CHAPTER THREE

Dogs' (*Canis lupus familiaris*) behavioral adaptations to a human-dominated niche: A review and novel hypothesis

Clive D.L. Wynne*
Arizona State University, Tempe, AZ, United States
*Corresponding author: e-mail address: clivewynne@gmail.com

Contents

Advances in the Study of Behavior, Volume 53
ISSN 0065-3454
https://doi.org/10.1016/bs.asb.2021.03.004

Hundreds of millions of people share their homes with dogs, and billions more have dogs near their domiciles (Rowan, 2020). Dogs are the most numerous and widespread larger mammal (besides humans, of course) in the world. The purpose of this chapter is to weigh the possible explanations for how this state of affairs could have arisen. A scientifically secured understanding of the capacities of dogs would have significant implications in at least two directions. First, understanding dogs' adaptations to life in human proximity would have consequences for how people structure their lives alongside dogs. Each species in this symbiosis has the potential to bring benefits, but also do harm, to the other. An empirically-grounded understanding of the niche that dogs occupy within the human-dominated world could help people maximize those benefits while minimizing the harms. Second, in an era of unprecedented human-driven extinctions, understanding how one animal has succeeded in adapting to human activity may shed light on how and why others have failed. Many other animal species have also adapted to human proximity, including birds such as pigeons (*Columba livia*: e.g., Audet, Ducatez, & Lefebvre, 2016) and other mammals including other canids such as coyotes (*Canis latrans*: e.g., Mitchell, Strohbach, Pratt, Finn, & Strauss, 2015). Most of these other species, however, seem to have achieved this adaptation without the close and affectionate interaction with people which is so characteristic of dogs (Coppinger & Coppinger, 2016).

Around 40% of households in the United States harbor a dog (AVMA 2008: numbers in other developed countries are slightly lower, Rowan, 2020). However, only around 17–24% of the world's dogs live as pets in first-world homes (Lord, Feinstein, Smith, & Coppinger, 2013). Most dogs live on the fringes of human settlements in the developing world as feral, village or community dogs (Coppinger & Coppinger, 2001). Even in developed countries dogs can cause appreciable harm to humans. For example, in the United States dogs are responsible for around 12,400 bites to people every day (Gilchrist, Sacks, White, & Kresnow, 2008). Outside the First World, the harms of dogs may be much more significant. For example, more than 55,000 people per year die of rabies, mainly in Asia and Africa where dogs are the most important vector (World Health Organization, 2013). Notwithstanding these costs and the scarcity of practical benefits to dog cohabitation in the modern world (Rodriguez, Greer, Yatcilla, Beck, & O'Haire, 2020) the majority of first-world respondents view their pet dogs as family members (Serpell, 2004), and even in developing nations, large portions of the population are at least ambivalent and many express quite positive attitudes to the dogs on their streets (Bhattacharjee et al., 2020; Fielding & Mather, 2001).

In this chapter, I start by contextualizing the study of the dog-human relationship by sketching what is known about the origins of dogs before considering different theories of dogs' putative uniqueness that attempt to account for their success in a human-dominated world. I conclude that much current research into dogs is barking up the wrong tree. The search for evolved innate cognitive structures that could account for dogs' success in an anthropogenic world ("cognitive instincts") failed to take account of the intensity and intimacy of individual dog's lives in human proximity. I then outline relatively uncontroversial and well-established findings in the basic behavioral biology of dogs, including affiliative and attachment-related behaviors, which should inform our understanding of their more complex and cognitive behaviors. I outline how it is in dogs' social behaviors that the solution will be found. Dogs' ability to solicit care from humans is crucial to their success in human environments and yet has received much less research attention. Finally, I consider domains where more research is needed if the riddle of dogs is to be solved.

1. The origins of dogs

Much about the origins of dogs remains controversial, but several useful points have been established by geneticists, genomicists, archeologists and their hybrids. Certain wolves at one or several locations around the world adapted to human proximity by scavenging on the residues of human foraging (Larson et al., 2012; Morey, 2014; Perri, 2016). The earliest proposed dates of archeological remains of canids that can be distinguished from wolves are over 30,000 years ago (in Siberia: Germonpré, Lázničková-Galetová, & Sablin, 2011; Germonpré et al., 2009). The earliest find that is broadly accepted as from a dog rather than a wolf dates to around 14,000 years ago (in Germany: Nobis, 1981). Estimates from genomic analysis of the time of the last common ancestor of the dog and the gray wolf are in the range of 15–23,000 years ago (Bergström et al., 2020; Frantz et al., 2016; Perri, 2016; Perri et al., 2021). It is worth noting that the time point of the last common ancestor of dog and wolf is not the same as the point at which the dog and wolf would have become phenotypically (including behaviorally) distinguishable. To this day there remain many discriminable eco-morphs of wolf—from the large thick-coated wolves of the artic, to the much smaller Arab wolves of the Levant (Pilot et al., 2014; Stronen et al., 2013). Thus, to say that the last common ancestor of dogs and wolves lived 15–23,000 years ago is not to say that an animal discriminably distinct from a wolf and recognizable to modern observers as a dog arose at that time.

It implies solely that the wolves from whom dogs are descended last shared an ancestor with other groups of wolves at that time. The evolution to an animal that can be morphologically or behaviorally discriminated from wolves and therefore could be called a "dog" may have come many thousands of years later (Larson et al., 2012).

Although there is much that is contested in the early origins of dogs, certain conclusions can be drawn from the undisputed facts. First, all dogs are descended from wolves and only wolves (Larson et al., 2012; Wayne, 2012; Wayne & Ostrander, 2007). Second, dogs arose at least 14,000 years ago (Nobis, 1981). It follows from these two facts that, third, dogs arose during the last ice age and fourth, the domestication of dogs occurred before the domestication of any other species of animal or even plant—dogs thus arose when people were still entirely dependent on hunting and gathering (Larson et al., 2012; Perri, 2016). Earlier proposals that dogs came into being at the end of the last ice age and beginning of the Holocene as part of a package of changes occurring at the beginnings of agriculture (e.g., Coppinger & Coppinger, 2001) are, consequently, clearly refuted.

There may be an enumerable list of relatively uncontroversial facts around the origins of dogs, but much remains unclear. One of the vibrant continuing controversies concerns the nature of the earliest human-dog symbiosis. Some authors argue that early proto-dogs accompanied human hunters at an early point in the genesis of the dog, enhancing human hunting success and possibly even contributing to the ability of *Homo sapiens* to out-compete *Homo neanderthalenis* (Schleidt & Schalter, 2003; Shipman, 2017). Others argue that proto-dogs would have made poor hunters' companions (for a number of reasons, including the lack of benefit of dogs for humans who with their excellent vision were already well-able to hunt in the relatively open terrain of the Pleistocene, see Larson et al., 2012; Perri, 2013; Wynne, 2019). Rather, this latter group suggests, dogs would have arisen as scavengers of human foraging remnants with limited direct benefit to their human hosts (besides possibly cleaning camp, Russell, 2011).

From these origins, there is no dispute that, with the warming of the planet starting around 12,000 years ago, dogs accompanied people around the globe. The first evidence of human concern for dogs is careful burials that became more elaborate and numerous as the planet warmed. Perri (2013) proposes that this increase in intentional burials indicates that dogs were becoming more useful to people as hunting aids. Dogs' sensitive noses and small size relative to humans enabled them to chase down prey in denser tropical and temperate forests which were replacing the open steppe and colder-climate forests in many parts of the world. Unlike their wolf ancestors, dogs have difficulty completing a kill and thus need human assistance for successful hunting of larger prey—establishing the conditions for a mutually dependent symbiosis (Perri, 2013).

As time went on, dogs found numerous additional roles. Dogs' ability to form attachments to many species combined with a spontaneous tendency to bark when perceiving a threat underlies their propensity to warn groups of humans, as well as other domesticated animals, of the approach of intruders and potentially engage with them (Musil, 1928). This capacity was probably extremely important to early livestock herders, although the actual ability to herd—that is, to force livestock to move on direct command—likely arose in dogs only much later, and only in environments where major predators had been extirpated (de Planhol, 1969). Dogs kept solely as companions can be identified in the Roman era (Bodson, 2000). Dogs were a significant source of labor—pulling wagons, turning meat on spits, and so on—right up until the early 20th century (Ritvo, 1987).

Thus, the role of dogs has altered over the millennia and yet they have always been able to adapt to their changing niche. Dogs today in first-world homes probably provide as little practical support to their human hosts as dogs have ever done and yet the level of resourcing they are provided is likely also unprecedented. The price they pay for this is greatly restricted control over their lives. First-world pet dogs must negotiate with their human hosts every aspect of life, from opportunities to urinate and defecate, what and when they may eat, to their selection of mates and even whether they are reproductively viable.

2. Adaptation to a human-dominated niche

Over the past half century several theories have been proposed to account for dogs' success in the human-dominated world. I will briefly mention two accounts that have proposed a cognitive aspect to dogs' adaptation to the human environment before moving on to the (in my view) more viable theories involving adaptation of social behavior independent of more cognitive factors.

2.1 Cognitive hypotheses

Diverse definitions of "cognitive" exist in the literature. Originally the term was introduced into psychology to indicate a break from behaviorist interpretations of behavior solely in terms of conditioning and to emphasize behavior generated by internal representations of external stimuli (Miller, 1962; Pearce, 2008). Given the difficulty in establishing whether an animal is experiencing an internal representation and in demonstrating that a complex behavior cannot be explained in terms of simpler conditioning processes (which amounts to the logical impossibility of proving a negative), more recent definitions of cognition in animals emphasize the complexity of the behavior to be explained. Categories of cognition in animals include reasoning, problem-solving, memory and concept formation (Wynne & Udell, 2020).

2.1.1 Problem-solving hypothesis

During the 1980s Harry Frank and his wife Martha raised a number of dog and wolf pups in order to closely compare their cognitive development. Frank (1980) argued that the wolf niche favors group hunting and thus cognitive adaptations including foresight, mental representation and an understanding of means-end relationships. Since dogs have been relieved of the selection pressures for hunting live prey in their symbiosis with humans, Frank argued they lost these forms of cognition in place of tractability in the human partnership (Frank & Frank, 1982). From these considerations the Franks derived a number of testable hypotheses. They predicted that dogs would perform better than wolves (i) on problems where cues to task solution were arbitrarily selected by the experimenter rather than intrinsic to the problem situation, (ii) where reinforcement is administered by the experimenter rather than directly from the rest of the problem environment and (iii) that dogs would also perform better where the behavior required of them had no direct functional link to the outcome. On the other hand, wolves should outperform dogs where the connections between action and consequence were more intrinsic to the problem situation and where the task demanded "*cognitive* processes, such as foresight, planning, mental representation (imagery), and serial organization of behavior" (Frank & Frank, 1987, p. 144, emphasis in the original).

Using their hand-reared wolf and malamute dog pups Frank and Frank carried out a series of experiments to test their hypotheses. These included tests of behavioral inhibition such as requiring the dog or wolf to stand on a wooden platform; visual and auditory discriminations; as well as problem-solving tasks. The problem-solving tasks included a detour test; a task where the animal had to extract a food dish from a wooden box; and a maze test.

Initially Frank and Frank reported that their findings supported their theory of the fundamental cognitive differences between wolves and dogs.

However, by the end of their project they reported significant caveats to their earlier findings (Frank & Frank, 1987). The first concern was that their attempts to match early experiences for the wolf and dog pups were not entirely successful. This mitigated the extent to which differences in behavior could be ascribed to phylogenetic differences rather than ontogenetic ones. The importance of matching ontogenetic experience in attempting to characterize wolf-dog differences in behavior is a theme which will be returned to below. Second, their studies had only used a single breed of dog—malamutes (for idiosyncratic reasons, see Feuerbacher & Wynne, 2011, for more on the history of the project). Frank and Frank (1987) noted that dog pups from other breeds tested in some of the same tasks by other researchers had been reported to perform more like the wolves in their studies than the dogs. For example, basenjis studied by Scott and Fuller (1974, originally published 1965) performed like Frank and Frank's wolves on problem-solving tasks, and much better than the dogs Frank and Frank studied. Third, the observed differences in behavior between dogs and wolves might not be determined by differences in styles of problem solving but by different responses to confinement or sensitivity to contingencies of reinforcement (Frank & Frank, 1987). Finally, Feuerbacher and Wynne (2011) noted that the distinction between human-directed training problems (which dogs were predicted to excel at) and problem-solving tasks (which wolves were expected to perform better on) was not entirely firm and that some tasks reported in Frank, Frank, Hasselbach, and Littleton (1989), for example, could be interpreted in either direction.

In sum, the pioneering project of Frank and Frank is now largely of historical interest. It illustrates the extreme difficulty of successfully carrying out comparative behavioral research even on two such closely-related species and highlights that successful comparative work needs to take account of the phenotypic variety in dogs (and, indeed, in wolves) to enable meaningful conclusions to be drawn, as well as the problems in establishing truly comparable populations for analysis.

2.1.2 Human-like social cognition hypothesis

More recently, Hare et al. have proposed a number of related hypotheses centering on the claim that dogs developed "human-like social skills" as a by-product of domestication. This proposal is known as the "domestication hypothesis": namely that dogs, as a direct consequence of selection during domestication, developed abilities in interpreting human actions and intentions that exceed those of all other nonhumans and indicate aspects of theory of mind only seen in *Homo sapiens* (e.g., Hare, 2017; Hare, Brown, Williamson, & Tomasello, 2002; Hare & Tomasello, 2005). Thus, according to Hare et al. (2010, p. E6), "the unusual skills of domestic dogs in using human communicative cues most likely evolved during and as a result of human domestication." Riedel, Schumann, Kaminski, Call, and Tomasello (2008) went so far as to argue that these kinds of skills, though they are known to be highly dependent on ontogenetic experience in our own species (Lakatos, Soproni, Dóka, & Miklósi, 2009; Morissette, Ricard, & Décarie, 1995), arise in dogs without significant developmental component. "Human exposure has no major effect on dogs' ability to use human-given communicative cues," (Riedel et al., 2008, p. 1012).

