cacophony of crazy, excited dogs charging up and down alongside the fence. (pp. 119-120)

Wynne's anecdote clearly shows the strong desire of dogs to engage socially with humans. Unlike wolves, dogs seem to find interacting with humans to be highly rewarding. But dogs do not respond that way unless they have been socialized to humans soon after birth (Wynne & Udell, 2020). Socialization requires close contact with and handling by humans. Unsocialized dogs often respond to humans with fear and aggression.

Why do socialized dogs and wolves respond so differently to humans? To answer this question, we first will look at research on a human neurodevelopmental disorder called "Williams-Beuren syndrome" (WBS). This syndrome is marked by extreme friendliness and a strong desire to interact with others including strangers. The unusual social behavior of people with WBS is similar to that of dogs. This similarity led canine researchers to wonder if the biological factors underlying WBS might help them understand the social behavior of dogs.

What is WBS?

WBS is a congenital disorder comprising a cluster of physical, physiological, psychological, and behavioral symptoms (Martens et al., 2008; Waz & Lee, 2022). People with WBS show greatly increased sociability. Sociability is the degree to which one seeks out others and interacts with them in social activities. People with WBS express three psychological characteristics associated with their heightened sociability (Järvinen et al., 2013; Jones et al., 2017; Woodruff-Borden et al., 2010):

- They experience low levels of social anxiety.
- They focus their attention primarily on other people
- They are driven to interact with others.

WBS and Social Anxiety

Infants typically develop "stranger anxiety" (i.e., a fear of unfamiliar people) before their first birthdays (Sroufe, 1977). Infants with WBS, however, rarely develop stranger anxiety (Sampaio et al., 2018). In fact, these infants often stare directly into the eyes of nearby strangers unlike most other infants who tend to avoid looking at strangers' faces once they develop stranger anxiety.

People with WBS also rarely develop other common types of social anxiety that tend to appear later in childhood and adolescence. For example, few people with WBS develop "performance anxiety," which is anxiety resulting from a fear of being judged negatively by others (American Psychiatric Association, 2013).

This lack of social anxiety in WBS Typically continues through the rest of life.

WBS and Attentional Bias to Others

WBS is characterized by a strong tendency to focus attention on nearby people and to ignore other events, even potentially rewarding ones (Jones et al., 2000). For example, a child with WBS might ignore a piece of candy in order to converse with a stranger. This characteristic is known as "attentional bias to social stimuli." In one experiment, toddlers with WBS performed a task that required them to watch an adult hide a toy behind a barrier so that they could retrieve it later. But rather than watching where the toy was placed, the toddlers looked instead at the adult's face while smiling and talking continuously.

WBS and Social Interactions

Attentional bias in WBS is usually coupled with a strong drive to interact with others:

> Infants, toddlers, children, and adults with [WBS] frequently come directly up to and begin engaging strangers. Parents report attempts to train their [WBS] child (e.g., adolescent daughter) not to talk to strangers—to no avail. The parent may then watch in private horror as their [WBS] daughter walks up to a complete stranger in a public place, looks him right in the eye and then asks in a friendly and engaging manner, "Are you a stranger?" (Jones et al., 2000, p. 31)

It seems that people with WBS find interacting with other people to be highly rewarding. As noted earlier, dogs also seem to find interacting with people to be highly rewarding. Similarities like this one are what led canine researchers to look to research on WBS to develop hypotheses about the biological causes of dog sociability.

What Is Hypersociability?

The increased sociability observed in WBS often is referred to as "hypersociability." Hypersociability consists of two of the psychological characteristics listed above:

- attentional bias to social stimuli and
- a strong drive to interact with others.

Both aspects of hypersociability are illustrated in the following anecdote shared by a deaf person who worked with young WBS research participants:

> The [WBS] children … typically come right up close to me, look me in the face, smile broadly at me, and talk to me even though I sign to them that I can't hear or speak. They seem to be fascinated, continuing to smile and talk to me, all the time looking right into my face while they try to imitate my signs. (Jones et al., 2000, p. 36)

This anecdote reveals the endearing personalities of WBS children. But it also hints at a potential difficulty in their social interactions: they seem to have little awareness of subtle social signals, primarily nonverbal, that provide a fuller picture of what others are thinking and feeling (Haas et al., 2009).

