Comparisons of laterality between wolves and domesticated dogs (*Canis lupus familiaris*)

By

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Abstract

I compared laterality in *Canis lupus familiaris* (domesticated dog) with: *Canis lupus occidentalis* (Canadian Rocky Mountain wolves), *Canis rufus* (red wolves), *Canis lupus baileyi* (Mexican wolves), and *Canis lupus arctos* (Artic wolf), all related. Each wolf species was grouped into a single category and was compared to domesticated dogs. The methods performed on domesticated dogs were the Kong™ test and the step test. For wolves the PVC test was created to simulate the Kong™ test and a step test for comparison. My hypothesis was that *Canis lupus familiaris* and *Canis lupus* will show consistent lateralized preferences between both species. The significance of this study is that laterality in *Canis lupus familiaris* has been studied multiple times with varying results. The purpose is to determine the possibility of laterality in *Canis lupus familiaris* being a conserved trait. This study has the potential to give greater meaning to laterality and the benefits of right or left sidedness or handedness. The total amount of paw touches recorded under each category, for the step test in dogs were 280 (50.5%) left and 274 (49.5%) right, for the Kong™ test there were 278 left (50.3%) and 275 right (49.7%). In wolves, the step test 119 left (70%) and 51 right (30%), for the PVC test 447 (48.3%) left and 478 right (51.7%). When comparing the dogs' pawedness you find that, the step test had 40% of dogs preferring their left paw, 10% of dogs preferring their right paw, and 50% ambidextrous. The Kong™ test had 20% of dogs preferring their left paw 10% preferring their right paw, and 70% ambidextrous. When comparing the wolves' pawedness you find that the step test had 40% of wolves preferring their left paw, 40% of wolves preferring their right paw, and 20% ambidextrous, the PVC test had 11.2% of wolves preferring their left paw, 44.4% of wolves preferring their right paw, and 44.4% are ambidextrous.

Introduction

Laterality is the specific function of the left and right cerebral hemispheres; which may be responsible for both motor responses and the favored processing of stimuli. Lateralization may also have the potential to predict general behaviors and responses (Tomkins, Thomson, and Mcgreevy 2010). Human laterality has been a large topic of study for many years; more recently researchers have begun looking into the handedness of other vertebrates including cats, whales, amphibians, and dogs. These studies have shown that laterality may be a feature of all mammals and other vertebrates; leaving the question of whether non-human species have a consistent handedness and whether or not this handedness is consistent across the population (Wells 2002). In *Canis lupus familiaris* (domesticated dog) laterality has been studied, but with inconsistent results; mainly because the methods used to research their laterality have been inconsistent. The complexity of the task has also shown to influence the paw used to complete the task (Batt *et al.* 2008). The most recent approaches used to study dog laterality include: the Kong™ test, involving the dog toy Kong™ and observing the paw first used to grasp the toy; the first step test, involves having the dog walk downstairs and observing which paw stepped first (Tomkins, Thomson, and McGreevy 2010).

This study compares laterality in *Canis lupus familiaris* with: *Canis lupus occidentalis* (Canadian Rocky Mountain Wolves), *Canis rufus* (Red Wolves), *Canis lupus baileyi* (Mexican Wolves), and *Canis lupus arctos* (Artic Wolf). Each wolf species is grouped into one category and is compared to domesticated dogs. The methods performed on domesticated dogs are the Kong™ test and the first step test based on previous studies by Tomkins, Thomson, and McGreevy and Batt *et al.* For wolves the PVC (polyvinyl chloride) test was created to simulate the Kong™ test and a stepping testing for comparison. My hypothesis is that *Canis lupus familiaris* and *Canis lupus* will show consistent laterality between both species.

The significance of this study is that laterality in *Canis lupus familiaris* has been studied multiple times with varying results. I compared *Canis lupus familiaris* with *Canis lupus* laterality in order to look at the possibility that laterality is a conserved trait. Meaning, a gene that has remained unchanged as domesticated dogs evolved from wolves. This study has the potential to give a more significant meaning to laterality and the benefits of right or left handedness.

The domestic dog is a member of the Canidae family which includes thirty five species that deviated over the last ten million years. There are three major groups of the Canidae family: red fox-like canids, South American canids, and wolf-like canids; these three groups account for approximately ninety three percent of all living canids (Figure 1). As members of the order Carnivora, meaning animals that eat on flesh, they share many of the carnivorous characteristics, including: prominent canine teeth, molars for crushing and grinding, and a shorter alimentary canal. In a recent classification (Figure 2), the major divisions are Feliformia (cats) and the Caniformia (dogs) which is believed to have occurred between the Eocene and the Paleocene approximately forty to sixty million years ago (Evans and de Lahunta 2012).