Human-like social cognition can be conceptualized in terms of the seven domains of theory of mind outlined by Heyes (1998). Heyes (1998) defined theory of mind in animals as an animal "… believ[ing] that mental states play a causal role in generating behaviour and infer[ing] the presence of mental states in others by observing their appearance and behaviour under various circumstances" (p. 102). She identified several methodologies that may indicate behavior governed by theory of mind and some evidence of success in dogs has been reported on five of these seven theory-of-mind methodologies, including imitation (Bräuer, Bös, Call, & Tomasello, 2013; Miller, Rayburn-Reeves, & Zentall, 2009; Range, Virányi, & Huber, 2007; Topál, Byrne, Miklósi, & Csányi, 2006), deception (Heberlein, Manser, & Turner, 2017), role taking (Miklósi, Polgárdi, Topál, & Csányi, 2000; Topál, Erdõhegyi, Mányik, & Miklósi, 2006), and understanding the implications of what others can and cannot see (Cooper et al., 2003; Gácsi, Miklósi, Varga, Topál, & Csányi, 2004; Johnston, Huang, & Santos, 2018; Udell, Dorey, & Wynne, 2011). In addition, substantial evidence has been presented in the literature that dogs are sensitive to the implications of human pointing gestures and even of human gaze (citations below). These claims of theory-of-mind-like abilities in dogs are particularly noteworthy in view of the difficulties in demonstrating similar theory-of-mind-like skills in nonhuman primates (e.g., Heyes, 1998; Povinelli & Eddy, 1996; Povinelli & Vonk, 2003).

In the following subsections, I briefly review evidence from three domains where human-like social skills have been demonstrated in dogs in studies from multiple laboratories. These are (Section 2.1.2.1) Point and gaze following; (Section 2.1.2.2) Understanding the implications of what others see; and (Section 2.1.2.3) Imitation.

2.1.2.1 Point and gaze following

Numerous studies demonstrate that pet dogs will follow a wide range of different human pointing gestures to locate hidden food rewards (Bräuer, Kaminski, Riedel, Call, & Tomasello, 2006; Hare et al., 2002; Hare & Tomasello, 2005; Kaminski & Nitzschner, 2013; Téglás, Gergely, Kupán, Miklósi, & Topál, 2012; Udell, Dorey, & Wynne, 2008). Most pet dogs will follow human gestures made with hands and arms as well as legs and feet (for reviews see Lea & Osthaus, 2018; Udell, Dorey, & Wynne, 2012; Miklósi, 2015). Early reports claimed that this ability was unique to dogs since it was not initially observed in wolves (Hare et al., 2002) nor in humans' closest relatives, chimpanzees and bonobos (Bräuer et al., 2006; Hare & Tomasello, 2005; Kaminski & Nitzschner, 2013; Téglás et al., 2012). Subsequent studies have established that hand-reared wolves can perform on the task to a similar level as pet dogs (Gácsi et al., 2009; Udell et al., 2008) and many other species have also been shown capable of following human pointing gestures given prior experience around people. This list now includes not just members of domesticated species (goats: Kaminski, Riedel, Call, & Tomasello, 2005; pigs: Nawroth, Ebersbach, & von Borell, 2014; horses: Dorey, Conover, & Udell, 2014; Malavasi & Huber, 2016) but also individuals from non-domesticated species (dolphins: Pack & Herman, 2004, Xitco, Gory, & Kuczaj, 2001; a gray seal: Shapiro, Janik, & Slater, 2003; sea lions: Malassis & Delfour, 2015; bats: Hall, Udell, Dorey, Walsh, & Wynne, 2011). In a review, Krause, Udell, Leavens, and Skopos (2018) identified 38 species from diverse taxa which have been found to follow at least some human pointing gestures. The status of chimpanzees remains ambiguous. Individuals from this species follow human gaze (for a review see Itakura, Das, & Farshid, 2017) but do not appear to follow human gestures in laboratory tests (Kirchhofer, Zimmermann, Kaminski, & Tomasello, 2012). However, a review and meta-analysis of the data on dogs' and nonhuman primates' abilities to follow human gestures concluded that apparent differences between species were subject to systematic confounds (Clark, Elsherif, & Leavens, 2019). These included the use of a barrier between the pointing person and the animal for primates but not dogs and other species, along with differences in task-relevant preparation of the subjects (Clark et al., 2019). It is worth noting that earlier researchers who raised a chimpanzee in their home like a human child, found that their charges were inclined to follow human pointing gestures (Hayes, 1951; Kellogg & Kellogg, 1933).

Several lines of evidence implicate the importance of appropriate life experiences rather than purely phylogenetic factors for dogs (and other species) to follow human gestures. Dogs living in less close daily contact with people than typical household pets are less likely to follow gestures (D'Aniello et al., 2017; Udell, Dorey, & Wynne, 2010). Dogs living in animal shelters who do not follow points spontaneously can quickly acquire the ability to follow human gestures both through very brief explicit training (Lazarowski & Dorman, 2015; Udell et al., 2010) and also through the kinds of human interaction that pet dogs living in a human home typically experience (Jarvis & Hall, 2020). Udell, Hall, Morrison, Dorey, and Wynne (2013) observed that pet dogs could improve at following human points even within the brief experience of a typical testing session.

Testing of a wider range of dog populations, including shelter-living dogs, street dogs in India, as well as laboratory and other kennel-living dogs show reduced performance in following gestures—often at chance levels (Bhattacharjee et al., 2017; Lazarowski & Dorman, 2015; Udell et al., 2010; though see also Bhattacharjee, Mandal, et al., 2020, for evidence of successful point following in about half the Indian street dogs approached). Interestingly, although pet dogs more readily follow proximal cues than distal ones (that is to say, cues where the pointing hand is very close to the object pointed to rather than about 0.5 m distant from it: Udell et al., 2013), street dogs in west Bengal, India, were more likely to follow distal cues (Bhattacharjee, Mandal, et al., 2020). This may be because street dogs are more likely to interact with people at greater distances than do pet dogs.

The fact that dogs are reluctant to ignore points that are not informative—or that even indicate a location which can be clearly seen to be devoid of food (Dwyer & Cole, 2018; Kundey et al., 2010; Petter, Musolino, Roberts, & Cole, 2009; Pongrácz, Hegedüs, Sanjurjo, Kővári, & Miklosi, 2013; Szetei, Miklósi, Topál, & Csányi, 2003) has been adduced as evidence of a priority to attend to human intentional actions over the evidence of their own senses (Hare, 2017). These results are more parsimoniously explained, however, by considering the lives of pet dogs. Pet dogs are routinely reinforced for following human gestures to find things and often punished for seeking food independently when they, for example, remove food from kitchen counters or investigate garbage containers. Given these extensive, albeit undocumented, reinforcement histories it should not be surprising that in the context of a brief experimental test such dogs may continue to follow a cue that has been reinforced in the past even if it is being extinguished during the experimental sessions.

As well as following ostensive points, dogs in at least some studies also show sensitivity to the direction of an individual's gaze. Agnetta, Hare, and Tomasello (2000) and Met, Miklósi, and Lakatos (2014) found that dogs did not succeed in following human gaze at a group level. However, Wallis et al. (2015) reported that brief training was sufficient to bring a group of 145 border collies to follow human gaze into distant space. Dogs may use also use their own gaze alternation to draw owner's attention to hidden toy (Marshall-Pescini, Colombo, Passalacqua, Merola, & Prato-Previde, 2013; Miklósi et al., 2000; Persson, Wright, Roth, Batakis, & Jensen, 2016).

In sum, the evidence of dogs' ability to follow human pointing gestures and gaze direction, as well as use gaze alternation to bring people's attention toward things certainly indicates a high level of sensitivity to these cues of human attention. However, these abilities are not unique to dogs nor are they automatic or innate for them. Rather, they appear to develop in many species that live in intimate proximity with human beings and depend on them for fulfillment of their daily needs.

2.1.2.2 Understanding the implications of what others can and cannot see

Another aspect of theory of mind and human-like cognition which is relatively amenable to study in animals is the understanding that another individual's ability to see something influences that individual's knowledge of what is around them.

In the so-called begging task, an individual has to select one of two similar-looking people to approach and solicit for food. One of the people can see the subject (and her eyes are clearly visible to it) while the other is rendered inattentive by having her vision obscured in some obvious way. Gácsi et al. (2004) reported that pet dogs were more likely to beg for food from a woman who could see them than one who could not; however, performance was more accurate when the inattentive woman turned her back than when she wore a blindfold. Similarly, Cooper et al. (2003) found that dogs were more likely to ignore a person whose face was obscured behind a book than a bucket. Udell et al. (2011) extended these findings by demonstrating that neither dogs nor hand-reared wolves demonstrated an undifferentiated ability to respond to signals of human attention. Rather, the kinds of signals that pet dogs, shelter-living dogs, and hand-reared wolves were attentive to varied in a manner consistent with the living conditions of the three groups of canids. Pet dogs were sensitive to the widest range of human cues, responding appropriately to people whose vision was obscured by turning their backs or placing a book in front of their eyes. However, even the pet dogs did not reliably respond differentially to a person with her head in a bucket compared to a person holding an identical bucket next to her head. Shelter-living dogs were also sensitive to a person turning her back, but not to a book (or a bucket). The performance of hand-reared wolves living in a sanctuary was very similar to that of shelter dogs. Udell et al. (2011) interpreted these findings, as well as those of Gácsi et al. (2004) and Cooper et al. (2003), as indicating that dogs do not have any special inborn capacity to perform better than other canids on perspective-taking tasks. Rather, the life experiences of the individual animals under test are determinative of the kinds of cues to which different individuals are sensitive. Even pet dogs were insensitive to the largest occlusion of attention in Udell et al.'s (2011) study—the bucket—because dogs do not usually see people with a bucket on their head. However, pet dogs (in a university town) are accustomed to people placing books in front of their faces and ceasing to interact with them. This signal is not, however, familiar to wolves or shelter-living dogs.

The begging task shows that dogs can, with suitable experience, become sensitive to humans' visual access to the world and the consequences that can follow on from that for them. The limits of this ability clearly implicate individual life experience, rather than any inborn capacities, in this ability. The limited data available from hand-reared wolves support this interpretation.

Claims for pet dogs' sensitivity to the importance of vision as a means of gaining information were made in a study by Kaminski, Pitsch, and Tomasello (2013). These researchers simply ordered dogs not to take some food which was placed within the dogs' reach. A human remained in the room with the dogs and food throughout the test. The dogs were more likely to take the food when illumination was reduced (so the human could not see the dog's actions) than when the room was normally illuminated. Interestingly, the dog's behavior was impacted by the illumination level around the food rather than around the human watching the food. However, if there was no human present, the dogs approached the food more rapidly in the dark than when it was illuminated. This may imply that dogs are more sensitive to the state of being in the dark rather than understanding anything about human's visual access in the dark, perhaps because scavenging food in the dark is less likely to be chastised.

Further evidence of pet dogs' sensitivity to human visual access comes from a study by Kaminski, Tomasello, Call, and Bräuer (2009). In this study, dogs were seated on one side of a pair of barriers: one transparent, the other opaque. The experimenters placed two identical toys on the dog's side of the barriers–one next to each barrier. On the other side of these barriers sat a human experimenter who could only see one of the toys (the one behind the transparent barrier). Each dog was ordered to "Bring it here," and the question of interest was which of the two identical toys the dog would bring to the experimenter. The dogs were more likely to approach and bring the toy that was behind the transparent barrier–that is the one the human experimenter could also see. This tendency was reduced if the experimenter faced away from the dog and the barriers, or if the toys were placed on the experimenter's side of the barriers. Kaminski et al. (2009) concluded that this finding indicates that the dogs were sensitive to the human's visual access to the toys, though it is left unexplained why the dog should prefer bringing the toy which the human can also see.

2.1.2.2.1 Guesser-knower task A more elaborate paradigm which assesses some of the same issues as the begging task is the Guesser-Knower experiment, originally developed for chimpanzees by Povinelli, Nelson, and Boysen (1990). The essence of this task is that a subject is confronted by two (human) informants. One of these informants, in a manner that is made obvious to the subject, has knowledge of where something desirable to the subject is located. For example, this person may have watched while a third person placed a treat underneath an upturned container. This person is termed the "Knower." The other person, known as the "Guesser," did not see where the treat was located—and her ignorance is also communicated to the subject. For example, in Povinelli et al.'s original experiment, a chimpanzee was allowed to watch while one person hid a treat under an upturned container in the presence of two other people. The chimpanzee was unable to see which container had been baited because a screen was placed in the way to obscure its vision. However, the chimpanzee could clearly see that there were two other people in the experimental room, one of whom (the Guesser) had a bucket over his head and thus—like the chimpanzee itself—could not know which container had been baited; but the other human in the room had unobscured vision of which container had been baited. Once this scenario had been set up with one of the containers baited, the Guesser and the Knower each pointed at one container and the chimpanzee was given the opportunity to select a container and given the contents if it selected appropriately. Chimpanzees performed only at a very poor level on this task even after over one hundred trials (Povinelli et al., 1990).