Nonverbal Communication and Theory of Mind

We are "social animals" (Aronson, 1972): we are immersed in social groups from birth to death. This immersion in social groups requires us to constantly adjust our behaviors to the ever-changing behaviors of others—to adapt to our social environments in order to achieve our social goals. In order to adapt and interact meaningfully with other people, we must infer what they are thinking and feeling. These inferences require us to interpret not only what other people are saying, but also how they say it.

The ability to infer what others are thinking and feeling draws on a set of cognitive skills collectively called Theory of Mind (Wellman, 2017). *Theory of Mind* (ToM) allows us to infer the internal mental states, intentions, beliefs, desires, and feelings of others from their external behaviors

(Kliemann & Adolphs, 2018; Schaafsma et al., 2015). For example, if someone says that she is "doing fine" with a strained smile, a shaky voice, and tears in her eyes, we will infer that she is not really doing fine regardless of what she said. With ToM, we are able to take the perspective of others—to see the world through their eyes, so to speak.

People with WBS, on the other hand, show lower levels of ToM (Toth, 2019). In the example of the sad girl, they might be more likely to focus on her spoken words and to misinterpret her smile as expressing happiness (Haas et al, 2009).

How Can WBS Help Us Understand Dog Sociability

Let's now try to answer the question asked earlier: why do socialized dogs and wolves respond so differently to humans? Canine researchers have proposed two hypotheses to answer this question (Wynne & Udell, 2020):

- Dogs evolved a human-like ToM, which is based in cognition. Cognition refers to the skills and abilities that form the basis of knowing the world.
- Dogs evolved the trait of hypersociability, which is based on emotion. These emotions involve the feelings, desires, and motivations underlying social attachments.

Hypothesis 1: Theory of Mind

Just like humans, dogs are highly social animals. Dogs must constantly adjust their behavior not only to the ever-changing behavior of other dogs, but also to the behavior of humans because they depend on humans for their survival. Thus, the evolution of ToM would be highly adaptive for dogs.

Dogs express some behaviors consistent with ToM. For instance, dogs recognize the emotions felt by humans from their facial expressions and vocalizations (Albuquerque et al., 2016). In addition, dogs find hidden food when a human points to its hiding place (Hare et al., 2002).

However, these behaviors are not unique to dogs. Socialized wolves also go to a spot to find food when a human points to it (VonHoldt et al., 2017; Wynne, 2019; Wynne & Udell, 2020). In fact, other animal species, including rats, go to a spot when a human points to it. Rats are unlikely to have human-like cognitive abilities such as perspective-taking. Furthermore, most animals do not perform this feat unless they have had extensive experience with humans. This finding suggests that the animals learn to go anywhere a human points because this behavior has been rewarded in the past.

Hypothesis 2: Hypersociability.

As noted earlier, hypersociability has two aspects: attentional bias to people and a strong drive to engage others socially. The hypersociability hypothesis states that the special bond between dogs and humans is an emotional one, not one based on advanced cognitive abilities like ToM (Wynne, 2019). To test the hypersociability hypothesis, canine researchers developed tasks that measured "human-directed sociability" in dogs and socialized wolves (Von Holdt et al., 2017). These tasks measured three aspects of human-directed sociability: attentional bias to people, desire to interact with a familiar person, and desire to interact with a stranger.

The first task measured attentional bias to people. The task required dogs and wolves to figure out how to open a box that contained a small piece of summer sausage. Dogs and wolves performed this task under two conditions: a human was either present or absent. In both conditions, socialized wolves focused their attention on opening the box, and almost all were successful. Dogs, on the other hand, spent more time looking at the human when one was present and much less time looking at or trying to open the box. But whether a human was present or absent, few dogs were successful at opening the box and getting the reward.