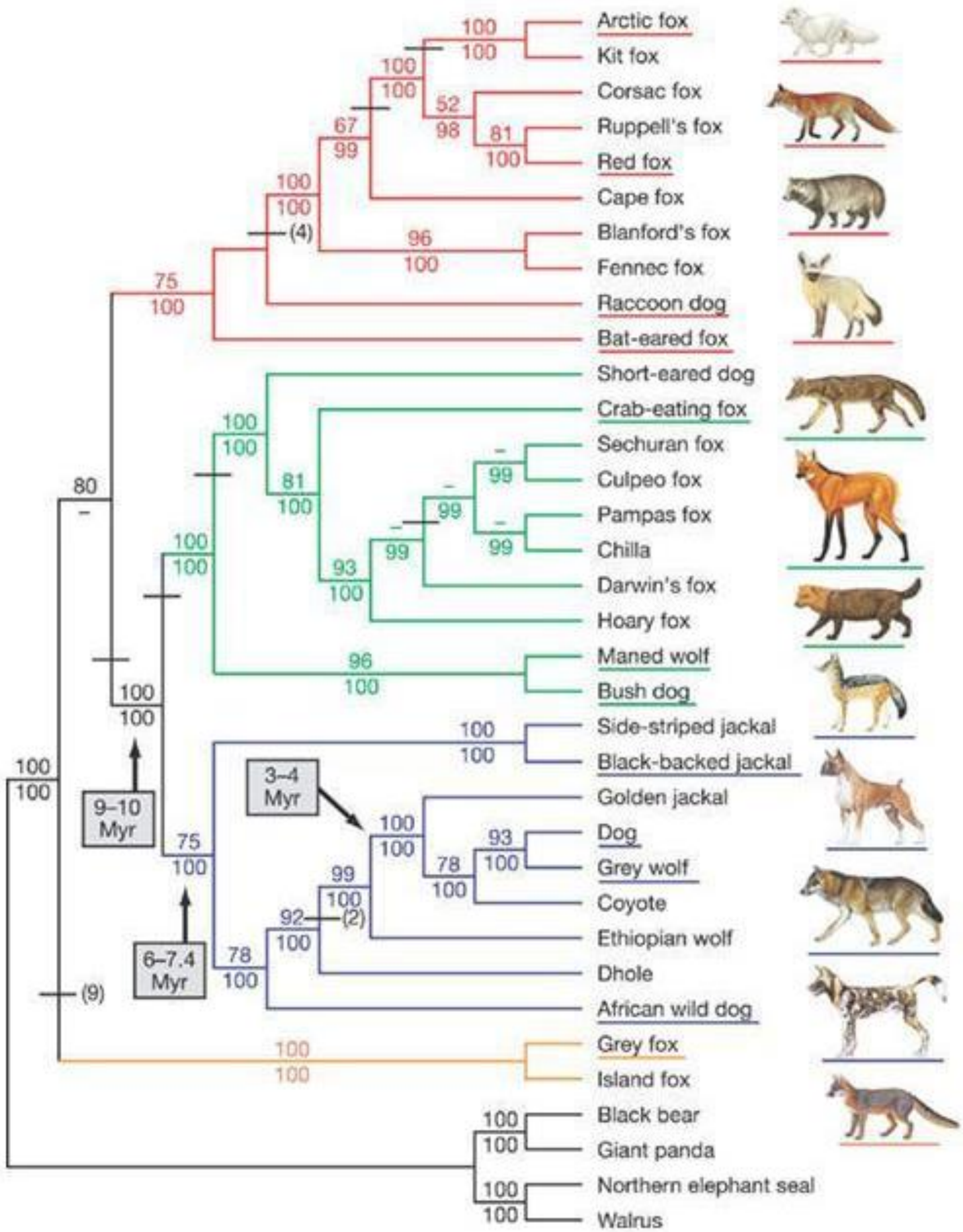

Figure 1-Phylogenetic relationships among canids: In red, are the red fox-like canids; in green, are the South American canids; in blue, are the wolf-like canids; and in orange are the island fox canids (Marshall-Pescini and Kaminski 2014).