In the first test of dogs' capacities of this kind, Cooper et al. (2003) reported briefly (as part of a survey of several tasks) that 14 of 15 dogs chose the Knower on the first trial, however, on subsequent trials performance quickly fell to chance. Maginnity and Grace (2014) replicated this experiment and reported findings from 16 dogs which were allowed to watch while one experimenter (the Knower) baited one of four containers. The presence of a barrier made it impossible for the dog to see which container the Knower had baited, but the dog could see that baiting had taken place. With baiting completed, the Knower removed the screen so the dog could now clearly see the four containers and the Guesser joined the Knower in the room. After a brief delay, both Guesser and Knower pointed and gazed toward one of the containers. The Knower indicated the container she had previously baited: The Guesser pointed at one of the unbaited containers. If the dog chose correctly, it received the food reward and verbal praise: incorrect responses led to the owner calling the dog back to a starting position and the next trial. Further conditions explored the impact of having the Guesser present but not handling the food while the baiting occurred. Generally, the dogs chose above chance but were less successful when the Knower did not handle the food. Maginnity and Grace were careful to point out that the dogs could have learnt an associative rule such as "Choose the container that is pointed at by the person whose eyes looked at the container during baiting" (p. 1390). Given, as they note, pet dogs' extensive experience observing people preparing food for their consumption, it is quite plausible that dogs may have detected relationships between people gazing toward food and then indicating its location by gesturing.

Catala, Mang, Wallis, and Huber (2017) replicated Maginnity and Grace's (2014) study and compared dogs' performance under three conditions. In the Guesser Absent condition the Guesser was not present while the container was baited. In the Guesser Looked Away condition, the Guesser was present during baiting but gazed ostentatiously in a different direction from where the baiting took place. In a third, control, condition, the "Guesser" was present during baiting, looked ostentatiously at the baiting operation, but then pointed at an unbaited container (and thus was not so much "guessing" as willfully misdirecting). Dogs' performance was above chance in the two experimental conditions (Guesser Looked Away and Guesser Absent), but performance in the control "Guesser" Present condition was also close to significantly above chance ($p = 0.064$) and not very different from performance in the Guesser Looked Away condition (means 61.7% and 56.2% respectively—no statistical comparison was reported). Catala et al. noted that: "The dogs' confidence in the informant who was in the position to see the relevant event (food hiding) might possibly emerge from an awareness of the superior knowledge state of the Knower over the

Guesser, but a more parsimonious explanation of this behaviour is in terms of generalization from similar situations in everyday life (Udell et al., 2011). Pet dogs may have experienced reinforcement in similar, but not identical situations." (p. 588).

Johnston et al. (2018) carried out a partial replication and extension of the studies of Maginnity and Grace (2014) and Catala et al. (2017). In this study only two containers were used and the performance of dogs in choosing between containers indicated by an informed (Knower) and uninformed (Guesser) individual was compared under conditions in which the two people indicated their choices by pointing, by placing a block colored to match the two people's shirts (red and blue—which may not be very discriminable colors for dogs: Siniscalchi, d'Ingeo, Fornelli, & Quaranta, 2017), or by grasping the container to indicate their choice. Johnston et al. noted that the dogs chose the baited cup at above chance levels only in control conditions in which they were allowed to see the cup being baited with food. When the screen was in place so that the dogs did not have direct visual access to the baiting action, the dogs chose at random between containers indicated by the Guesser and Knower, no matter what form the informants' indications took.

The complexity of the Guesser-Knower task makes interpretation of findings difficult. It does not appear, overall, that dogs—even pet dogs living in human homes – have any exceptional capacity to interpret the implications of a human seeing or not seeing baiting actions being carried out, and the limited evidence of some success in certain conditions of some of the studies in the literature may well relate, as Catala et al. (2017) noted, from the dogs' particular experiences around people preparing and providing food to them.

2.1.2.3 Imitation

The ability to imitate the actions of another individual is a more complex form of understanding the implications of what one sees, and true imitation is considered a form of theory of mind understanding (Heyes, 1994). True imitation must be distinguished from observers simply having their attention drawn to an object or location (stimulus or local enhancement, respectively), or showing emulation rather than imitation (meaning that the animal learns about the outcome of the action rather than repeating the course of action itself: Wynne & Udell, 2020).

In an early report of a limited from of imitation in a dog, Topál, Byrne, et al. (2006) described one service dog that had been trained by his owners to repeat nine previously trained actions on a specific command, “Do it!” The owner would carry out one of the previously trained actions, say “Do it!” to the dog, and the dog would be expected to repeat the demonstrated action. Topál et al. found the dog to be successful with an average accuracy of 72% when the commands were demonstrated by the owner. The dog achieved a similar level of accuracy on four of the nine commands with an unfamiliar demonstrator (the remaining five were either not attempted or not reported). Topál et al. proceeded to ask the owners to demonstrate moving a bottle to a new location and then asking the dog to “Do it!”—an apparently completely novel task for the dog. Here the dog was completely successful in repeating the demonstrated action in all details in 16 out of 60 cases. A further six cases were “close” to the correct response. Since there were five possible bottles that could be moved to any one of five possible target locations and thus $6 \times 5 = 30$ possible movement sequences these performance levels were above chance.

Huber et al. (2009) also reported on a single pet dog that had been trained to match its behavior to one of eight demonstrated actions on the command, “Do it!” When tested with actions that were novel but contained previously trained elements the dog was also usually accurate, but the errors it made consisted of carrying out other trained actions—suggesting problems in memory, such as interference. When given completely novel actions to imitate the dog never succeeded on the first attempt.

Fugazza and Miklósi (2014) extended the use of the Do-as-I-Do paradigm in dogs to retention intervals of up to one and a half minutes, more trained behaviors (20), and a larger group (8) of dogs. They also introduced two-action tests. Two-action tests are important because they control for the possibility that the dogs are not truly imitating the human demonstrator, but instead are showing stimulus or local enhancement or emulation.

Fugazza and Miklósi (2014) only presented two forms of the two-action control test. In one, the human demonstrator either looked inside a box or touched it with the hand. Both actions had the same null outcome, the box was unchanged by the interaction. In the other two-action test, the demonstrator either walked around a tube (which had no effect) or knocked it over. Performance was generally at a very high level, significantly above chance, in all conditions. However, the fact that one of the actions in this two-action test had no outcome reduces the interest in the result since no outcome can be achieved in an unlimited number of ways. Fugazza, Pogány, and Miklósi (2016) further examined dogs’ performance in the two-action control procedure and found the dogs generally matched the human action at a high level though performance was negatively impacted by a spatial bias when objects were displaced.

Further two-action tests using the Do-as-I-Do method were reported by Fugazza, Petro, Miklósi, and Pogány (2019). In these tests, the human demonstrator opened an apparatus. Dogs were more likely to use their paws (which was considered imitation of the human's hand/arm movement) if there was no outcome than if there was a goal (in which case they used their mouths). Fugazza et al. interpret these findings as indicating that when the dogs could observe the goal this overshadowed what they had observed of the human's actions, whereas when there was no goal they remembered and imitated the person's action more precisely. This interpretation of the findings depends on assumptions about what part of a dog's body is analogous to a human hand and arm and also what kinds of outcomes might overshadow memory for what other kinds of actions.

Do-as-I-Do is not the only method that has been used to assess imitation in dogs. Kubinyi, Topal, Miklósi, and Csanyi (2003) had pet dogs observe a human demonstrator push a lever either left or right to release a ball from a box. This experimental design, known as the bidirectional procedure, is attractive because the observer sees how a demonstrator operates a single manipulandum in one of two possible ways (Heyes & Dawson, 1990). This controls for any facilitation toward the manipulated object created by seeing a demonstrator interact with it. When the observer dogs were given an opportunity to operate the lever themselves, although dogs in the experimental groups were more likely to contact the lever than dogs in control groups who had not seen the owner operate it, they were not more likely to push the lever in the direction demonstrated to them. Thus the study did not provide evidence for imitation in dogs.

Range et al. (2007) developed a form of two-action task with another dog, rather than a human, as the demonstrator. The demonstrator dog was trained on command to depress a hanging rod by pushing down on it with a paw (in control tests there was a strong preference among dogs to use their mouth to operate this rod but use of the mouth was never demonstrated). Observer dogs watched the demonstration 10 times and were then given the opportunity to operate the apparatus themselves. An additional interesting complexity was that in some cases the observer had a ball in its mouth, but in other demonstrations the observer's mouth was empty.

When observer dogs were given the opportunity to operate the mechanism themselves, these dogs (all of whom had seen the demonstrator use its paw) were only inclined to imitate the demonstrator and use their paws if the demonstrator's mouth was empty. If the demonstrator was carrying a ball in its mouth, the observers were less likely to imitate. Range et al. interpreted this finding as implying that the dogs not only engaged in true imitation (because they used a less preferred way of operating the apparatus when that was demonstrated to them), but they also showed selective imitation by only copying the demonstration in the condition where the demonstrated actions were not justified by a visible condition (the ball in the demonstrator's mouth). This latter finding would be important because it would indicate an additional level of theory of mind in the observing dogs—that they are taking account of the demonstrator's available actions before choosing to imitate or not.

This finding has been challenged because it breaks with established procedures in this field by only demonstrating one of the two possible actions (no observers ever saw the demonstrator use its mouth) and the observers had been pretrained to operate the rod—both with their paws and their mouths (Kaminski et al., 2011). This is particularly noteworthy because the novelty of the behavior expressed by an observer is considered a defining characteristic of true imitation (e.g., Heyes, 1994).

A subsequent attempt by Kaminski et al. (2011) to replicate Range et al.'s (2007) finding by assessing whether dogs would selectively adjust their behavior to take account of the "rationality" of the demonstrator's actions (such as using a hand when the mouth is full, or a leg when the hands were full) did not replicate Range et al.'s findings and concluded that, although dogs closely monitor demonstrator's actions, they likely do not take the rationality of the demonstrator's behavior into account when choosing to mirror what others do. These findings remain controversial (Huber, Range, & Virányi, 2012).

Similarly, Mersmann, Tomasello, Call, Kaminski, and Taborsky (2011) found that dogs were not more likely to walk around an obstacle in the same direction as a human demonstrator, nor was their ability to solve an instrumental problem (a puzzle box which could be opened in two different ways) improved by watching a skillful demonstrator—whether that individual was human or dog. Mersmann et al. concluded that the benefits to observers of seeing demonstrators complete actions were more likely stimulus and local enhancement than true imitation. Similar conclusions were drawn by Tennie et al. (2009).

Miller et al. (2009) reported greater success in observing true imitation in pet dogs using a bidirectional control procedure and a dog as the demonstrator. In all conditions each observer dog watched as a screen moved either left or right to obtain food from an experimenter. In control conditions the screen was moved by the experimenter behind the apparatus in such a way that the observer dog could not see the means by which the screen was made to move. In experimental conditions, a trained demonstrator dog pushed the screen either left or right. In additional conditions a human demonstrator moved the screen in view of the observing dog. The observer dogs were more likely to push the screen in the direction demonstrated if the demonstrator was another dog than a human and both demonstrators evoked greater levels of imitation in the observer dogs than when the screen moved without a visible operator.

Evidence for imitation in dogs remains unclear—especially in the best-controlled paradigms like the bidirectional control procedure, which controls for other possible interpretations such as stimulus or local enhancement and emulation. In any case, species uniqueness for dogs is not claimed in this domain. True imitation has been shown in a range of species including birds (pigeons: Epstein, 1984; Kaiser, Zentall, & Galef, 1997; quail: Akins & Zentall, 1999; Dorrance & Zentall, 2001; Budgerigars, Mui, Haselgrove, Pearce, & Heyes, 2008; Parrots, Moore, 1992; see Zentall, 2006, for a review), rats (Heyes, Jaldow, & Dawson, 1994; Heyes, Jaldow, Nokes, & Dawson, 1994; Mitchell, Heyes, Gardner, & Dawson, 1999); primates (Bugnyar & Huber, 1997; Call, Carpenter, & Tomasello, 2005; Custance, Whiten, & Bard, 1995; Ferrari et al., 2006; Hayes & Hayes, 1952; Myowa-Yamakoshi & Matsuzawa, 1999, 2000; Russon & Galdikas, 1993; Stoinski & Whiten, 2003; Subiaul, Cantlon, Holloway, & Terrace, 2004; Voelkl & Huber, 2000, 2007; Whiten & Custance, 1996) Cetaceans (Whales, Panova & Agafonov, 2017; dolphins, Richards, Wolz, & Herman, 1984; Jaakkola, Guarino, & Rodriguez, 2010—for a review Rendell & Whitehead, 2001) see Zentall (2013) for a review. Most pertinently to the present discussion, imitation has also been reported in wolves (Range & Virányi, 2014) and thus cannot be considered part of any domestication adaptation package.

It is also worth noting that imitation is not an important aspect of training dogs. Dogs in close relationship with people are not noted for their tendency or ability to imitate human actions. Working dogs, for example, are not typically trained by having a human demonstrate the desired behavior (be that herding or guarding livestock, using the nose to detect contraband or explosives, guiding blind people across streets while wearing a harness, etc.).

2.1.2.4 Critique of human-like social cognition hypothesis

The claim that dogs possess human-like forms of social cognition that are unique among nonhuman animals has been empirically refuted. In the case of following human gestures and gaze, individuals from 38 different animal species have been demonstrated to have at least some capacity of this type. True imitation has been more readily demonstrated in several species of bird than in dogs where findings remain controversial.

The more complex forms of theory of mind awareness such as demonstrated in the Guesser-Knower studies have produced only constrained evidence of success in dogs and they have not been matched by comparison studies in wild canids without which claims of exceptional skill in dogs are without content. The results of studies in great apes are as controversial as those in dogs.