The second task assessed the desire of dogs and socialized wolves to interact with a familiar person (i.e., their owner or caretaker). The person sat in a chair placed in the center of a circle one meter in diameter and encouraged the dog or wolf to approach. Observers recorded the amount of time the dog or wolf spent within the circle. Dogs spent much more time within one meter of the familiar person than wolves did.

The third task assessed the desire of dogs and socialized wolves to interact with a stranger. The procedure was similar to the one used in the previous task with the familiar person. The researchers predicted that dogs would spend more time than wolves within one meter of the stranger. Although dogs spent more absolute time near the stranger, the difference between dogs and wolves was not statistically significant. This result, however, may have been due to the small number of dogs and wolves observed (18 dogs and 10 wolves).

In summary, although dogs may show some signs of human-like perspective taking, socialized wolves do not differ with respect to ToM. But dogs and wolves show large differences in sociability. The "attentional bias" task clearly demonstrated the different degrees of sociability in the two subspecies:

> Wolves did show social interest in their caretakers, approaching them for greetings when they entered during the sociability test in this study. However, they then returned to other activities…., whereas the prolonged greeting of [domestic] dogs … would be considered exaggerated or hypersocial. (VonHoldt et al., 2017)

In other words, dogs are more similar in their social behavior to people with WBS than they are to socialized wolves. The most likely cause of this difference is selection for hypersociability beginning early in the domestication process.

Puppy Love: Neoteny and the Evolution of Hypersociability in Dogs

Wolves and dogs differ in several ways with respect to sociability and the development of attachments to humans (Herbeck et al., 2022; Wynne, 2019; Wynne & Udell, 2020):

- Wolves require intensive daily contact with humans to form attachments, whereas dogs require only short periods of daily contact.
- Wolves can bond with humans only during the first few weeks of life. Dogs can bond with humans throughout their lives.

Because the “sensitive period” for forming social attachments is so short in wolves, they are able to bond closely with only a small number of humans. But dog domestication has resulted in an extension into adulthood of the sensitive period for forming attachments to humans. Furthermore, dogs do not need much contact with humans to develop strong bonds with them. Dogs, therefore, can bond with many humans over their lives. In short, domestication has resulted in adult dogs expressing some of the behaviors and traits characteristic of juvenile wolves. The continuation into adulthood of traits characteristic of juveniles of the ancestral population is known as *neoteny* (Price, 1999; Wynne, 2019).

Artificial selection for social bonding with humans beyond the first weeks of life probably resulted in the evolution of dog hypersociability (Herbeck et al., 2022):

- Ancient humans selected for decreased fear of and aggression towards humans.
- The decreased fear and aggression aided the formation of social attachments.
- Humans then selected dogs that formed stronger social attachments with humans.
- The strongest social attachments were demonstrated by hypersociable behaviors.

Selection for the formation of strong social attachments over many generations led to an extension of the sensitive period for forming such attachments from the first weeks of life to later and later stages of development. In other words, the period of "puppy love" eventually extended into adulthood.

The fact that dogs form social attachments to humans well beyond the sensitive period of wolves may be related to the reduced/absent stranger anxiety shown by infants with WBS. The decreased anxiety to unfamiliar people shown by these infants allows them to form social attachments to new people more easily than other infants. Could something like reduced "stranger anxiety" form the basis of hypersociability in dogs? And more generally, can our understanding of the biological causes of WBS help us understand the development of hypersociability in dogs?

Heredity and WBS

Although WBS is not usually passed from one generation to the next, heredity is still the most important cause of the syndrome. Heredity refers to the transmission of biological units called genes, which are bits of chemical information arranged along chromosomes. Chromosomes are threadlike bodies located in the nucleus of cells. Humans typically have 46 chromosomes, 23 of which are inherited from fathers and 23 from mothers.