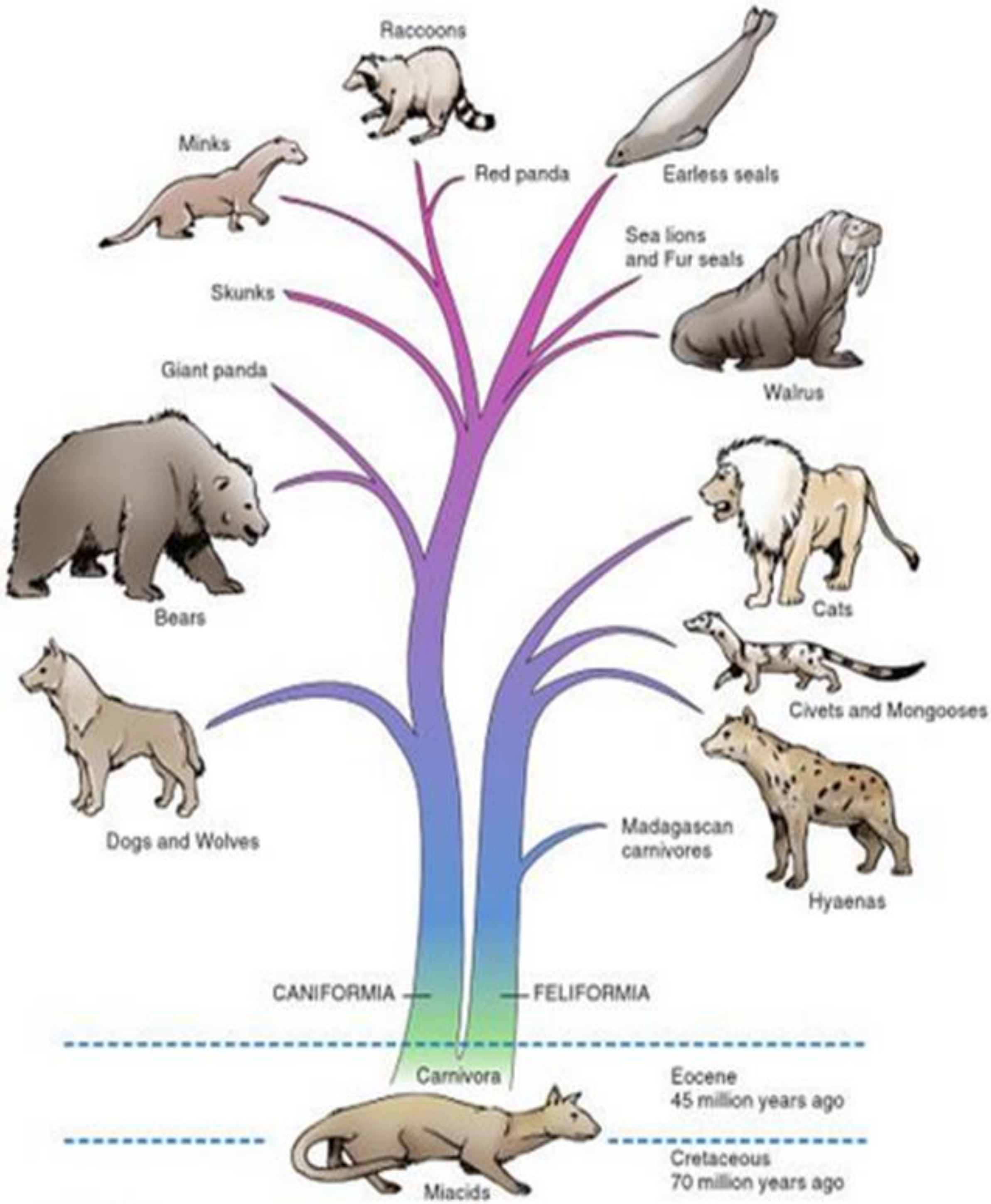

Figure 2- Members of the order Carnivora, separating into the two major groups of Caniformia (dog-like) and Feliformia (cat-like), (Evans and de Lahunta 2012).

Domestic dogs are most closely related to wolf-like canids; *Canis lupus* (gray wolves) are the closest living relative to the domestic dog and share 99.9 percent of their DNA (Science 2015). They have a close affiliation with coyotes, golden jackals, and Ethiopian wolves. All members of the genus *Canis* have the potential to interbreed and produce fertile offspring. The coywolf is a species that suggests that this is possible. Closest to the *Canis* genus are dhole and African wild dogs, although there exact relationship to *Canis* is still unknown (Marshall-Pescini and Kaminski 2014). Understanding dog evolution contributes to the understanding of the domestication process, as well as the lives of prehistoric humans (Science 2015).

Canids are believed to have separated from other mammals around forty million years ago. This is signified by encephalization involving: expansion of the prorean gyrus at the anterior end of the neocortex, an increase in the amount of infolding of the frontal lobe, and an expansion of the prefrontal cortex; this process also caused an architectural reorganization of the brain. It appears that this occurred in conjunction with the taxonomic diversification and expansion of the global grasslands during the late Miocene or early Pliocene (Marshall-Pescini and Kaminski 2014). There are multiple theories for what drove these changes in the brain. This includes the diversification of the environment; this is unlikely because increasing brain size is energetically expensive making it more likely that the cause would have to be a major adaptive advantage. This led to the theory that pack hunting may have been the driving cause, but encephalization appears to have occurred in all three living clades of canids and most smaller canids do not hunt in packs; the most shared trait among canids is monogamy making this the most likely cause. Monogamy refers to a single male and female mating exclusively with each other over multiple reproductive cycles; this theory is favored because it corresponds with studies that have shown that species living in pair bonded social systems have the largest brains (Marshall-Pescini and Kaminski 2014).

Canids are the most widespread family and inhabit every continent, except Antarctica. Hunting strategies among canids vary, ranging from species that feed solely on fish and insects to hypercarnivore species that hunt in packs. Sociality and hunting cooperatively are closely linked in canids; species that hunt in packs are known to be more social. Researchers have found that pack hunting may be the driving force for steering canid sociality. Leading to the question of whether canid species live in larger groups so they can hunt larger prey, or does availability of larger prey oblige them to larger groups? More recent studies have concluded that wolves in groups larger than four appear to have a significantly reduced hunting success due to an increase in “free riders” that do not assist in the take down of prey, but reap the rewards (Marshall-Pescini and Kaminski 2014).

Among evolutionary scientists the main question of dog evolution is why were wolves or an ancestor of wolves, able to domesticate into today’s dog? Collected data shows, grey wolves are genetically, morphologically, and behaviorally the closest living relative to domesticated dogs. Specific canid characteristics may be responsible for their ability to be domesticated. As monogamous creatures this may have allowed them to establish long term relationships with one individual, in the case of domestication, humans. What is still unknown is the direct cause of this relationship, were wolves just in the right place at the right time? The social behavior of many species is still poorly understood with some basic information missing for many species. Most studies focused on the social behavioral ecology of the species; there has been little data collected on the relationship of social behavior in regards to: social organization, affiliate relationships, coalition-alliance formation, and group dynamics (Marshall-Pescini and Kaminski 2014).

There have been numerous theories proposed for domestication processes. Dogs have been an extremely successful species, wherever there are humans there are dogs. The first species to be domesticated by humans was dogs and canid remains have been found with humans over one hundred thousand years ago that were wolf-like, with signs of domestication (Marshall-Pescini and Kaminski 2014). Morphological features used to determine domestication in prehistoric canid skulls have been shortening of the facial region and the reduction in tooth size. Wolves have been found with humans over expansive time spans and location, signs of domestication on canid skulls found near humans only late in the Pleistocene period. A significant example of this is the Natufian site in Mallaha, Israel. The Natufian people were thought to have been hunters and gatherers with stable settlements and are thought of as the earliest farmers. The importance of dogs to the Natufian people is clear by their joint burials of dogs and humans (Figure 3), also the jewelry excavated with decorative dog head designs. These findings suggest a change in the way humans viewed dogs and dogs' significance to the Natufian society (Marshall-Pescini and Kaminski 2014).

Figure 3- Natufian burial of dog and human (Science 2015).

During the late Pleistocene age (2.5 million years ago through 11,700 years ago) and early Holocene age (11,700 years ago through the present), humans began to settle and agriculture began to replace hunter gather societies. Agriculture led to the domestication of plants and animals; human agriculture is closely connected to the first findings of dog specimens. Researchers have suggested that wolves may have approached human settlements, wolves may have continuously lived around human settlements, and wolves may have survived living off of human waste and leftovers. The self-domestication hypothesis depends on the domestication of wolves based on selection against aggression or fear. This is believed to be unintentional, humans did not actively pick certain individuals based on their perception of them being less aggressive; instead wolves that were less aggressive or less fearful towards humans had an advantage (Marshall-Pescini and Kaminski 2014).