In studies where putatively unique social-cognitive skills are being tested for in dogs, the animal subjects are being expected to attend to and comprehend the implications of *human* visual access. In almost every case, these have been pet dogs living in human households. To compare the behavior of these animals, who by the time they are 1 year old have probably spent over 4000 h within 2 m of a human with laboratory reared animals is not a viable method to draw phylogenetic comparisons.

Rather than view the cognitive performance of a few dozen first-world pets as indicative of innate abilities of the subspecies *Canis lupus familiaris*, it is surely at least as likely that the results obtained are specific to the life experiences of the particular subjects under test. At a minimum, some effort to test dogs with diverse life experiences is essential before concluding that a skill is even widespread in dogs—never mind indicative of phylogenetic significance.

2.2 Social ecology and behavioral development of dogs

While the possibility of behavioral adaptations in the cognitive domain has attracted a great deal of research effort over the last 20 years which has in turn led to vibrant controversy, there are many behavioral adaptations in other domains which have been studied for much longer and about which there is considerably less controversy. These are adaptations in the domains of social and foraging ecology as well as behavioral development.

2.2.1 Reproductive behavior

Lord et al. (2013) reviewed the reproductive behavior of dogs in the context of the other members of the genus *Canis*. Unlike wolves and other wild canids which generally do not reproduce until their second year of life, both male and female dogs are reproductively active already in their first life year (Boitani & Ciucci, 1995; Ghosh, Choudhuri, & Pal, 1984; Lord et al., 2013; Wandeler, Matter, Kappeler, & Budde, 1993).

Again, unlike wolves, free-living dogs do not form pair bonds. Although most female dogs are not technically promiscuous, they typically mate with a number of males while in estrus (Cafazzo et al., 2014; Pal, Ghosh, & Roy, 1999). Males do not commonly guard females during estrus or stay with them during pregnancy and birth (though see Pal, 2005, for some evidence of paternal guarding of mothers and litters). Females reproduce every 7 months on average (Boitani, Ciucci, & Ortolani, 2007; Macdonald & Carr, 1995) and males are continuously reproductively active (Gipson, Gipson, & Sealander, 1975; Haase, 2000; Lord et al., 2013).

Female dogs give birth to a litter of pups ranging in number from 3.5 to 7.0 (in purebreds, Borge, Tønnessen, Nødtvedt, & Indrebø, 2011: only limited data are available from free-ranging dogs. Pal recorded a mean litter size of 5.83 (±1.57) from six pregnancies in Katwa town, West Bengal, India—not all of whom need have the same father (Hollinshead, Ontiveros, Burns, Magee, & Hanlon, 2020). Mothers have sole responsibility for the pups and nurse them for around 5–11 weeks (Martins, 1949; Pal, 2005, 2008; Scott & Fuller, 1974). At the end of that period the pups are entirely on their own. There is no paternal care or support from young of earlier litters (Bonanni & Cafazzo, 2014; Martins, 1949; Mech & Boitani, 2003; Pal, 2008) though there are sporadic reports of paternal care including regurgitation (Malm, 1995; Pal, 2005; Paul, Sen Majumder, & Bhadra, 2014) and play and protection (Pal, 2005; Paul et al., 2014) as well as allonursing from other females denning in the same location at the same time (Daniels & Bekoff, 1989a; Pal, 2005; Paul et al., 2014).

Females enter estrus approximately every 7 months starting in the first year of life. Reproduction is not typically seasonal (Boitani et al., 2007; Engle, 1946; Gipson et al., 1975; Lord et al., 2013), though it can be responsive to seasonal resource availability, as in India where mating takes place from October to March so that pups are born in the late monsoon season and winter (Chawla & Reece, 2002; Oppenheimer & Oppenheimer, 1975; Pal, 2001, 2008). In general, however, unlike wild canids who hunt live prey, the food source of dogs does not in occur in seasonal pulses because humans discard waste uniformly over the year (Coppinger & Coppinger, 2001).

This pattern of reproductive behavior contrasts quite starkly with wolves who do not usually start reproducing until their second year of life at the earliest and form potentially life-long pair bonds. They are typically monogamous (Kleiman & Eisenberg, 1973; Macdonald & Moehlman, 1982; Mech, 1970) which is otherwise rare in mammals (Kleiman & Malcolm, 1981) and fathers provision mothers while they are nursing and then continue to support their young by regurgitation—as do siblings from the prior season or two. Reproduction is strictly seasonal with mating in December through March and pups born in March through June (with variation due to latitude: Haase, 2000; Mech, 2002; Rausch, 1967).

Unlike wolf pups who stay with their parental pack for 2 or 3 years (Mech, 1981; Peterson, Woolington, & Bailey, 1984; Rausch, 1967), dog pups are rejected by their mother around 11 weeks of age at weaning (Pal, 2005). Pups start foraging around 8 weeks of age by following their mothers to food sources. They may also beg for food from people but are less effective than adult dogs in obtaining food during the weaning and post-nursing stages of life (Lord et al., 2013; Macdonald & Carr, 1995; Pal, 2008).

First year pup survival is reported as low as 5% or less from Boitani, Francisci, Ciucci, and Andreoli (1995) in central Italy and Beck (1973) in Baltimore, MD. Paul, Sen Majumder, Sau, Nandi, and Bhadra (2016) reported 19% survival in free-ranging dogs in India (with nearly two thirds of mortality being human influenced). Bonanni and Cafazzo (2014) reported a much higher 50% survival to 1 year in a suburb of Rome, Italy.

The radically different reproductive behavior of dogs compared to wolves is clearly related to their different foraging ecologies (Marshall-Pescini, Schwarz, Kostelnik, Virányi, & Range, 2017). Wolves primarily hunt live prey—ungulates that are typically larger than they are and that can be successfully captured and killed only by the coordinated action of a group of adults (Mech, 1981). Although the coordination required of a wolf pack may not be as cognitively demanding as has been assumed (Muro, Escobedo, Spector, & Coppinger, 2011), it is still a necessarily social and cooperative activity. The result of a successful wolf hunt is a quantity of meat greater than one wolf could consume on its own, and since the other individuals in its pack are its kin it would not be in the dominant individual's interest to attempt to prevent other pack members from feeding (Mech, 1970). Dogs, on the other hand, live in human proximity (Coppinger & Coppinger, 2001; Sen Majumder, Paul, Sau, & Bhadra, 2016) where they forage on human waste, including feces—a foraging style that typically does not depend on coordination with conspecifics (Atickem, Bekele, & Williams, 2010; Butler & du Toit, 2002; Vanak & Gompper, 2009).

2.2.2 Flight distance

Another behavioral difference between dogs and wolves that is clearly related to the different feeding ecologies of the two subspecies is flight distance. Flight distance is simply the linear distance at which an animal interrupts ongoing activity as a response to the approach of a potential predator—including human. The flight distance of wolves scavenging on trash dumps in Scandinavia to human approach has been estimated at around 200 m (Karlsson, Eriksson, & Liberg, 2007). Daily experience around pet dogs suggests that flight distance for dogs is highly variable. Many pets will allow even unfamiliar people to approach and touch them, implying a flight distance of zero. Free-ranging dogs around villages in rural Ethiopia had flight distances around 5 m (Ortolani, Vernooij, & Coppinger, 2009). Bonanni & Cafazzo (2014) in a study of free-roaming dogs in a suburb of Rome, Italy, reported that the dogs they studied typically showed fear reactions toward approaching people. Even after 2–3 months of habituation experimenters had to observe from 20 to 50 m distance.

This reduction in flight distance in dogs is likely an adaptation to foraging by scavenging on human trash as it increases the time a dog—compared to a wild canid—will spend foraging near human beings.

Where there is so much dispute over subtle potential differences in behavior between dogs and wolves on cognitive tests it is remarkable that the large, clear-cut, and uncontroversial differences in reproductive and foraging behavior between wolves and dogs are not more often discussed and taken into consideration when formulating accounts of the success of dogs in the modern world. This seems to be a consequence of a generally anthropocentric, and sometimes frankly anthropomorphic, approach to dog behavior and cognition where human-like qualities are considered more important than aspects of behavior that are more strongly related to canine niches.

2.2.3 Behavioral development

In the most recent thorough comparison of sensory development in dogs and wolves, Lord (2013) concluded that sensory development in these two subspecies is similar, with olfaction developing by the second week of life, audition by Week 4 and vision by Week 6. Behavioral development has a different timeline, however. Wolf pups are already exploring their environment at 2 weeks of age (Frank & Frank, 1982; Packard, 2003) whereas dog pups do not actively approach and investigate objects until 4 weeks (Fox, 1964; Rheingold, 1963; Scott & Fuller, 1974). The implication of the similarity of sensory development in dogs and wolves observed by Lord (2013), combined with the difference in age of first mobility and exploration found in several prior studies, is that wolves discover their environments while still largely blind and deaf, whereas dogs do not explore until their ears and eyes are functional.

Lord (2013) suggests that this has implications for the critical period for social imprinting in dogs. The critical period for social imprinting is a time-limited phase early in an individual's life when it learns what kinds of beings to seek for social relationships throughout life. This process is crucial for the development of species identification (Hess, 1959; Lorenz, 1937; Scott & Fuller, 1974) and exposure to other species during this period can result in inter-species socialization (Scott & Fuller, 1974), which is crucial for dogs to form relationships with humans—in other words, to be tamed.

The critical period for social imprinting starts with the ability to explore (Hess, 1959; Scott & Marston, 1950) and ends with the onset of fear toward novel stimuli which then inhibits further exploration (Freedman, King, & Elliot, 1961; Hess, 1959; Scott & Fuller, 1974; Scott & Marston, 1950). No direct study of the duration of the critical period for social imprinting appears to have been carried out in wolves, but accounts of attempts to hand-rear wolves, as well as observations of the onset of fear toward novel stimuli in wolf pups, are taken to imply that this period starts around 2–3 weeks of age and is complete 4 weeks later (Klinghammer & Goodmann, 1987; Woolpy & Ginsburg, 1967; Zimen, 1987). The only direct study of the duration of the critical period for social imprinting in dogs concluded that dogs remain sensitive for at least 9 weeks of age (Freedman et al., 1961; also reported in Scott & Fuller, 1974).

Lord (2013) noted that the fact that dogs do not start exploring until 4 weeks of age implies that they have all of their senses available to them at the onset of the critical period for social imprinting, whereas when wolves begin to explore at 2 weeks, only olfaction is fully functional. On the basis of her sensory data, which indicates dogs show initial fear responses at 8 weeks, compared to wolves' initial fear responses becoming apparent at 6 weeks of age, Lord argued that the critical period for social imprinting in dogs and wolves has the same duration, it is just 2 weeks later in dogs than wolves. The crucial difference between the subspecies then lies in the higher level of sensory development in dogs than wolves during this period.

Clearly the critical period for social imprinting is crucial to how it is possible that many dogs and a tiny number of wolves have formed social relationships with human beings. Changes in this process must contribute to why it is so much easier to tame dogs than wolves. And yet the scientific understanding of this process in these two closely-related but behaviorally diverse canids is still weak. There is only one direct study on social imprinting in dogs, and none at all in wolves. In the sole study of dog imprinting, Freedman et al., 1961, also reported in Scott and Fuller (1974), reported that dogs that were not exposed to human contact until 14 weeks of age—compared to dogs so exposed at 9 weeks of age (no group was exposed at any point intermediate between nine and 14 weeks), behaved toward people, "…like little wild animals and could be tamed only in the way in which wild animals are usually tamed, by keeping them confined so that they could not run away and feeding them only by hand, so that they were continually forced into close human contact." (Scott & Fuller, 1974 p. 105). The vagueness of this comment is deeply frustrating. If Scott and Fuller meant to imply that, even though the critical period for social imprinting had passed these dogs were nonetheless tamable, albeit with some extra effort, then this would undermine the widely-accepted identification of social imprinting with "taming" (e.g., Coppinger & Coppinger, 2001). Unfortunately, all authors of this study are deceased and no comparable study has been reported since.

2.3 Social relationships

The above discussion of social development indicates that this is a domain where there has been significant evolution from wolf to dog. In this section we focus in on the question of social relationships in dogs.

2.3.1 Inter-species relationships

Even the most casual observation of dogs makes clear that they are remarkable for their willingness to form social relationships with members of other species; from the ubiquitousness of "man's best friend," (Voltaire, 1764/1824) to the rancher's dog guarding livestock to whom it is socially attached (Coppinger & Coppinger, 2014). This has been studied extensively in forms of attachment tests originally developed for the analysis of mother-infant relationships in the human species.

2.3.1.1 Attachment tests

Many dog owners report that they perceive their pets as family or friends (e.g., Archer, 1997; Barker & Barker, 1988; Serpell, 2004; Voith, 1985), and several studies have attempted to measure the strength and intimacy of that relationship. One widely deployed test of emotional connection or attachment is modeled on the Strange Situation Procedure from human developmental psychology which was developed from Bowlby's (1958) theorizing about mother-infant bonds by Ainsworth and Bell (1970).

Ainsworth (1989) defined "attachment" as an affectional bond which is a "relatively long-lasting tie" (p. 711) that may exist between parents and children, in sexual pair bonds, and among friends. It is characterized by "a need to maintain proximity, distress upon inexplicable separation, pleasure or joy on reunion, and grief at loss." In addition there is, in secure attachments, "security and comfort… and yet the ability to move off from the secure base provided by the partner." (p. 711).