As shown in Figure 3, chromosomes come in pairs, one from each parent, and are numbered from the largest (*chromosome 1*) to the smallest (*chromosome 22*). The X and Y chromosomes, which make up the twenty-third pair, are distinguished not on the basis of size, but on the basis of function: they are associated with sex development. Females have two X chromosomes, and males have one X and one Y.

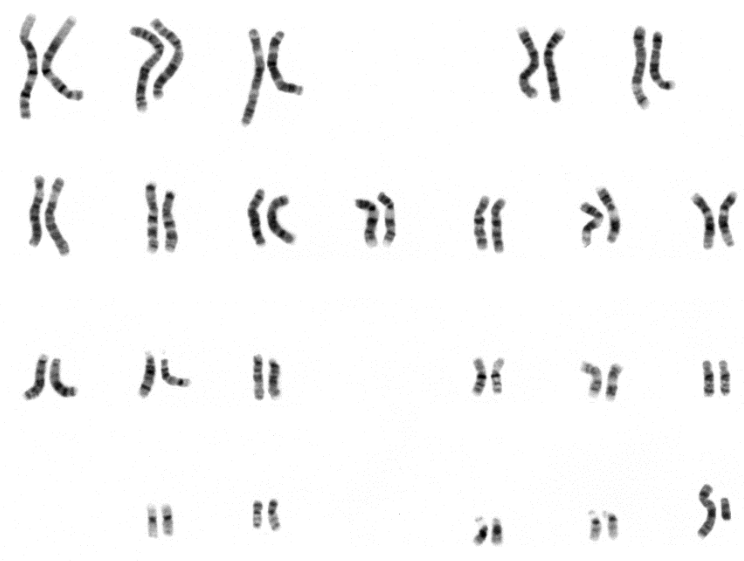

Figure 3. A karyotype of a human male showing the 23 pairs of replicated chromosomes. The 23rd pair consists of an X and a Y chromosome. Female karyotypes are similar except that the 23rd pair consists of two X chromosomes.

Each chromosome contains a molecule of deoxyribonucleic acid (DNA). Genes are arrayed along chromosomes and consist of short segments of the DNA molecule. Each gene on a chromosome has a corresponding gene on the paired chromosome.

Many genes produce biochemicals used to make proteins. These proteins are used in bodily development. Let's look closely at an example of how genes function during development.

Most of us have heard of the A, B, and O blood types. The gene associated with these blood types is on Chromosome 9 (Ah-Moye et al., 2014). Each of the two chromosomes contain a blood-type gene, and each gene makes a biochemical used to produce proteins. Although the two corresponding genes are associated with the production of the same protein category, the particular biochemical made from each may differ a bit. That is, the gene may have different variants. The A-B-O blood-type gene has three main variants: the A, B, and O variants. If one chromosome of the pair has the A variant and the other chromosome has either the A or the O variant, the individual will express blood type A. The other blood types develop when other combinations of the gene variants are inherited.

Sometimes a gene is deleted during the production of sperm and eggs, which means that its protein-building product does not get produced. WBS is associated with the deletion of 25 to 28 adjoining genes on one of the two *chromosomes 7* in what is referred to as the *Williams-Beuren (WB) Critical Region* (Järvinen et al., 2013; Morris, 2010; Waz & Lee, 2022). Thee other *chromosome 7* has the complete set of genes, which means that people with WBS have only one copy of each gene in this region rather than the normal number of two copies. Because these individuals have only half the normal number of genes in the WB Critical Region, their cells make only half the amount of the protein-building product of each of these genes.

Although researchers have not identified all of the deleted genes responsible for the physical, psychological, and behavioral features of WBS, they have identified several that are important for sociability and related traits, such as empathy (Sampaio et al., 2018; Toth, 2019; Von Holdt et al., 2017). They identified these genes by observing how partial deletions of the WB Critical Region affect a person's behavior. Two genes, GTF2I and GTF2IRD1, stood out in these studies. These two genes code for "transcription factors," which are proteins that bind to particular sequences of DNA. When a transcription factor binds to a DNA sequence, it increases or decreases the activity of any gene containing that sequence. Each transcription factor, therefore, affects the activity of many genes.