An extensive set of experiments by Russian evolutionary biologist, Dmitri Belayev, applied selection pressures supervised during domestication by selecting for tameness and against aggression in *Vulpes vulpes* (silver fox). Tameness has been defined as the raising of wild animals with human contact, whereas domestication has been defined as the process of genetic selection resulting in an animal that has become substantially different from its ancestor. Foxes were divided into different groups based on their reaction toward a human hand reaching toward their cage. The three groups were: the non-domesticated group, which exhibited aggressive reactions; the intermediate group, which showed no signs of aggression toward the hand but no friendliness; the domesticated group, which displayed friendliness towards hands of caretakers (Marshall-Pescini and Kaminski 2014). After several generations the domesticated group showed clear signs of paedomorphic features including floppy ears and curly tails. This indicates that selection against aggression or fear towards humans can lead to behavioral and morphological changes in canid species. It was a common assumption that changes between dogs and their ancestors were the products of trait by trait selections akin to natural selections. It is more likely that these traits were inadvertent outcomes reinforced through artificial selection (Marshall-Pescini and Kaminski 2014).

Recent discoveries have challenged the belief that dog characteristics started late in the Pleistocene and early Holocene, since archaeological findings have traced the genetic origins of domestic dogs. The evidence includes skulls possessing clear signs of domestication found in Goyet Cave in Belgium and in the Altai Mountains in Russia (Marshall-Pescini and Kaminski 2014). Radiocarbon dating determined that skulls are over thirty thousand years old and are currently the oldest remains available. When the DNA of these skulls was compared to modern dog breeds, modern wolves, and prehistoric wolf specimens scientists concluded that the thirty thousand year old skulls were dog, not wolf. This new evidence indicates that the site of the origin of dogs was Europe. Skeptics of this research point out that this may just be an abnormal looking wolf, or possibly an early dog that did not give rise to today's canines (Science 2015). Additionally, there were also indications of sequences from modern dogs with ancient European specimens and with European wolves, but there has not been any association with modern wolf sequences from the Middle East or East Asia with today's dogs. If this recent evidence is accurate, then the story of how wolves became dogs is altered, because humans were still hunters and gathers at this time. Humans began settling at the end of the Pleistocene and the early Holocene, making it more likely that wolves followed humans while hunting and fed on leftovers. There have been ancient bones found with gnawing marks from larger mammals of the Pleistocene period, found near human remains; the marks were also comparable marks left by modern wolves. This supports the idea that wolves assisted in hunting or the possible existence of a proto dog (Marshall-Pescini and Kaminski 2014).

In order for relationships between humans and wolves to have lasted and developed to this extent, the relationship would have had to provide substantial advantages to both species, most likely the intake of food. A theory that humans may have learned to follow wolves to their selected prey and that the presence of wolves or a proto dog increased the hunting success, so food would be shared. The likely theory is that once prey was detected by wolves and the hunting began the faster wolves would chase down the prey and humans would finish the kill using weapons or tools (Marshall-Pescini and Kaminski 2014). This can be tied into the self-domestication hypothesis; this may have been the first wave of domestication that occurred between humans and wolves. A change in temperament due to self-domestication would still have a selection advantage in wolf individuals that were less fearful and aggressive around humans and more likely to join these hunting scenarios. It is likely that another wave of domestication occurred when humans began to settle and established agriculture, some ten thousand years ago, according to archaeologists. Humans and wolves coexisted leading to advantages that were significant enough for both species to continue maintaining proximity, a symbiotic relationship (Marshall-Pescini and Kaminski 2014).

The process of domestication caused both morphological and social changes in dogs. Domestication in dogs' morphology is similar to that of other domesticated species. When compared to wolves, dogs have: reduced cranial capacity, smaller teeth, and a greater variety of fur pigmentation (Figure 4). Dogs today have a variety of paedomorphic characteristics such as large eyes and short noses (Science 2015). These features may be linked to selection against aggression, or to return puppy-like features. The social differences between dogs and wolves include: the lack of pair bonding as the primary mating strategy, differences in parental investment, decrease in cooperative hunting strategies, and less stability in social groups. This information is not exact because approximately eighty three percent of dogs worldwide live without direct human influence (Marshall-Pescini and Kaminski 2014). Selective pressures associated with domestication that may have affected dogs social cognition comes from research showing that dogs seem to have extraordinary skills in understanding human forms of communication. This is most likely due to dogs evolving cognitive skills during domestication that are functionally equivalent to humans. Dogs outperform other species when it comes to their understanding of cooperative communicative signals including wolves. In identical environments what dogs and wolves learn originates from their performances and sensitivity and will inform us about the domestication process, more studies that are comparable are required (Marshall-Pescini and Kaminski 2014).