The Strange Situation Procedure (SSP) was developed to mimic the mild social stressors of everyday life where a child may become separated from a caregiver but soon reunited (Ainsworth & Bell, 1970). Briefly, a child, typically under 2 years of age, is given an opportunity to explore a novel room in the company of his mother, a stranger enters the room and the mother sneaks away. A few minutes later the mother returns and comforts the child before leaving with the stranger so that the child is completely alone. After a few more minutes the stranger returns followed finally by the mother.[1]

Primarily two aspects of the child's behavior are used to assess the nature of attachment to the mother: First how much he explores when the mother leaves him with the stranger; second how he responds to the mother's return (Ainsworth, Blehar, Waters, & Wall, 1978). Securely-attached children are identified by their willingness to explore in their mother's presence, distress when she leaves and happiness on her return, combined with a readiness to be comforted quickly by the mother. Children who respond differently can be categorized in several ways depending on their response to the stranger and the reunion with the mother.

Starting with Topál, Miklósi, Csányi, and Dóka (1998) several studies have looked at the behavior of pet dogs in the SSP. Unfortunately, as Rehn, McGowan, and Keeling (2013) point out, most studies on dogs have coded behavior rather differently from the recording of human behavior in the same test. Whereas studies on children, as noted above, code the nature of the child-caregiver attachment relationship into one of a small set of categories, most dog studies (with notable exceptions including Rehn et al., 2013; Topál et al., 1998; Thielke & Udell, 2019, 2020; Wanser,

---

[1] I have used male and female pronouns here to clarify the roles: both male and female children are routinely tested; fathers are less commonly tested than mothers, but the procedure can be used with both parents as well as other caregivers.

Simpson, MacDonald, & Udell, 2020; Wanser & Udell, 2019) have simply noted the presence or absence of attachment as identified by marked differences in the dogs' behavior toward its owner and the stranger (e.g., Mariti, Carlone, Ricci, Sighieri, & Gazzano, 2014; Mongillo et al., 2013). Nonetheless, there is now abundant evidence that adult dogs living in human homes react to their owner in the SSP in a manner comparable to that of securely-attached children toward their caregivers.

Gácsi, Topál, Miklósi, Dóka, and Csányi (2001) used the SSP to show that dogs living in an impoverished shelter environment showed signs of attachment toward a person after having just been handled three times for 10 min. This is similar to Feuerbacher and Wynne's (2017) finding that shelter dogs given brief exposure (10 min) to two unfamiliar people rapidly developed an apparently arbitrary preference for one of the two people.

The complexity of the SSP brings with it some difficulties in interpretation. For example, Rehn, Handlin, Uvnäs-Moberg, and Keeling (2014) noted that the dog's reaction to being reunited with the owner (equivalent to the child's reunion with his mother) depended on the owner's behavior when returning to the room where the dog had been left. If the person ignored the dog when she returned, the dogs were less effusive in their greetings than if the person responded with physical and verbal contact. Udell et al. (2021), however, did not replicate this finding on a larger sample of dogs and owners. In their study, there was no significant effect of the manner of the owner's return on the dog's behavior.

The dog's behavioral responses may also fail to correlate with the owner's self-reports of attachment to the dog. Rehn, Lindholm, Keeling, and Forkman (2014) found that the dog's attachment as measured in the SSP did not reflect owner's responses on a survey of their attachment to the dog, though an association was found with the amount of time that the human and dog interacted daily, which is consistent with Mariti et al.'s (2011) finding that dogs expressed most intense attachment in the SSP to the person who walked them most.

2.3.1.2 Other tests of dog-human social connectedness

Simpler tests also indicate dogs' attachment to their owners. For example, Horn, Huber, and Range (2013) studied pet dogs' use of a person as a secure base by presenting the dog with a manipulative task and comparing how long it spent trying to solve the task either alone or with the owner present in the room. They found that the dogs manipulated the task longer with owner present than when alone. Gácsi, Maros, Sernkvist, Faragó, and

Miklósi (2013) investigated the impact of owner presence on dogs' response to the approach of a threatening stranger. They found that heart rate variability, a measure of physiological stress, was higher when the dog was alone when the stranger approached compared to when it had its owner with it.

Jakovcevic, Mustaca, and Bentosela (2012) introduced a simple test for inter-species sociability in which an unfamiliar human sat on a chair inside a 1-m-radius circle and the latency and proportion of time a pet dog chose to spend inside the circle was recorded. The person was passive for 2 min followed by a 2-min period in which the person solicited contact with the dog. Dogs that sought out more human contact were also found to gaze more at a person in a separate test where food was in sight of the dog but out of its reach.

2.3.1.3 Possible uniqueness of dog-human social connectedness

Taken together the tests discussed in preceding Sections 2.3.1.1 and 2.3.1.2 indicate that pet dogs show signs of attachment to the humans with whom they live, and also that these emotional connections can develop remarkably rapidly. In themselves, however, they do not demonstrate that attachment to people is a unique characteristic of the dog-human relationship. Rather few studies have looked for similar patterns of behavior in any other species. The most interesting comparison is to dog's wild ancestors, wolves. Gácsi et al. (2005) compared the reactions of hand-reared wolf pups and dog puppies at 3–5 weeks of age given a choice between their human caregiver and either a nursing bottle, an unfamiliar adult dog, a familiar age-matched dog, or an unfamiliar human experimenter. Although dogs displayed more social behaviors toward the humans, the overall patterns of preference differed little, with both dogs and wolves preferring the familiar human in most tests. The same population of wolves was tested on the SSP at 16 weeks of age alongside an age-matched group of dogs (Topál et al., 2005). Topál et al. concluded that the wolves, unlike dogs, did not show signs of attachment to their human caregivers.

Hall, Lord, Arnold, Wynne, and Udell (2015) tested up to 10 wolf pups on the SSP at 3, 5 and 7 weeks of age. The wolves showed clear differential responses to their caregiver compared to a stranger, with strong effects on reunion with the caregiver after separation. These findings are consistent with the hypothesis that wolf pups can be securely attached to their human caregivers. Comparison of Topál et al.'s (2005) findings with those of Hall et al. raises the possibility that wolves may show attachment to a caregiver at an early age but, possibly unlike dogs, this attachment may fade as the animal matures. A recent study, however, shows attachment to the handler in adult, hand-reared wolves and thus indicates that for wolves in continuing human contact attachment does not decline with age (Lenkei, Újváry, Bakos, & Faragó, 2020) leaving Topál et al.'s results anomalous. One possible explanation was proposed by Hall et al. They noted that Topál et al.'s wolves, though initially hand-reared, had already been relocated to a wolf "farm" between 2 and 4 months of age and thus their human interactions had been substantially attenuated which may account for their lower levels of attachment to human caregivers.

Bentosela, Wynne, D'Orazio, Elgier, and Udell (2016) compared the performance of pet dogs and human-reared wolves on the simple test instigated by Jakovcevic et al. (2012) in which a human sits on a chair and the animal's latency and duration of proximity to the person is measured. In addition to the unfamiliar person used in Jakovcevic et al., Bentosela et al. also measured the animals' responsiveness to a familiar person in the chair. In all conditions, dogs displayed strikingly more prolonged interest in the human than did the hand-reared wolves. Dogs spent more time in proximity to an unfamiliar individual than wolves did with a familiar one and dogs showed effectively no latency to approach familiar or unfamiliar people.

In a rare use of the SSP with animals other than dogs or wolves, Lundberg, Hartmann, and Roth (2020) found limited evidence for attachment to humans for horses. The horses sought human proximity during the reunion phase, but exploratory behavior was similar in the presence of the owner and the stranger. Vitale and Udell (2019) tested cats in a simplified SSP and reported that the majority of juvenile and adult pet cats showed a secure attachment style—a pattern of results similar to that found in human children and dogs.

Thus it would appear that secure-attachment-like behavior may not be entirely unique to dogs, but the intensity seen in adult dogs appears to be unlike anything observed in other species, particularly wolves.

2.3.2 Intraspecific relationships

Curiously, although there is considerable research into dogs' social interest in people, there is relatively little available research on social relationships among dogs. The available findings indicate a quite different pattern of intraspecific relations among dogs than are reported between dogs and human caregivers. This creates a puzzle that needs more attention.

Separation of puppies from their mother leads to distress (Fredericson, 1952; Pettijohn, Wong, Ebert, & Scott, 1977) and yet, quite unlike the reports of adult dogs separated from their human caregivers in attachment tests noted above, separation of two adult dogs that lived together in a kennel had no detectable effect on their behavior (posture, movement, and vocalizations) or glucocorticoid stress hormones (Tuber, Sanders, Hennessy, & Miller, 1996). Even when placed in a novel environment, the dogs' behavioral and endocrine responses were no different whether they were alone or with their kennel mate. Only the presence of a human caretaker reduced the response to this mild stressor and the dogs were more often seen soliciting social behavior from the human than from the kennel mate (Tuber et al., 1996).

Mariti et al. (2014) tested pairs of dogs living together in the same household in the SSP with one dog in each dyad acting as the "caregiver" for the other. The dogs showed fewer signs of stress toward the stranger when the cohabitant dog was present, however, the dogs were less stressed in the presence of the stranger than when alone—which is not consistent with secure attachment in humans. They also maintained more contact with the stranger after reunion with her than toward their familiar dog partner. The studies of Tuber et al. (1996) and Mariti et al. (2014) seem to indicate that dog-dog affectional bonds are not as strong as those between dogs and humans. Why this might be needs further investigation.

Free-ranging dogs in studies from various parts of the world show a range of forms of social organization. It should be noted that these studies are ethological in nature and involve passive observation of the animals, quite unlike the experimental studies carried out on pets and other captive dogs noted above. Several studies have reported dogs as typically solitary or dyadic (in India: Sen Majumder et al., 2014; Zimbabwe, Butler, Du Toit, & Bingham, 2004; Baltimore, MD: Beck, 1973; New York, NY: Rubin & Beck, 1982; Berkeley, CA: Berman & Dunbar, 1983, Newark, NJ: Daniels, 1983; Cd. Juarez, Mexico and Navajo reservation: AZ, Daniels & Bekoff, 1989a; Daniels & Bekoff, 1989b; Ethiopia: Ortolani et al., 2009). At the other extreme, at least one study has reported almost no (fewer than 1 in 1000) solitary animals (Italy: Bonanni & Cafazzo, 2014). Several studies have reported group sizes in a range from 11 to 28 (Baltimore, MD: Beck, 1973; Alaska: Gipson, 1983; Italy: Macdonald & Carr, 2016; India: Sen Majumder et al., 2014). Bonanni and Cafazzo (2014) studying dogs in a suburb of Rome, Italy, found groups ranging from 6 to 27 members. Larger groups can include multiple adult females depending on the availability of food, the breeding status of females and season (Sen Majumder et al., 2014).

Living in groups may offer advantages in terms of protection against threats. Free-ranging dogs in India have been reported to be bolder toward people when they are in groups than solitary (Bhattacharjee, Sau, & Bhadra, 2020). Larger groups may also be able to hunt larger prey (Bhadra, 2014; Butler et al., 2004; Vanak & Gompper, 2009).

Although some of the observed difference in group sizes may be due to different assessment methods at different locations and times, it appears that dog social structure is very flexible. Whether these differences are due to genetic differences in populations of free-ranging dogs around the world, or adjustment to different environmental conditions such as density of food is presently unknown.

2.3.2.1 Dominance, cooperation and competition

The possibility of dominance in dog social groups (and mixed dog-human groups) has become unnecessarily controversial in recent years as scholars and professional associations have attempted to react to questionable forms of animal interaction advocated by high profile trainers on television (in particular "Dog Whisperer with Cesar Millan," Sumner, 2004-2016). In reacting to these trainers' misapplication of the term "dominance," several authors have attempted to deny the relevance of dominance to dog social behavior (e.g., American Veterinary Society of Animal Behavior, 2008; Bradshaw, Blackwell, & Casey, 2009; McGreevy, Starling, Branson, Cobb, & Calnon, 2012; Yin, 2007). Dominance, however, does not need to be a controversial concept. It is simply a tendency for certain individuals to have somewhat consistent preferential access to constrained resources (Dugatkin, 2020). The existence of dominance relationships does not have to imply agonistic behavior, indeed, the function of dominance is to limit conflict: "dominance relationships become established not because higher ranking individuals reinforce their status by being aggressive or showing formal dominance signals but because lower ranking individuals recognize supremacy by showing formal submissive signals" (Schilder, Vinke, & van der Borg, 2014, p. 186). Active conflict is most likely when perceived asymmetries are small. Formal dominance and submissive signals (ritualized behaviors which indicate recognition of higher and lower status respectively) serve to reduce contests and antagonistic interactions.

Dominance in ethology is correctly identified as a property of relationships between individuals, but since it depends on relatively stable qualities of individual animals, contrary to the claims of Langbein and Puppe (2004), Bradshaw et al. (2009) and others, relatively stable differences between individuals may contribute and influence dominance relationships. Thus "submissiveness" has been recognized a trait in dog personality (Jones & Gosling, 2005) as has "leader/dominan[ce]" (Ákos, Beck, Nagy, Vicsek, & Kubinyi, 2014). A similar trait of "boldness" was identified by Svartberg (2005). It is particularly noteworthy that dominance-related temperament traits have been identified even though current tests of dog temperament or personality include little or no assessment of dog-to-dog social interactions (e.g., Flack & De Waal, 2004; Svartberg & Forkman, 2002).

Hierarchical social structures and dominance signaling have been observed in free-living dogs in Italy by Bonanni, Cafazzo, Valsecchi, and Natoli (2010), Bonanni et al. (2017), Silk, Cant, Cafazzo, Natoli, and McDonald (2019) and Cafazzo, Valsecchi, Bonanni, and Natoli (2010); in Spain (Font, 1987) and India (Pal, Ghosh, & Roy, 1998; Sen Majumder et al., 2014); at a U.S. dog day-care center (Trisko & Smuts, 2015); in group housed dogs in the Netherlands (van der Borg, Schilder, Vinke, & de Vries, 2015) and in pet dogs playing at a dog park in the U.S.A. (Bauer & Smuts, 2007).