When all WBS genes except GTF2I and GTF2IRD1 are deleted, people with WBS do not exhibit hypersociability. This result suggests that GTF2I and GTF2IRD1 need to be deleted in order for hypersociability to develop. When the WB Critical Region is mostly intact, but GTF2I is deleted, people express low levels of social anxiety but no other features of WBS.

The reliability of these findings, however, is questionable because they are based on a small number of cases. People rarely have a partially deleted WB Critical Region. So researchers looked elsewhere for evidence that deletions of specific genes caused the hypersociable behaviors of WBS.

Researchers found that they could collect large sample sizes in other mammals that have the WB Critical Region, such as mice. In what are known as "knockout mice," researchers inactivate single genes so that they no longer produce proteins (Koppet al., 2019). With knockout mice, researchers have found that the effects of genes in the WB Critical Region are similar to their effects in humans. For example, when mouse researchers inactivate GTF2IRD1, which mimics the gene deletion in WBS, mice engage in more positive social interactions and fewer negative (aggressive) interactions towards unfamiliar mice.

Recently, researchers performed a Critical test of the idea that the two GTF genes produce the symptoms of WBS. They did this by inactivating GTF2I and GTF2IRD1 in a line of mice (Kopp et al., 2019). The results showed that the two genes may be necessary, but are not sufficient, to produce the symptoms of WBS (Sampaio et al., 2018).

Another way to study the effects on sociability of genes in the WB Critical Region is to look at what happens when these genes are duplicated. Gene duplications occur when a portion of the DNA containing a gene appears more than once along a chromosome because of copying errors. Gene duplications in the WB Critical Region should produce behaviors opposite to those of WBS. Researchers have confirmed this prediction: people with gene duplications in the WB Critical Region show higher levels of separation anxiety or lower levels of prosocial behaviors (Sampaio et al., 2018).

Taken together, findings such as those described above provide compelling evidence that genes in the WB Critical Region, particularly GTF2I and GTF2IRD1, are linked to differences in sociability in humans, mice, and perhaps dogs and other mammals.

Heredity and Hypersociability in Dogs

Dogs and wolves have 39 pairs of chromosomes and contain a WB Critical Region on Chromosome 6 (VonHoldt et al., 2017; VonHoldt et al., 2018). If these genes have functions similar to those in the WB Critical Region of humans and mice, then dog hypersociability may be due to evolutionary changes in this region. In fact, Canine researchers found that genes in this region have been subjected to intense artificial selection throughout the domestication of dogs (Li et al., 2013).

Geneticists have identified a number of genes in this region important for dog hypersociability (VonHoldt et al., 2017). Two of these genes are the transcription factors, GTF2I and GTF2IRD1, which, as discussed earlier, also are important for hypersociability in humans with WBS. The effects of GTF2I and GTF2IRD1 seem to be primarily on brain development in dogs (Li et al., 2013). The effects on brain development are unsurprising: the development of psychological and behavioral traits often depend on brain activity (Kolb & Whishaw, 2021; MacLean et al., 2019).

Conclusion

Sociability is a trait essential to the survival and reproductive success of all "social mammals." In the case of dogs, their extreme sociability extends beyond species boundaries to include humans. Because of their dependence on humans, the extreme sociability of dogs has made them remarkably successful reproductively compared to their cousin, the grey wolf. The population of dogs worldwide is about 400 million, whereas wolves' number only about 200,000 (Harari, 2014). In the United States, about 90 million dogs are kept as pets (Wynne & Udell, 2020). Assuming that there are about 135 million households, that makes one dog for every 1.5 households. Many humans, it seems, place great importance on their relationships with dogs (Sykes, 2018). If we are to develop a more-complete understanding of human nature, we need to consider why this is so.