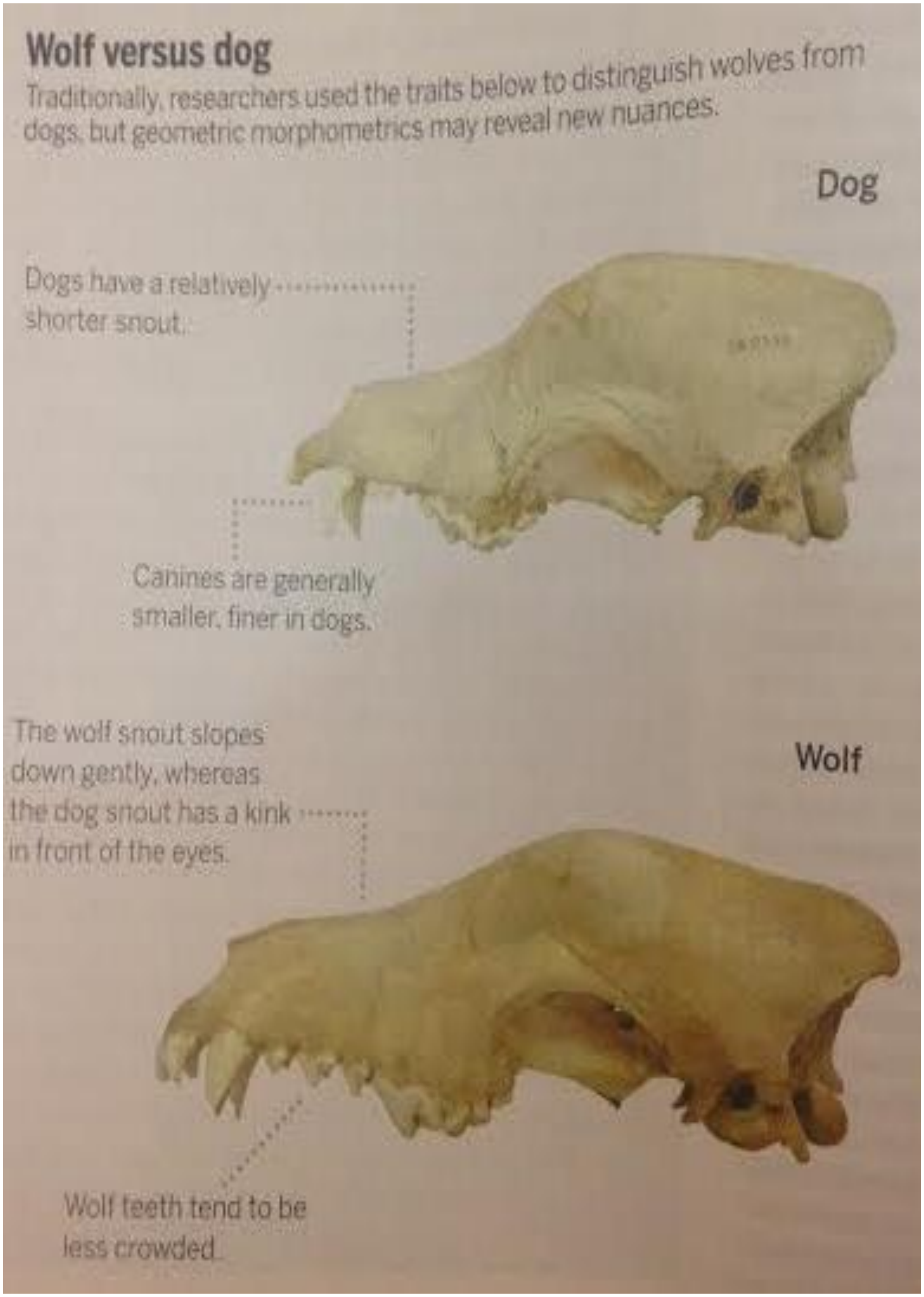

Figure 4- Differences in the skeletal structure of dogs and wolves (Science 2015)

The causes of genetic changes during dog domestication have two main modes. The first cause being, mutations that remained through fixation and then crossed into additional breeds. The second cause being, dogs that were bred to maintain specific traits. This type of selection causes clusters, or halotypes which are sets of DNA variations that are typically inherited together, for the genes possessing specific phenotypes and behavioral functions (Wayne and vonHoldt 2012). When the halotypes shared between dogs and gray wolves were analyzed the origins were shown to be derived from Middle Eastern or European wolves; this agrees with the archeological evidence discussed previously. Interestingly, when mitochondrial DNA (mtDNA) is examined the evidence indicates an East Asian origin. Mitochondrial DNA is extranuclear double stranded DNA that is found in mitochondria and is typically inherited maternally. This genetic information is complicated by backcrossing, a hybrid crossed with a species that is the same as one parent. The mtDNA is believed to have originated in East Asia because the highest variation occurs there (Wayne and vonHoldt 2012). The genetic diversity in modern dogs is highest in Asian dog breeds. In the past dogs regularly interbred with wolves, and the highly travelled trade routes leading to China may be the link to the diversity in this region (Science 2015).

The domestic dog is a unique species because of its phenotypic variation; this variation in dogs, as one species none the less, is greater than that found in thirty five species of wild canids. Not only do domesticated dogs have large variation in their phenotypes, but the variations in behavior including: hunting, swimming, herding, and aggression. Domesticated dogs are the only large domesticated carnivore; dogs have the ability to physically harm us, but we keep them as pets. Two bottlenecks during dog evolution have been discovered by the genome project; one occurring during the first domestication event that was altered by backcrossing and the other being the inbreeding of dogs in order to maintain specific breeds (Kirkness *et al.* 2003). Domestic dog breeds are the result of artificial selection, each breed represents extreme phenotypic diversity that maintain high levels of autozygosity, these are genes in a homozygote that are copies of the same ancestral gene as a result of mating between related individuals (Wayne and vonHoldt 2012). Research conducted on the dog genome has recorded a genetic basis for: ear type, body size, coat color, leg length, and cranial dimensions (Kirkness *et al.*2003). The majority of these genes are linked with early domestication. The significance of this is in that the morphological diversity of dogs reflects variation in a relatively small number of genes. This contrasts other domesticated species in that quantitative traits often are influenced by a large number of major and minor genes that, in aggregate, explain only small fraction of phenotypic variation. Dogs' having only a few genes responsible for morphological diversity was most likely caused by discrete point mutations, and followed by fixation through intense inbreeding (Wayne and vonHoldt 2012).