In free-living dogs, dominant individuals are more likely to lead group movements (Bonanni et al., 2010), and have higher copulatory access (Cafazzo et al., 2014)—which is consistent with the concept of dominance as applied to other species (e.g., Flack & De Waal, 2010).

Bauer and Smuts (2007) studied dogs playing together at a park and reported that, although there were role reversals in behaviors including chasing and tackling, even as roles were repeatedly swapped, some behaviors never reversed, including mounts, muzzle bites, and muzzle licks, suggesting they were stable indicators of dominance status.

Pal et al. (1999) as well as Pal (2003, 2005) concluded that free-ranging dogs at their study site in India did not establish dominance hierarchies but these studies relied mainly on aggressive interactions which may not be an appropriate measure given that formal dominance signals may have served to minimize agonistic interactions. Bonanni and Cafazzo (2014) reanalyzed data from Pal et al. (1998) and concluded that these dogs showed highly statistically significant linear hierarchies.

Boitani et al. (Boitani & Ciucci, 1995; Boitani et al., 2007: see also van Kerkhove, 2004) have suggested that dog groups lack the hierarchical social structure and strong bonds that are typical of wolf packs. This conclusion was partially driven by the presence of multiple breeding individuals in the absence of a test of hierarchy (Bonanni et al., 2017). Cafazzo et al. (2010) noted social hierarchies which influenced reproductive behavior even though the overall mating system was promiscuous.

Considering the wide range in group sizes that have been observed at different sites, it seems possible that different patterns of social organization may be present in different places and at different times. This could include the possibility that not all dog groups may show dominance hierarchies. Bradshaw et al. (2009) presented results from a group of neutered male dogs in which no overall ranking could be found (though some behaviors were consistent markers of dominant and subordinate relationships). Schilder et al. (2014) point out, however, that this was a group of neutered dogs of the same sex, with no resources to compete over and thus any dominance hierarchy may have been greatly muted.

Two studies have thoroughly investigated social networks in groups of dogs. van der Borg et al. (2015) studied formal dominance and submission signals in a group of 16 dogs living in kennels studied during outdoor group exercise and play opportunities. They identified several clear signals of social ranking and, on an established scale of the degree of linearity of a hierarchy which ranges from (1) despotic, through (2) tolerant, (3) relaxed to (4) egalitarian (Flack & De Waal, 2004), dogs were found to be "tolerant." This means that they had a moderately steep linear social hierarchy and large asymmetries in postural signaling with mild to moderate aggression. This places dogs in a similar position to several macaque species (e.g., Balasubramaniam et al., 2012). Silk et al. (2019) reported comparable results from a group of 25–40 dogs ranging freely in a suburb of Rome, Italy. Silk et al. found a sex and age-graded network of linear dominance in which older and male animals were typically dominant over younger and female ones. They found that networks of submission, ritualized dominance and aggression were broadly consistent with each other.

That groups of dogs raised together show higher rates of aggression toward each other than groups of similarly-raised wolves has been known for some time (e.g., Feddersen-Petersen, 1991, 2007; Frank & Frank, 1982). In an interesting study with a surprising outcome, Feddersen-Petersen (2004) raised mixed packs of dogs (poodles) and wolves. At 4 months of age male poodles outranked age- and sex-matched wolves and obtained preferential access to food and preferred locations. Feddersen-Petersen noted that agonistic interactions appeared in dog groups earlier than in wolves and persisted longer. The frequency of aggressive interactions in packs of poodles during the first life year resembled that of jackals—which are solitary in adulthood and thus have little need to learn to build social networks—rather than wolves (Feddersen-Petersen, 1991).

Dogs have also been shown to have more severe social hierarchies and dominance-related behaviors than wolves. For example, Dale, Quervel-Chaumette, Huber, Range, and Marshall-Pescini (2016) presented a carcass to groups of dogs and wolves which had been raised similarly (human-socialized at an early age and living in captive same-species groups). Subordinate wolves spent as much time feeding on the carcass as more dominant individuals, but subordinate dogs stayed away from the carcass which was then monopolized by more dominant individuals. In a similarly simple but telling test, Range, Ritter, and Virányi (2015) offered pairs of equivalently reared, group-living, human-socialized dogs and wolves a food item that could either be shared or monopolized. In wolves, dominant individuals tolerated subordinate animals cofeeding on the same food resource. In dogs, on the other hand, subordinate animals were seldom able to feed because the dominant individual monopolized the available food.

This difference in dominance severity also shows in tests of cooperation comparing dogs and wolves. For example, Marshall-Pescini et al. (2017) compared the performance of similarly-raised group-living dogs and wolves on a task which required each of two animals to pull strings simultaneously for either of them to obtain a reward. Despite similar levels of engagement and interest in the task, wolves outperformed dogs. Indeed, dogs were never successful. These authors concluded that dogs' and wolves' different conflict management strategies were responsible for the results.

Ostojić and Clayton (2014) reported success of pairs of pet dogs tested on a string-pulling task similar to that used by Marshall-Pescini et al. (2017). However, unlike the dogs tested by Marshall-Pescini et al., Ostojić and Clayton's animals received extensive pretraining and they also lived together in human households where owners may often train dogs not to engage in resource conflicts and thereby promote tolerance (Marshall-Pescini et al., 2017).

Successful cooperation has been observed in dogs in a paradigm where pairs of dogs could not both enter into a food area together. Bräuer et al. (2013) and Bräuer, Stenglein, and Amici (2020) investigated a task in which two openings were mounted in a transparent barrier. Only one of these openings could be open at any one time and a human operator controlled which was open by moving a sliding door. On the further side of the barrier from the animals were bowls containing food. As a dog approached an opening, the experimenter closed it, thereby revealing the other opening. Only after the first dog had passed through did the experimenter move the opening so that the other dog could enter the food-containing section of the apparatus. Consequently, if both dogs approached one opening, they would never access food. The only way to get to the food was if the dogs each approached a separate opening. Bräuer et al. (2013) found that dog dyads were successful on this task, however, the animals did not monitor each other's behavior. In other words, the task was not cooperative *sensu stricto* because each dog acted independently. Bräuer et al. (2020) compared the performance of human-habituated wolves to that of pet dogs on this task and did not find an overall effect of subspecies on successful task performance or latency to task completion.

Unlike the string-pulling task reported by Marshall-Pescini et al. (2017) where the steeper social hierarchy of dogs led to failure because the pairs of dogs did not want to simultaneously approach the same food source, in Bräuer et al. (2013), (2020), the subordinate dogs' willingness to stay away from the dominant animal rather paradoxically led to success on the task and the appearance of cooperation. The successful outcome thus resulted from two individuals striving to keep out of each other's way.

Overall, the more intense social hierarchy of dogs compared to wolves leads to low levels of cooperation in feeding tasks unless the dogs have been trained or otherwise shaped by humans to act cooperatively.

2.3.2.2 Unsolvable and solvable tasks

Miklósi et al. (2003) offered two simple problems to both hand-reared juvenile wolves and dogs raised in human families. They were confronted by a desirable food item trapped inside a container: in one condition, this was a plastic bin with a lid screwed shut onto it; in the other, a piece of meat attached to a rope inside a cage. First, each animal was exposed to the apparatus with the food freely accessible (because the lid had not been attached to the bin and the cage door had not been closed). Then the wolves and dogs were exposed to the experimental condition with the container closed. In the initial phase, no differences between the species were noted; however, once the container was closed, the wolves continued to work on the problem, whereas the dogs reduced the amount of time they attempted to open the container and instead gazed more at their nearby owner or caretaker. Miklósi et al. interpreted these findings as indicating a "genetic predisposition in dogs" for "'human-like' communicative behaviors." (p. 764). However, the authors did not report any data on the success of the dogs and wolves in opening the closed containers. A more parsimonious interpretation of their findings is that the wolves, with their more powerful jaws, simply did not perceive the closed containers as impenetrable. From personal observations of wolves interacting with objects at Wolf Park, IN, I would not expect an adult wolf to perceive a "commercial container for household litter" (p. 765) to be something it could not break into. It is possible the wolves did not look around at the nearby human because they simply did not perceive the problem as one requiring human intervention (Marshall-Pescini et al., 2017).

A test of kennel-reared dogs with limited human contact on this task found that they were less likely to gaze at human than breed- and age-matched pet dogs (D'Aniello & Scandurra, 2016). Dogs trained for agility—a sport that requires intense coordination with humans—were faster to look back at the owner than dogs trained for search and rescue—a more independent activity (Marshall-Pescini, Valsecchi, Petak, Accorsi, & Previde, 2009). Further, two studies on pet dogs found that gazing at the owner increased with age (Konno, Romero, Inoue-Murayama, Saito, & Hasegawa, 2016; Passalacqua et al., 2011). However, Brubaker and Udell (2018) failed to find any difference in the tendency to persist on a solvable task between pet dogs and dogs trained for search and rescue, though search and rescue dogs, when given encouragement, were more likely to solve the task and less likely to look at their human when encouraged to solve the task. These findings are all more consistent with the hypothesis that life experience is crucial to an animal's response to an unsolvable task than with explanations building on inherited genetic factors.

Marshall-Pescini et al. (2017) performed an extended study on dogs' and wolves' responses to unsolvable tasks by including free-ranging dogs (in India) and carrying out more thorough analysis of the animals' persistence in attempting to open the containers. They found that persistence was a key determinant of the tendency to look to a nearby human for assistance. Although wolves gazed at the person less than any of the dog groups tested, in an analysis only of animals that looked at the human at some point (which was most of the dogs and four of 15 wolves), persistence was a major predictor of latency to look back and there was no effect of subspecies. Marshall-Pescini et al. drew particular attention to the readiness with which the street dogs looked back at the nearby human when this person was not in any sense the dogs, "human partner." It seems unlikely that a dog living on the streets would be expecting assistance in opening a food-containing box from a nearby human. This points to the importance of considering a dog's ecology and living conditions when interpreting its behavior toward a person.

Udell (2015) extended Miklósi et al.'s (2003) finding by presenting hand-reared wolves, pet dogs, as well as dogs living in an animal shelter, with a fully solvable puzzle box. In this study, a piece of food was placed inside a transparent plastic box with a thick piece of rope inserted in its lid for ease of opening. Udell added two conditions to Miklósi et al.'s design. As well as a condition with the owner or caregiver present, she included a condition where the animals were left to attempt the puzzle box on their own. She also included a condition for those animals that did not open the box in their owner's presence where the owner was instructed to provide vocal encouragement. Here, even though the container and its closure were designed to be openable by both dogs and wolves, only 5% of dogs went ahead and opened the container in the human-present conditions, compared to 80% of wolves. Performance was mildly—but not statistically significantly—improved when the animals were alone. Further, encouragement from the owner/caregiver had a modest, albeit statistically significant, impact on the unsuccessful dogs' performance. These results provide some support for the hypothesis that dogs have a greater readiness than wolves to gaze at a nearby human to solicit assistance in solving problems. This readiness could stem from genetic or experiential factors. This study does not entirely address the question whether the dogs and wolves perceived the problem as equally difficult. It is possible that, although the task in Udell (2015) was amenable to solution by dogs just as by wolves, nonetheless, the dogs still perceived it as more difficult and therefore were more inclined to solicit human assistance.

Brubaker, Dasgupta, Bhattacharjee, Bhadra, and Udell (2017) compared human-socialized wolves, pet dogs and Indian street dogs on Udell's (2015) solvable task. They also found that wolves were more likely to open the container than dogs, and in addition observed that the free-living dogs looked back at humans more than any other group of canids tested. This further emphasizes the danger of assuming that dogs gaze at people in order to solicit assistance or indeed in any communicative manner.

Bhattacharjee et al. (2017) also investigated free-living street dogs in India on the solvable task developed by Udell (2015), but in addition they exposed the dogs to a piece of chicken inside a closed transparent plastic bag. This, they argued, was a familiar problem for a street dog, since they commonly find food remnants in bags. Bhattacharjee et al. found that the dogs were more successful on the familiar than the unfamiliar task and showed negligible interest in soliciting assistance from a nearby experimenter in the familiar task condition. For the unfamiliar solvable task, the dogs were more likely to not only look at the nearby person but explicitly beg from him.

Lazzaroni et al. (2019) compared free-ranging dogs (in Morocco), with pet dogs and dogs living in captive packs on an impossible task. They found that the free-ranging dogs were less persistent on the task than the other two groups of dogs. They did not believe this was due to less experience around similar objects but rather due to the free-ranging dogs having less experience of human-mediated object interaction. In a subsequent study, Lazzaroni et al. (2020) again compared free-ranging dogs in Morocco and pet dogs on an impossible task. In this study, they added three new conditions to the standard condition in which a human stands nearby. In one the dog was left alone to attempt to get the food, in a second a "dummy" human (a piece of cardboard shaped, colored, and sized to match a person) was placed nearby, and in the third a large piece of cardboard, not shaped like a human, was nearby. They found that pet dogs and free-ranging dogs showed similar levels of persistence in the task across all four conditions. However, pet dogs looked at the human more than did the free-ranging dogs. Lazzaroni et al. (2020) concluded that the looking back is not a problem-solving strategy but rather relates to the animals' persistence, the saliency of the stimuli offered and possibly also to the animals' past experience of human- and object-mediated reinforcement.