We humans have strong emotions associated with our social worlds. In fact, large areas of the brain are dedicated to social emotions such as empathy, jealousy, guilt, attraction, etc. (Kolb & Whishaw, 2021). We have a strong need to develop and maintain social attachments (i.e., a strong need for affiliation; Murray, 1938). It seems that the devotion that many humans feel for their dogs is associated with their need for affiliation. This explains, I propose, why ancient humans started to domesticate wolves and selected dogs to be hypersociable: dogs satisfy our most fundamental social emotional needs.

We humans have achieved some remarkable things over our short time on earth. We have split the atom, traveled to the moon and back, created massive civilizations, cured diseases that annihilated much of the world's population just a few centuries ago, and so on. But our greatest achievement, I argue, is the domestic dog. We have crafted a companion that satisfies our most basic affiliative needs in a universe that sometimes seems to take little notice of our existence. We are here for a very short time and then we are gone. If we are lucky, we have a small number of people who care about us through our lives. But our dogs are the closest thing to complete acceptance and unconditional love that we could ever hope to attain.

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Image References

Figure 1.

URL: https://www.ancient-origins.net/history/26000-year-old-child-footprints-found-alongside-paw-prints-reveal-oldest-evidence-human-021235

accessed 7 Sep 2022

Title: 26,000-Year-Old Child Footprints Found Alongside Paw Prints Reveal Oldest Evidence of Human-Canine Relationship

Date: 18 Feb 2017

Figure 2.

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Figure 3.

URL: https://en.wikipedia.org/wiki/File:NHGRI_human_male_karyotype.png#filelinks

accessed 7 Sep 2022]

The image is in the public domain.

References

Ah-Moye, D., Davies, C., Goody, J., Hayward, P., & Frewin, R. (2014). *Introduction to Hematology and Transfusion Science: Metabolic and Clinical Aspects,* 497. http://dx.doi.org/10.1016/B978-0-7020-5140-1.00026-2

Albuquerque, N., Guo, K., Wilkinson, A., Savalli, C., Otta, E., & Mills, D. (2016). Dogs recognize dog and human emotions. *Biology Letters, 12*(1), 20150883. https://doi.org/10.1098/rsbl.2015.0883

American Psychiatric Association. (2013). *Diagnostic and Statistical Manual of Mental Disorders (5th ed.).* https://doi.org/10.1176/appi.books.9780890425596

Aronson, E. (1972). *The Social Animal*. New York: Viking.

Freedman, A. H., Gronau, I., Schweizer, R. M., Ortega-Del Vecchyo, D., Han, E., Silva, P. M., ... & Novembre, J. (2014). Genome sequencing highlights the dynamic early history of dogs. *PLoS Genetics, 10*(1), e1004016. http://dx.doi.org/10.1371/journal.pgen.1004016

Freedman, A. H., & Wayne, R. K. (2017). Deciphering the origin of dogs: From fossils to genomes. *Annual Review of Animal Biosciences, 5*, 281-307. http://dx.doi.org/10.1146/annurev-animal-022114-110937

Haas, B. W., Mills, D., Yam, A., Hoeft, F., Bellugi, U., & Reiss, A. (2009). Genetic influences on sociability: Heightened amygdala reactivity and event-related responses to positive social stimuli in Williams syndrome. *Journal of Neuroscience, 29*(4), 1132-1139. http://dx.doi.org/ 10.1523 /1N EU ROSCI.5324-08.2009

Harari, Y. N. (2014). *Sapiens: A Brief History of Humankind.* Random House.