Domesticated dog forepaw laterality has also been studied, but with inconsistent results; mainly because the methods used to research such laterality have been inconsistent. These methods include: the removal of a blanket off their head, the removal of tape off their nose, paw used to remove food from a Kong™ toy, and a stepping test. The complexity of the task has also shown to influence the paw used to complete the task. The most recent approaches used to study dog laterality include: the Kong™ test, involving the dog toy Kong™ and observing the paw first used to grasp the toy; the first step test, involves having the dog walk downstairs and observing which paw stepped first. I used the step test and Kong™ test as measurements of motor laterality in dogs, as did Tomkins, Thomson, and McGreevy, who found that the stepping test had 46% of dogs preferring their right forepaw, 30.1% preferring their left forepaw, and

23.9% were ambidextrous. During this study they also performed the Kong™ test, which tallied 23.9% of dogs preferring their right forepaw, 28.3% preferring their left forepaw, and 47.8% were ambidextrous. The stepping test indicated strong laterality, but the Kong™ test indicated weaker lateralization (Tomkins, Thomson, and McGreevy 2010). There has been some evidence that dogs that are left pawed have different immune responses from dogs that are right pawed and that dogs with less lateralization are more fearful. Additionally, weak lateralization means that one hemisphere has a lessened ability to inhibit the other. Studies have also shown that dogs that are more lateralized have greater confidence and are more relaxed when exposed to new stimuli. Being lateralized may be a direct consequence of structural asymmetries in the brain (Siniscalchi and Quaranta 2014).

This study compares forepaw laterality in domesticated dogs with wolves. Each wolf species is grouped into one category and is compared to domesticated dogs. The grey wolf is the domesticated dog's closest living relative and they share 99.9 percent of their DNA. This research has the potential to show whether lateralization is consistent between dogs and wolves, plus any potential benefits of lateralized behavior.

Materials and Methods

The materials used in performing laterality tests on dogs included: classic red Kong™ toy for large dogs (4 inches long), frozen and filled with a quarter cup of Beneful dog food, a quarter cup of College Inn chicken broth, and both ends sealed with Skippy peanut butter; a dog leash; a small set of stairs; and a video camera. The dog population used in this experiment varied in breed and age containing medium to large sized dogs. The breeds included three black Labrador retrievers, one yellow Labrador retriever, two German Shepherds, and four mixed breeds.

The stepping test documented the dog stepping down off a small set of stairs and the paw that they step with first was recorded. In some cases the dogs were leashed in order for them to continuously go up and down the stairs. When performing the stepping test I would have the dog step ten times and I would be on the left side for five of the steps and on the right side for the other five, in order to decrease bias. The sets of stairs are not the same in every trial because each trial was conducted at the dog owner's home. The stairs vary in size from one step to four, in each circumstance only the first step was recorded. The methods of the Kong™ test involved placing the Kong™ toy in a location that was unbiased to either paw; if the dog followed the command the preferred method was to place the Kong™ toy between the two front paws while the dog is laying down (Figure 5). Variances in how the Kong™ toy was given to each dog occurred based on the dogs behavior. These variances include the dog sitting instead of laying down, throwing the Kong™ toy and having the dog retrieve it. I would then record up to ten paw touches during each trial. The stepping test was always conducted first, followed by the Kong™ test. These tests were conduct approximately one week apart each time over a period of eight weeks.

Figure 5- Black Labrador Retriever, Hannah completing the Kong™ test.

The materials involved in performing the laterality test on wolves included: PVC pipe (sixteen inches long and four inches wide) filled with either dead small rats, dead chicks, hot dogs, or cold cuts; also twine with either dead small rats, dead chicks, hot dogs, or cold cuts hung from it. The species of wolves used in this experiment varied including: five *Canis rufus* (Red Wolves), three *Canis lupus occidentalis* (Canadian Rocky Mountain Wolves), one *Canis lupus arctos* (Artic Wolf), and three *Canis lupus baileyi* (Mexican Wolves). The method for performing this experiment on wolves varies at each location.

At the Trevor Zoo in Millbrook, New York three Red Wolves were tested using three PVC pipes that were placed in the enclosure and tied to the base of a raised platform. Each PVC pipe was placed on a separate corner. On the raised area above the platform three pieces of one meter long twine were tied around the top of three posts, on the end of each piece of twine hung one of the meats mentioned above (Figure 6). The platform used in this experiment was chosen because of its visibility to record with a Go Pro camera. Each paw touch on the PVC pipe was recorded; if two paws were placed on the PVC pipe at one time then only the first paw to touch the pipe was recorded. In order for the wolves to retrieve the food hung from the top of the posts they had to step up onto the platform, the first paw to be placed on the platform when stepping was recorded. From September 2014 through November 2014, these wolves were tested once day a week with two trials during that day, and each trial lasted a maximum of two hours. In December 2014 and January 2015 they were tested once a day for ten days for a total of twenty trials. One of the red wolves never interacted with either the PVC pipes or the platform, and was not included in the results.

Figure 6- Red wolf, Luna completing the step test at the Trevor Zoo, Millbrook, New York.

At the Wolf Conservation Center in South Salem, New York one Artic Wolf was tested and three Canadian Rocky Mountain Wolves were tested. At the Wolf Conservation center only the PVC test was conducted. The three Canadian Rocky Mountain Wolves were in one enclosure and the Artic Wolf was in a separate enclosure. The experiment would be performed first on the Artic Wolf, when first starting to work with the Artic Wolf three PVC pipes were tied to a post and his paw touches were recorded; overtime he ended up cutting the rope leading instead to tossing the PVC pipes into his enclosure one at a time and recording his paw touches on each pipe. This was the method used consistently with the three Canadian Rocky Mountain wolves in order to avoid them fighting over the pipes. The pipes would be tossed neutrally so that each wolf retrieved a pipe then the paw touches for each wolf would be recorded on a digital video camera and documented after the trial was complete (Figure 7). These trials started in November 2014 and were completed in March 2015; there were a total of ten trials that lasted approximately forty-five minutes each. One of the Canadian Rocky Mountain wolves did not interact with the PVC pipe so she was not included in the results.

Figure 7- Canadian Rocky Mountain wolf, Nikai, completing the PVC test at the Wolf Conservation Center, South Salem, New York.