These studies of dogs' behavior when confronted with tasks in which they attempt to obtain a piece of food while a human is close by are not easily explained with an hypothesis that relies entirely on inherited tendencies to seek human assistance. Rather there are several reasons why a dog might look at a nearby human while it is foraging. One could certainly be an expectation, which would not be surprising given the lives many dogs lead with humans, that the person may facilitate access to the food. But other possibilities include that the dog may be made anxious by the static proximity of a human being. This does not seem to have entered the peer-reviewed literature, but I have seen street dogs in Moscow, Russia, and in Nassau, Bahamas, who were unperturbed by hundreds of pedestrian commuters passing them by, but if an observer stopped and observed a dog for more than about a minute, the dog would get up and move away. Presumably, a human attending to a dog without offering food or other friendly interaction could be a possible danger to a street dog. In making cross (sub-) species comparisons it is also important to keep in mind that the same physical object may offer different affordances to diverse animals. A container that is unequivocally unopenable for a dog, may not appear impossible to a wolf—which could explain the wolf's continued attempts to open where a dog gives up and reverts to begging from a nearby human.

3. Theories of dog social uniqueness

Having reviewed a wide range of studies of dogs' social behavior I now turn to theories of dog uniqueness that have attempted to incorporate this aspect of dog behavior.

3.1 Theories of increased "friendliness" and decreased aggression

Several authors have suggested that dogs were selected to be more friendly and less aggressive than their ancestors, wolves. This idea may have originated with Lorenz (1954) and more recent proposals along these lines include Hare and colleagues' "Survival of the friendliest" (Hare, 2017; Hare et al., 2002; Hare & Tomasello, 2005; Hare, Wobber, & Wrangham, 2012) and "Emotional Reactivity" hypotheses (Hare et al., 2002; Hare & Tomasello, 2005) as well as the "Decreased emotional reactivity" thesis (Ostojić & Clayton, 2014) and Miklósi and Topál's (2013) "Inter-specific social competence" hypothesis. These theses share the idea that selection for more friendly and less aggressive individuals may have facilitated human-dog cooperative activity. Miklósi and Topál (2013) proposed that "evolutionarily novel, inter-specific social competence in dogs, … allowed for the establishment of a wide range of social relationships with humans, ranging from a strictly working relationship to being a family pet" (p. 290).

All proposals of this general form, however, are contradicted by the abundant evidence that dogs are not more "friendly," more socially competent, and less aggressive than wolves. Rather, as noted above, dogs in intra-species interactions unsupervised by people show more, not less, agonistic interactions than even closely-equivalently reared wolves. Dogs' social hierarchies are steeper than those of wolves. It is only in interaction with humans that dogs appear more tractable. A successful theory of the uniqueness of dogs' social behavior will need to account not just for dogs' relatively low levels of aggression toward people, but also their higher levels of aggression among themselves. The hypothesis that dogs may have an evolved capacity to recognize humans and adopt different patterns of social behavior toward them by virtue simply of their species identity is surely *ad hoc* and improbable given that mammals are not born recognizing even their own species identity (Hess, 1973; Lorenz, 1937) and thus are highly unlikely to have an inborn capacity to recognize another species.

3.2 "Relaxed selection" theory

Several authors have proposed that dogs, by coming under human control, have been exposed to relaxed natural selection and consequently their tolerant and acquiescent behavior toward people should be viewed as a consequence of human artificial selection (Boitani & Ciucci, 1995; Fox, 1978; Haase, 2000; Malm, 1995; Martins, 1949). This thesis is not viable because most dogs are still subject to natural, not artificial, selection and this could only have been more the case in the past than it is today. On a global scale, estimates of the proportion of dogs that are under direct human control are less than 30% of the total population of around 800 million dogs (Rowan, 2020). Free-ranging dogs may be 80% of world's dog population: (Boitani & Ciucci, 1995; Hughes & Macdonald, 2013; Lord et al., 2013). (Aside from the intrinsic uncertainty in estimates of this kind, it is also the case that just because a dog is free-ranging does not necessarily mean that it is not at least in part under human control). Even in the United States, where the vast majority of dogs live as pets in human homes, only around half of all matings are under human control (New et al., 2004). On the assumption that this value for the United States is modal for pet dogs around the world, then only around 15% (50% of 30%) of dog matings are arranged by humans. Although there is likely some human intervention in the form of postzygotic selection (i.e., culling of undesired offspring before they reach reproductive viability, Coppinger & Coppinger, 2001), nonetheless it is clear that the vast majority of today's dog population (and surely larger portions of dogs historically) are subject to natural rather than artificial selection. The direct, intentional, human impact on dog evolution remains relatively modest and was probably quite minor as recently as two centuries ago. Intense human selection for dogs is a modern phenomenon: most dog breeds are a product of the last 200 years (Parker et al., 2017; Pemberton & Worboys, 2015; Ritvo, 1987, 2010; Russell, 2018; Worboys, 2018; Worboys, Strange, & Pemberton, 2018). The proportion of dogs registered as purebred in the US with the American Kennel Club has been declining in recent decades. The total number of dogs registered reached a minimum of 477,354 in 2014 though it has increased to 587,691 in 2019 (Burgess, 2020). This represents less than 1% of all dogs in the United States.

3.3 Canine cooperation hypothesis

Range and Virányi (2015) argued that dogs' willingness to cooperate with humans is a consequence of wolves' natural capacity for cooperation. This corrects earlier theorizing that dogs are more socially tolerant and attentive than wolves but does not explain how and why people and dogs readily live in close cooperative inter-species groups and yet people and wolves do not.

3.4 Social ecology hypothesis

Marshall-Pescini et al. (2017) proposed that the differences in social behavior between dogs and wolves need to be understood in the context of adaptation to changed foraging ecology. As dogs experienced reduced need to cooperate in foraging when they shifted from hunting live prey to scavenging on human refuse this led to a change from pair-bonding with alloparental care to a more promiscuous mating system and mostly maternal care of young. Although this hypothesis contextualizes dog reproductive behavior within the subspecies' foraging ecology, like the related Canine Cooperation Hypothesis, it does not offer a behavioral mechanism for how dogs are more sociable with humans than with their own species.

3.5 A novel hypothesis: Super-dominance

Any successful theory of dog's success in a human-dominated world must handle three well-established facts.

3.5.1 Anthropocentric selection

Dogs evolved in a human context. They have adapted to a human world. As Marshall-Pescini et al. (2017) have argued, many changes in dogs' social behavior are functionally fit to the ecology in which dogs live—namely a scavenging rather than primarily hunting niche.

3.5.2 Hypersociability toward other species

Dogs are more easily socially imprinted onto humans and other species than are their wild ancestors, and, once imprinted, they retain higher levels of social interest in humans and other species throughout their lives than do wolves or (likely) other species (vonHoldt et al., 2017).

3.5.3 Conspecific competition

In their interactions with conspecifics dogs are more aggressive than wolves; they show higher rates of agonistic interactions and their formal dominance behaviors evince a steeper dominance hierarchy than among similarly-raised and kept groups of wolves.

The second and third points might be viewed as in contradiction: How can it be that dogs show more competition in conspecific groups and more cooperative interactions with human beings?

One solution would be to posit that dogs recognize the species identity of different beings and this recognition then activates different patterns of social behavior depending on the species: "Compete with other dogs; cooperate with humans." Such an account is surely *ad hoc* and improbable. It is improbable because mammals are not born recognizing their own species—never mind others (Hess, 1973). It is *ad hoc* because it provides no principled way of explaining the proximate behavioral mechanism by which a dog reacts in the way it does to different social actors and does not enable prediction of how dogs will react to species other than humans and dogs. Take, for example, a livestock guarding dog raised to guard and interact socially with sheep or goats: How does that dog know whether to compete for dominance with the livestock—as it would with a conspecific; or whether to cooperate with the sheep—as it would with a human?

A possible resolution of this apparent paradox is that enhanced sensitivity to dominance relations may not be a contradiction of dogs' seeking of sociable interaction with humans but its cause. The behavior that people perceive as "friendly" may be what is termed in behavioral biology "formal submission."

van der Borg et al. (2015) identified high posture and muzzle bite as formal dominance indicators, and tail wag along with low posture, passing under the head, and mouth lick as formal submission markers in a group of interacting dogs. Interestingly, as Schilder et al. (2014) note, these status-marking behaviors observed in dogs are similar to behaviors serving the same function in human relationships. Raised posture, as, for example, standing or sitting on an elevated seat or platform (Eibl-Eibesfeldt, 1997; Mignault & Chaudhuri, 2003); sitting straight up (Schwartz, Tesser, & Powell, 1982), and raised head (Carney, Hall, & LeBeau, 2005; Mignault & Chaudhuri, 2003; Zivin, 1977) are well-established formal dominance markers in humans, whereas lowered head and other forms of lower posture are related to submission (Kalma, 1991; Mignault & Chaudhuri, 2003; Rosa & Mazur, 1979). Submissive people also kneel and bow to and kiss those whose dominance they are respecting (Mignault & Chaudhuri, 2003).

When dogs seek proximity, "kiss," and solicit and react positively to being stroked they are in fact showing formal signs of submission. When people pass their hands over dogs' heads and backs, accept licks (especially on or near the mouth), and adopt postures in which they make themselves taller than their dogs, they are (unknowingly, of course) expressing formal dominance over their dogs. These formal dominance and submission behaviors shared between humans and dogs, combined with humans' control over resources including food, movement, shelter, and sexual access (which is total for pets and present albeit to a lesser degree for free-living dogs), establish dogs in a state of total social subordination which may well account for their widely-noted tractability and willingness to follow human leadership. Indeed, I propose—by analogy to the concept of a supernormal stimulus in ethology (Tinbergen, 1969)—to call the relationship of human to dog, "Super-dominance."

Dominance could provide a mechanism by which dogs behave differently toward social companions from diverse species without needing to assume that dogs recognize individuals' species membership and consequently apply different social rules. The pattern of social behavior that dogs adopt toward members of different species could depend on the extent to which individuals from that species show behaviors toward the dog that it perceives as expressing dominance, combined with the other species' ability to control dogs' access to resources. The behavior of the Super-dominant humans toward the dogs as they interact with the third species would also be expected to play a key role in dogs' attitudes toward that other species.

It should be noted that this bears no relation to the bowdlerized ideas of "dominance" promulgated by some popular dog trainers of the moment, such as Millan and Peltier (2007) and Monks of New Skete (2002). These authors' advocacy of coercion and aversive methods in dog training is irrelevant to discussions of dominance in human-dog social groups. The "positive" trainer who controls her dog's behavior with contingent treats is conveying her social dominance by controlling resources every bit as much as the enthusiast for "alpha rolls" and electronic-shock collars. Likewise, advice to assert dominance over one's dog by ensuring one is first to eat or walk through a doorway entirely misses the point of how social dominance is established and maintained. The human is dominant over the dog because she can open the door and controls the dog's access to food. Who eats or walks first is neither here nor there.

Although these seem to be distinct concepts, it is possible that heightened sensitivity to dominance relationships may account, at least in part, for dogs' "hypersociability" (vonHoldt et al., 2017) and their presumed extended period for social imprinting. In many species, subordinates seek the proximity of more dominant individuals, particular when reconciling after conflict (e.g., Aureli, Preston, & de Waal, 1999): perhaps the frequently noted human-proximity-seeking of dogs is related to their recognition that people are intrinsically dominant and control important resources. It is possible that the observed relations in the SSP and related tests of dog "attachment" to people may be (at least in part) submissive relations rather than attachment bonds. This might then also explain the extreme rapidity of apparent attachment revealed in the SSP and other tests (Feuerbacher & Wynne, 2017; Gácsi et al., 2001).

In itself Super-dominance theory does not explain extended social imprinting but it is interesting to note that studies of social imprinting in the dog have only ever concerned imprinting on humans. Perhaps the dogs' apparently extended critical period for social imprinting is an artifact of testing their reactions to humans, who, by virtue of the super-dominant posture, may offer a supernormal stimulus for imprinting (Gaioni, Hoffman, DePaulo, & Stratton, 1978).

4. Open questions

4.1 Publication trends

In the past two decades there has been an astonishing explosion of scientific interest in the behavior of dogs. Although there was a rich history of dog behavioral research throughout the 20th century (see Feuerbacher & Wynne, 2011, for an historical review), the most recent phase of dog behavioral research started in the late 1990s and has grown with particular rapidity since around 2005 (Aria, Alterisio, Scandurra, Pinelli, & D'Aniello, 2020).

Notwithstanding this exponential grown in peer-reviewed publications in recent years, there is a tendency for research to congregate in certain areas and omit other important domains. A lot of research is directed toward exceptional "human-like" capacities and ignores more basic questions. A number of issues important to understanding dogs' success in a human-dominated world have hardly been addressed.

4.2 Imprinting and formation of social bonds

Although it is widely believed that an individual dog's ability to form relationships with people rests on its being socially imprinted on humans during a critical phase in early life, this assertion rests on results from a single experiment carried out over 60 years ago (Freedman et al., 1961; also reported in Scott & Fuller, 1974). This experiment, understandably given its age, suffered a number of limitations. First, it did not include a group of pups exposed to people between nine and 14 weeks of age; second, it studied only one level of human exposure (albeit reportedly slightly differently in two publications describing the same experiment) and, finally and most critically, as noted above, it was vague about the possibilities of socializing the group only exposed to humans at 14 weeks. There do not appear to be any published studies exploring other parameters in dogs' social imprinting on humans, nor on dogs imprinting on any other species, not even conspecifics. Furthermore, there are no formal studies investigating social imprinting in wolves—thus rendering comparisons of dogs to their wild ancestors informal and speculative.