Hare, B., Brown, M., Williamson, C., & Tomasello, M. (2002). The domestication of social cognition in dogs. *Science, 298*(5598), 1634-1636. http://dx.doi.org/10.1126/science.1072702

Herbeck, Y. E., Eliava, M., Grinevich, V., & MacLean, E. L. (2022). Fear, love, and the origins of canid domestication: An oxytocin hypothesis. *Comprehensive Psychoneuroendocrinology, 9*, 100100. http://dx.doi.org/10.1016/j.cpnec.2021.100100

Hughes, J. F., Skaletsky, H., Pyntikova, T., Minx, P. J., Graves, T., Rozen, S., ... & Page, D. C. (2005). Conservation of Y-linked genes during human evolution revealed by comparative sequencing in chimpanzee. *Nature, 437*(7055), 100-103. http://dx.doi.org/10.1038/nature04101

Järvinen, A., Korenberg, J. R., & Bellugi, U. (2013). The social phenotype of Williams syndrome. *Current Opinion in Neurobiology, 23*(3), 414-422. http://dx.doi.org/10.1016/j.conb.2012.12.006

Jones, W., Bellugi, U., Lai, Z., Chiles, M., Reilly, J., Lincoln, A., & Adolphs, R. (2000). II. Hypersociability in Williams syndrome. *Journal of Cognitive Neuroscience, 12*(Supplement 1), 30-46. http://dx.doi.org/10.1162/089892900561968

Kliemann, D., & Adolphs, R. (2018). The social neuroscience of mentalizing: Challenges and recommendations. *Current Opinion in Psychology, 24*, 1-6. http://dx.doi.org/10.1016/j.copsyc.2018.02.015

Koch, E. M., Schweizer, R. M., Schweizer, T. M., Stahler, D. R., Smith, D. W., Wayne, R. K., & Novembre, J. (2019). De novo mutation rate estimation in wolves of known pedigree. *Molecular Biology and Evolution, 36*(11), 2536-2547. http://dx.doi.org/10.1093/molbev/msz159

Kolb, B., & Whishaw, I. Q. (2021). *Fundamentals of Human Neuropsychology (8th ed.).* New York: Worth.

Kopp, N., McCullough, K., Maloney, S. E., & Dougherty, J. D. (2019). Gtf2i and Gtf2ird1 mutation do not account for the full phenotypic effect of the Williams syndrome Critical Region in mouse models. *Human Molecular Genetics, 28*(20), 3443-3465. http://dx.doi.org/10.1093/hmg/ddz176

Li, Y., Vonholdt, B. M., Reynolds, A., Boyko, A. R., Wayne, R. K., Wu, D. D., & Zhang, Y. P. (2013). Artificial selection on brain-expressed genes during the domestication of dog. *Molecular Biology and Evolution, 30*(8), 1867-1876. http://dx.doi.org/10.1093/molbev/mst088

MacLean, E. L., Snyder-Mackler, N., VonHoldt, B. M., & Serpell, J. A. (2019). Highly heritable and functionally relevant breed differences in dog behaviour. *Proceedings of the Royal Society B, 286*(1912), 20190716. http://dx.doi.org/10.1098/rspb.2019.0716

Martens, M. A., Wilson, S. J., & Reutens, D. C. (2008). Williams syndrome: a critical review of the cognitive, behavioral, and neuroanatomical phenotype. *Journal of Child Psychology and Psychiatry, 49*(6), 576-608. http://dx.doi.org/10.1111/j.1469-7610.2008.01887.x

Miao, B., Wang, Z., & Li, Y. (2017). Genomic analysis reveals hypoxia adaptation in the Tibetan Mastiff by introgression of the gray wolf from the Tibetan Plateau. *Molecular Biology and Evolution, 34*(3), 734-743. http://dx.doi.org/10.1093/molbev/msw274

Morris, C. A. (2010). Introduction: Williams syndrome. *American Journal of Medical Genetics Part C: Seminars in Medical Genetics, 154(*2), 203-208. http://dx.doi.org/10.1002/ajmg.c.30266

Murray, H. A. (1938). *Explorations in Personality: A Clinical and Experimental Study of Fifty Men of College Age.* New York: Oxford University Press.