The final location for my study was Connecticut's Beardsley Zoo in Bridgeport, Connecticut where two Red Wolves and three Mexican Wolves were studied. The three Mexican wolves were in in one enclosure and the PVC pipes containing enrichment meats were secured to branches that were low to the ground so that the PVC pipes laid horizontally. The paw touch of each wolf was recorded. Additionally, three pieces of rope were hung from tree branches approximately four feet off the ground; each rope had one enrichment meat on the end of it. The paw used in order to reach for the enrichment meat was recorded. The three red wolves were in a separate enclosure and the three PVC pipes were secured around the base of a tree, so the PVC pipes laid horizontally on the ground. The paw touch of each wolf was recorded. In this enclosure two pieces of rope were hung approximately four feet of the ground with one enrichment meat hanging from the end. The paw used to reach for the hanging enrichment meat was recorded. Each of these tests were video recorded and then the data was recorded. This segment was conducted twice to three times a week through February and March, with a total of twelve trials each lasting an hour.

<u>Results</u>

The total number of paw touches recorded under each category, for the step test in dogs were 280 (50.5%) left and 274 (49.5%) right, for the Kong™ test there were 278 left (50.3%) and 275 right (49.7%). In wolves, the step test 119 left (70%) and 51 right (30%), for the PVC test 447 (48.3%) left and 478 right (51.7%), (Table 1). These results show all but the Wolf Step test was approximately 50 % for both left and right pawedness, indicating that there is no paw preference. The pawedness for every dog and wolf for each task was calculated using a laterality index, [R-L]/[R+L] x 100 (Table 2). R is the number of right paw touches; L is the number of left paw touches. The wolves were challenging to work with and even if they were exposed to the experiment not all of them participated. Although, Atka Zephyr, and Nikai were not given the step test because they were at the Wolf Conservation Center. When comparing the dogs' pawedness you find that, the step test had 40% of dogs preferring their left paw, 10% of dogs preferring their right paw, and 50% ambidextrous. The Kong™ test had 20% of dogs preferring their left paw 10% preferring their right paw, and 70% ambidextrous. When comparing the wolves' pawedness you find that the step test had 40% of wolves preferring their left paw, 40% of wolves preferring their right paw, and 20% ambidextrous, the PVC test had 11.2% of wolves preferring their left paw, 44.4% of wolves preferring their right paw, and 44.4% are ambidextrous (Figure 8). When comparing dogs and wolves, the results show that dogs have a tendency to be ambidextrous for both tasks and wolves have a tendency to be right pawed for both tasks.

Dog Total			Wolf Total		
	Left	Right		Left	Right
Step	280 (50.5%)	274 (49.5%)	Step	**119 (70%)**	**51 (30%)**
Kong	278 (50.3%)	275 (49.7%)	PVC	447 (48.3%)	478 (51.7%)

Table 1- Total amount of paw touches for dogs and wolves during each task.

Dog	Willow	Magnolia	Hannah	Ki	Rayne	Lily	Tucker	Molly	Ajax	Obi
Step	Ambi	Right	Ambi	Ambi	Left	Right	Left	Ambi	Ambi	Ambi
Kong	Ambi	Left	Ambi	Ambi	Left	Left	Left	Ambi	Ambi	Left

Wolf	Luna	PRA	Atka	Zephyr	Nikai	14	15	16	Harper	Ruby
Step	Left	Right	N/A	N/A	N/A	N/A	Left	N/A	Right	Ambi
PVC	Ambi	Ambi	Right	Left	Ambi	Right	Ambi	Right	N/A	Right

Table 2- Pawedness determined for every dog and wolf during each task; right, left, or ambidextrous (ambi). N/A means they did not interact with that part of the experiment and were not included in the data results.