Ostrander, E. A., Wayne, R. K., Freedman, A. H., & Davis, B. W. (2017). Demographic history, selection and functional diversity of the canine genome. *Nature Reviews Genetics, 18*(12), 705-720. http://dx.doi.org/10.1038/nrg.2017.67

Perri, A. R., Feuerborn, T. R., Frantz, L. A., Larson, G., Malhi, R. S., Meltzer, D. J., & Witt, K. E. (2021). Dog domestication and the dual dispersal of people and dogs into the Americas. *Proceedings of the National Academy of Sciences, 118*(6). https://doi.org/10.1073/pnas.2010083118

Price, E. O. (1999). Behavioral development in animals undergoing domestication. *Applied Animal Behaviour Science, 65*(3), 245-271. http://dx.doi.org/10.1016/S0168-1591(99)00087-8

Sampaio, A., Belsky, J., Soares, I., Mesquita, A., Osório, A., & Gonçalves, Ó. F. (2018). Insights on social behavior from studying Williams syndrome. *Child Development Perspectives, 12*(2), 98-103. http://dx.doi.org/10.1111/cdep.12263

Schaafsma, S. M., Pfaff, D. W., Spunt, R. P., & Adolphs, R. (2015). Deconstructing and reconstructing theory of mind. *Trends in Cognitive Sciences, 19*(2), 65-72. http://dx.doi.org/10.1016/j.tics.2014.11.007

Serpell, J. A. (2021). Commensalism or cross-species adoption? A critical review of theories of wolf domestication. *Frontiers in Veterinary Science, 8*, 281. http://dx.doi.org/10.3389/fvets.2021.662370

Signore, A. V., Yang, Y. Z., Yang, Q. Y., Qin, G., Moriyama, H., Ge, R. L., & Storz, J. F. (2019). Adaptive changes in hemoglobin function in high-altitude Tibetan canids were derived via gene conversion and introgression. *Molecular Biology and Evolution, 36*(10), 2227-2237. http://dx.doi.org/10.1093/molbev/msz097

Speakman, J. R., Van Acker, A., & Harper, E. J. (2003). Age-related changes in the metabolism and body composition of three dog breeds and their relationship to life expectancy. *Aging Cell, 2*(5), 265-275.

Sroufe, L. A. (1977). Wariness of strangers and the study of infant development. *Child Development*, 731-746. http://dx.doi.org/10.2307/1128323

Svartberg, K. (2006). Breed-typical behaviour in dogs—historical remnants or recent constructs?. *Applied Animal Behaviour Science, 96*(3-4), 293-313. http://dx.doi.org/10.1016/j.applanim.2005.06.014

Sykes, B. (2018). *Once a Wolf: The Science Behind Our Dogs' Astonishing Genetic Evolution.* New York: Norton & Co.

Toth, M. (2019). The other side of the coin: Hypersociability. *Genes, Brain and Behavior, 18*(1), e12512. https://doi.org/10.1111/gbb.12512

VonHoldt, B. M., Shuldiner, E., Koch, I. J., Kartzinel, R. Y., Hogan, A., Brubaker, L., ... & Udell, M. A. (2017). Structural variants in genes associated with human Williams-Beuren syndrome underlie stereotypical hypersociability in domestic dogs. *Science Advances, 3*(7), e1700398. http://dx.doi.org/10.1126/sciadv.1700398

Waz, W. R., and Lee, T. M. (2022). Williams syndrome. *UpToDate.* Retrieved February 13,2022, from https://www.uptodate.com/contents/williams-syndrome

Wellman, H. M. (2017). The development of theory of mind: Historical reflections. *Child Development Perspectives, 11*(3), 207-214. http://dx.doi.org/10.1111/cdep.12236

Woodruff-Borden, J., Kistler, D. J., Henderson, D. R., Crawford, N. A., & Mervis, C. B. (2010, May). Longitudinal course of anxiety in children and adolescents with Williams syndrome. *American Journal of Medical Genetics Part C, 154*(2), 277-290). http://dx.doi.org/10.1002/ajmg.c.30259.

Wynne, C. D. (2019). *Dog is Love.* New York:Mariner.

Wynne, C. D., & Udell, M. A. (2020). *Animal Cognition: Evolution, Behavior and Cognition.* Bloomsbury Publishing.