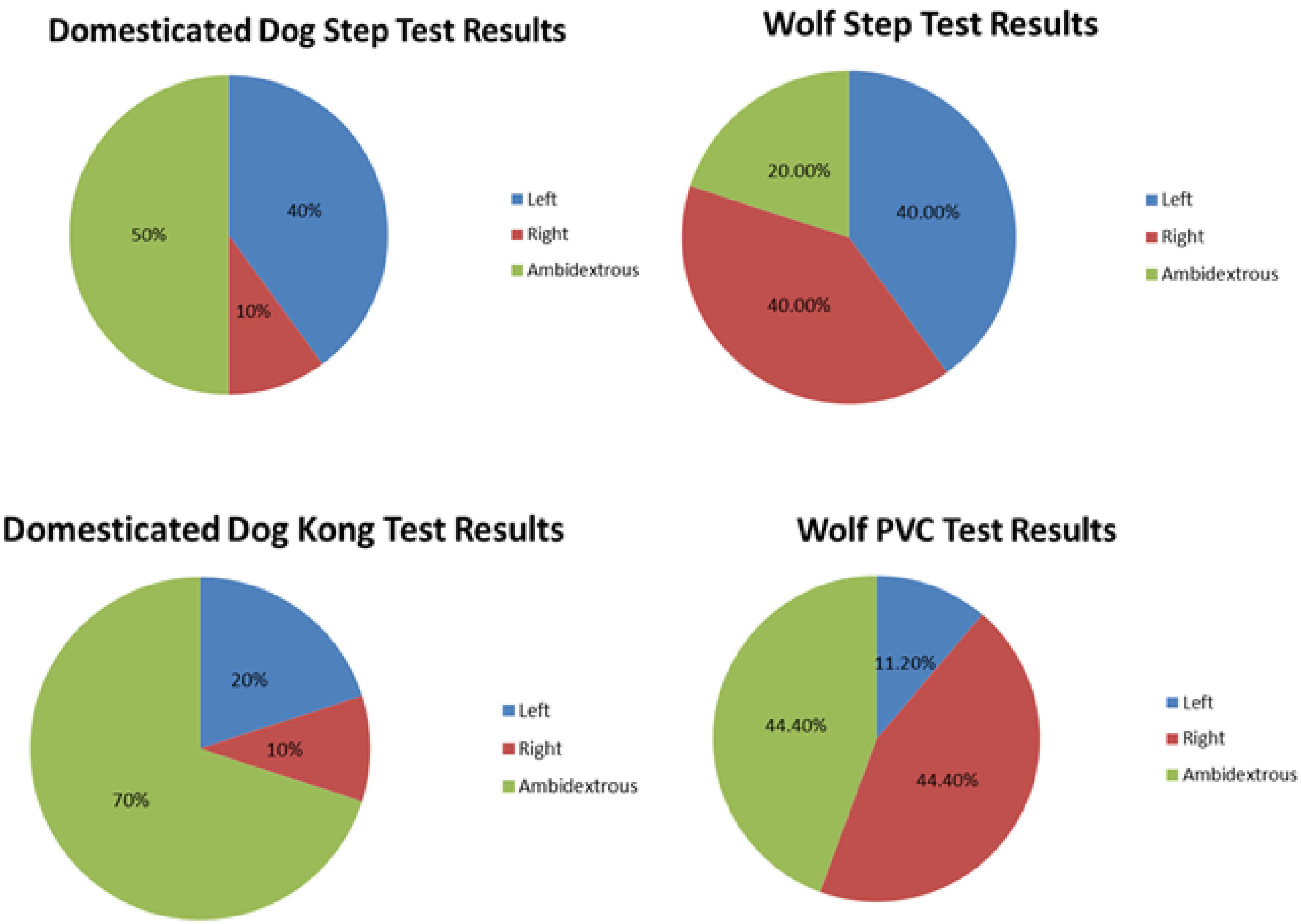

Figure 8- Percentages of right, left, or ambidextrous dogs and wolves for each task.

Discussion

Based on these results, laterality is not consistent between wolves and dogs. This data is also not consistent with Tomkins, Thomson, and McGreevy's findings, but all of the dogs in their study were between 13-17 months of age and neutered (2010). This was not taken into consideration here when selecting test subjects. The age ranges of the dogs vary from 8 months to 10 years of age. The age ranges for the wolves were 6 months to 12 years of age. Additionally this is a small population size and does not reflect the entire population. In Tomkins, Thomson, and McGreevy's study, one hundred and thirteen dogs were studied (2010). As far as I know, there have not been any studies conducted on wolf laterality prior to this experiment.

Laterality in dogs has been shown to have several implications including, dogs that are left pawed have different immune responses. Additionally, dogs that have no particular paw preference have been linked with more fearful behaviors, such as a greater fear of thunderstorms and a decrease in their ability to focus; though very little research has been conducted. Although this does correspond to the idea that lacking lateralization indicates that one hemisphere is unable to inhibit the other (Siniscalchi and Quaranta 2014). Also related, is that dogs that were found to be more lateralized during the Kong™ test had greater confidence (Batt *el al.*2008). Having a preferred right or left side may be caused by structural asymmetries in the brain; further research in dogs is required. Studying dog laterality may have the ability to find a potential link between emotion and cognition (Siniscalchi and Quaranta 2014).

The human-dog relationship is unique and ranges over tens of thousands of years. Scientists have found that dogs follow more human social cues than wolves or chimps; cues include facial expression and directional indications. This likely occurred as a part of domestication processes. In comparison to dogs, wolves need much longer interactions with humans in order to understand human gestures. Studies have been conducted on how this coevolution of dogs and wolves has impacted biological mechanisms (Science 2015). Researchers compared the levels of neurotransmitters in humans and dogs before and after they interact with one another. They found increased levels of: oxytocin, endorphins, dopamine, and prolactin in both humans and dogs. Such results may indicate the existence of a feedback loop that shifts oxytocin concentration in dogs that may have similar effects in humans. There has also been a correlation found between the length of eye contact maintained between an owner and their dog, and the amount satisfaction owners have with their dogs (Science 2015).

The domestication of wolves to dogs led to significant changes in behavior, phenotype, and sociality. Such differences imply that laterality would not be consistent between dogs and wolves, as these results indicate. Further research, with more subjects, is still necessary in order for firm determination. Additionally, future research could involve only the physiologic specialization of dog and wolf brains and how this compares with behavioral lateralization.

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Batt, L., M. Batt, J. Baguley, and P. McGreevy. 2008. Stability of motor lateralisation in maturing dogs. *Laterality* 5: 468- 479.

Evans, H.E. A.de Lahunta.2012. Miller's Anatomy of the Dog. Elsevier: St. Louis.

Kirkness E.F., V. Bafna, A.L Halpern, S. Levy, K. Remington, D,B. Rusch, A. L. Deicher, M. Pop, W. Wei, C. Fraser, C.J. Venter. 2003. The dog genome:survey sequencing and comparative analysis. Science 301: 1898–1903

Marshall-Pescini, S., J. Kaminski. 2014. The social dog: history and evolution. The Social Dog: Behaviour and Cognition, edited by J. Kaminski and S. Marshall-Pescini. New York: Elsevier. Pp. 3-26.

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Siniscalchi, M., A.Quaranta.2014. Wagging to the right or to the left:lateralization and what it tells of the dog's social brain. The Social Dog: Behaviour and Cognition, edited by J. Kaminski and S. Marshall-Pescini. New York: Elsevier 1: 373-393.

Tomkins, L. M., P. C. Thomson, P. McGreevy. 2010. First-stepping test as a measure of motor laterality in dogs (Canis familiaris). Journal of Veterinary Behaviour 5: 247-255.

Wayne. R., vonHoldt, B. 2012. Evolutionary genomics of dog domestication. *Mammalian Genome*. 23.

Wells, D. L. 2002. Laterialized behavior in the domestic dog, *Canis familiaris*. Behavioural Processes 61: 27-35.