Informal observations of dogs introduced to homes that already contain other species of pets such as cats, hint at the possibility that dogs may be able to form emotional bonds with individuals from species they did not interact with during the critical period for social imprinting. The possibility of a life-long openness to forming social connections has never been investigated. If it exists it might undermine the identification of "taming" with social imprinting and would have important implications for rehabilitation (or perhaps better, "habilitation") of dogs that have had difficult experiences and are being brought into a human home for the first time past 14 weeks of age. Given the centrality of socialization to dogs co-existence with humans it seems quite astonishing that the scientific knowledge base regarding this aspect of dogs' behavior is so inadequately secured.

4.3 What makes people want to care for dogs?

It is taken for granted in developed nations that people want to care for their pet dogs, and indeed vast sums of money are expended doing so (APPA, 2020). More surprisingly, people in less wealthy parts of the world also show detectable concern for dog welfare even when these animals may bring no tangible benefit and even appreciable harm. Thus Bhattacharjee, Sarkar, et al. (2020) surveyed attitudes to street dogs in India and found on balance slightly positive stances toward the dogs. In Port au Prince, Haiti, Fielding, Gall, Green, and Eller (2012) reported that over 40% of respondents fed street dogs and Fielding and Mather (2001) found that in the Bahamas, although street dogs were considered a nuisance, local people were generally tolerant toward them and more than half reported feeding dogs they did not own.

This positive attitude and willingness to expend resources on dogs would seem to lead naturally to the question: What is it about dogs that prompts people to want to care for them? However, only limited research has been carried out on this question. Chersini, Hall, and Wynne (2018) showed people images of dog puppy faces and found that they peaked in attractiveness around weaning age (approximately 8 weeks). Hecht and Horowitz (2015) showed people photographs of dog faces that had been manipulated in photo-editing software to exaggerate fit to Lorenz's (1943) Kindchenschema predictions, as well levels of humanization. Participants preferred images in line with some Kindchenschema predictions—such as larger eyes—and also preferred some human characters, such as colored irises. Neither of these studies investigated behavioral properties of dogs that may appeal to people, and only explored a small subset of the dimensions of potential physical attractiveness of dogs.

In a study that captures a small portion of the behaviors people find attractive in dogs under one set of circumstances, Protopopova and Wynne (2014) investigated aspects of the spontaneous behavior of dogs in an animal shelter that influenced potential adopters' decisions to take the dog home with them. Although the dogs were at liberty to express a large number of different behaviors, only two behaviors influenced adopters' decisions to take a dog home: Ignoring a person's play invitation (which had a more-than-100-fold negative impact) and resting in proximity to the person (which had a more-than-14-fold positive impact).

The literature needs more studies on different dog and human populations exploring what dogs do that attracts people to care for them. This could include exposing people to diverse dogs and asking them to rate the animals on multiple dimensions of attraction or finding other naturalistic ways to investigate human choices of dogs to live with—such as possibly at points of sale and adoption. It would also be valuable to investigate dog preferences among humans. Many pet dog owners express the opinion that their dog prefers men or women, but I am not aware of systematic studies of dog preferences among people.

4.4 What do people and dogs do together?

There is a surprising lack of research on how dogs and people spontaneously interact. A series of studies investigated the spontaneous reactions of a child and his or her pet dog, noted the importance of smell and touch to the dog, and that the child more often initiated contact than did the dog, but these studies have not led to an ongoing program of research (Filiâtre, Millot, & Eckerlin, 1990; Filiâtre, Millot, & Montagner, 1986; Millot, 1994; Millot, Filiâtre, Gagnon, Eckerlin, & Montagner, 1988).

At present, we do not know how much time dogs in different circumstances (pets, street dogs, etc.) spend in different levels of proximity to people, nor do we know what form the interaction of dogs and people takes under these different circumstances. Studies have not been reported indicating how this interaction varies with the age, sex, and other dimensions of the dog or the person in interaction. These data have therefore not been set in juxtaposition with people's perception of their dog's affection for them, the dog's attachment behaviors as measured in the SSP or similar procedure, and the person's reported emotional affiliation with the dog.

Lay people and the gray literature on dog behavior commonly report that dogs express their affection for people with tail wags and "happy" faces (e.g., McConnell, 2007) and yet there is an almost complete lack of scientific research into the behaviors of dogs that indicate affiliation toward people.

If dog behavior toward people is predicated on dominance relationships, as I propose here, then dogs should react differently toward people who express different levels of dominance toward them. The importance of raised posture for dominance implies that people of reduced stature should attract less submission from dogs than do taller people. It is well established that children are much more likely to be bitten by dogs than are adults (Chapman, Cornwall, Righetti, & Sung, 2000; Gershman & Sacks, 1994; Gilchrist et al., 2008), but of course the behavior of children toward dogs differs in many ways besides their stature. It would be interesting to know whether adult humans of reduced stature (such as people with dwarfism) also experience less submissive behavior from dogs and it would also be interesting to see experimental manipulation of dominance behaviors from people to dogs to test whether this alters the dog's behavior in predictable ways.

4.5 Can we identify social hierarchy in dog-human groups?

Very few studies have investigated dominance in dog groups and to my knowledge no study has been carried out looking for formal dominance behaviors in the interaction of dogs and people. Studies are needed that look for the formal dominance and submission behaviors that have been identified in groups of dogs and of people separately in interacting mixed-species groups of people and dogs. I predict that dogs will seek out people who are dominant over them and express a range of behaviors that are formal signals of submission. Furthermore, I predict that the humans in these relationships with dogs will interpret the dogs' formal submissive signals as signs of affection.

4.6 What are the intra-species social connections of dogs like?

In a literature with so many lines of evidence supporting the affiliation of dogs toward people, it is surely anomalous that there is so little sign of "attachment" between cohabiting dogs (Mariti et al., 2014; Tuber et al., 1996). This could be explored further with pet dogs using different forms of social stressor. There also appear to be no studies on the reaction of free-living dogs to separation from their social companions. Study of the social relationships among free-living dogs may help shed light on dog-human social relationships.

4.7 Social genetics

Ultimately, if there is something intrinsic to dogs that distinguishes them from wolves and from other species this should be identifiable in their genomes. The theories reviewed above which posit inherited differences in cognition have failed to lead to any identified genetic differences. Several studies have found differences in genes related to social behavior in dogs (Persson et al., 2016; Persson, Sundman, Halldén, Trottier, & Jensen, 2018; Persson, Trottier, Bélteky, Roth, & Jensen, 2017; vonHoldt et al., 2017, 2018). Presently the extent of the relevance of these genetic differences to the whole world of dogs is unknown, as the analyses have only been carried out on pet dogs. Hopefully, geneticists will be interested to pursue this question into free-living dogs as well, perhaps, in addition to archeological specimens. This would help identify the importance of social adaptations to the human-dominated niche.

5. Conclusions

Dogs are not a human creation in a direct sense. They came into being thousands of years before people had any idea that they could change the form or function of living beings by controlling their reproduction. Nonetheless, dogs evolved in close proximity to humans and their present form shows many signs of being adapted to succeeding in a human-dominated world.

The precise nature of these adaptations is a matter of current controversy. I have here considered and dismissed the proposal that dogs show special cognitive adaptations to their human-dominated niche. That is that they possess theory-of-mind-like capacities that are unique to their species. Although pet dogs are surely exquisitely sensitive to human actions and intentions, the patterns of success and failure both in dogs and in other species are more consistent with the proposal that it is living in close proximity to, and often in utter dependence on, humans that leads animals to be highly sensitive to human actions—independent of the species from which an individual is descended.

On the other hand, there are many areas of dog behavior that would not usually be labeled "cognitive"—behaviors involved in reproduction, foraging and sociality—where dogs differ greatly from even their closest relatives, wolves, and other wild canids. Dogs show much more fluid social structures, much less parental care, less-coordinated foraging, and steeper social hierarchies accompanied by more agonistic social behaviors than do wolves and other canid species. The social behavior of dogs with conspecifics stands in seldom-noted contradistinction to their behavior when living with humans. People in the first world typically refer to their dogs as "family members," and even in the developing world positive emotions are often reported toward street dogs. Given dogs' social behavior in same-species groups their behavior toward humans demands more explanatory attention.

Nearly 150 years ago, a deep thinker and dog lover, in what may be called the first work of comparative psychology, explored the possibility that religious feeling could have evolved. Darwin (1871, p. 470) wrote:

> *The feeling of religious devotion is a highly complex one, consisting of love, complete submission to an exalted and mysterious superior, a strong sense of dependence, fear, reverence, gratitude, hope for the future, and perhaps other elements. No being could experience so complex an emotion until advanced in his intellectual and moral faculties to at least a moderately high level. Nevertheless, we see some distant approach to this state of mind in the deep love of a dog for his master, associated with complete submission, some fear, and perhaps other feelings. The behavior of a dog when returning to his master after an absence, …, is widely different from that toward their fellows. In the latter case the transports of joy appear to be somewhat less, and the sense of equality is shown in every action. Prof. Braubach goes so far as to maintain that a dog looks on his master as on a god.*[2]

Darwin's perspective may today be recognized as a precursor to the view that dogs their human companions as highly dominant over them. I have coined the term "Super-dominant" to capture how humans' utter control

---

[2] The original reads: "Des Hundes Herr ist ihm sein Freund und sein Gott, den er nicht nur schützt und bewacht, den er nicht nur fürchtet, sondern dem er auch mit treuer Liebe anhängt." "The dog's master is his friend and his God, who he not only protects and guards, who he not only fears, but who he also follows with faithful love." (Braubach, 1869, p. 53).

over dogs' lives, combined with inadvertent use of behaviors that may be perceived by dogs as formal dominance signals, may influence dogs' behavior toward people. This notion in no way corresponds to the naïve use of the term "dominant" by certain popular dog trainers of the day but rather connects to the technical use of the term "dominant" in the classical ethological literature. Whatever the virtues of this neologism, a refocus of research on dogs and humans toward behavior in social interaction would be a valuable step with both practical and theoretical implications.

Acknowledgements

I am very grateful to Monique Udell, Debottam Bhattacharjee, Louise Barrett and two anonymous reviewers for their most helpful comments on an earlier draft. Responsibility for the text rests with the author. I also thank Maddies' Fund for research support.

References

Agnetta, B., Hare, B., & Tomasello, M. (2000). Cues to food location that domestic dogs (Canis familiaris) of different ages do and do not use. *Animal Cognition*, *3*(2), 107–112.

Ainsworth, M. D. S. (1989). Attachments beyond infancy. *American Psychologist*, *44*(4), 709–716.

Ainsworth, M. D. S., & Bell, S. M. (1970). Attachment, exploration, and separation: Illustrated by the behavior of one-year-olds in a strange situation. *Child Development*, *41*(1), 49–67.

Ainsworth, M. D. S., Blehar, M. C., Waters, E., & Wall, S. (1978). *Patterns of attachment. A psychological study of the strange situation*. Lawrence Erlbaum Associates, Inc.

Akins, C. K., & Zentall, T. R. (1999). Imitation in Japanese quail: The role of reinforcement of demonstrator responding. *Psychonomic Bulletin & Review*, *5*, 694–697.

Ákos, Z., Beck, R., Nagy, M., Vicsek, T., & Kubinyi, E. (2014). Leadership and path characteristics during walks are linked to dominance order and individual traits in dogs. *PLoS Computational Biology*, *10*(1). https://doi.org/10.1371/journal.pcbi.1003446, e1003446.

American Veterinary Society of Animal Behavior. (2008). *AVSAB position statement on the use of dominance theory in behavior modification of animals*. American Veterinary Society of Animal Behavior. https://avsab.org/wp-content/uploads/2018/03/Dominance_Position_Statement_download-10-3-14.pdf.

APPA. (2020). *Industry statistics and trends*. American Pet Products Association. https://www.americanpetproducts.org/.

Archer, J. (1997). Why do people love their pets? *Evolution and Human Behavior*, *18*(4), 237–259.

Aria, M., Alterisio, A., Scandurra, A., Pinelli, C., & D'Aniello, B. (2020). The scholar's best friend: Research trends in dog cognitive and behavioral studies. *Animal Cognition*. https://doi.org/10.1007/s10071-020-01448-2.

Atickem, A., Bekele, A., & Williams, S. D. (2010). Competition between domestic dogs and Ethiopian wolf (Canis simensis) in the Bale Mountains National Park, Ethiopia. *African Journal of Ecology*, *48*(2), 401–407.

Audet, J.-N., Ducatez, S., & Lefebvre, L. (2016). The town bird and the country bird: Problem solving and immunocompetence vary with urbanization. *Behavioral Ecology*, *27*(2), 637–644.

Aureli, F., Preston, S. D., & de Waal, F. B. M. (1999). Heart rate responses to social interactions in free-moving rhesus macaques (Macaca mulatta): A pilot study. *Journal of Comparative Psychology*, *113*(1), 59–65.

Balasubramaniam, K., Dittmar, K., Berman, C., Butovskaya, M., Cooper, M., Majolo, B., et al. (2012). Hierarchical steepness, counter-aggression, and macaque social style scale. *American Journal of Primatology*, *74*, 915–925.

Barker, S. B., & Barker, R. T. (1988). The human-canine bond: Closer than family ties? *Journal of Mental Health Counseling*, *10*(1), 46–56.

Bauer, E. B., & Smuts, B. B. (2007). Cooperation and competition during dyadic play in domestic dogs, Canis familiaris. *Animal Behaviour*, *73*(3), 489–499.

Beck, A. (1973). *The ecology of stray dogs: A study of free-ranging urban animals* (p. 116). Purdue University Press. E-Books.

Bentosela, M., Wynne, C. D. L., D'Orazio, M., Elgier, A., & Udell, M. A. R. (2016). Sociability and gazing toward humans in dogs and wolves: Simple behaviors with broad implications. *Journal of the Experimental Analysis of Behavior*, *105*(1), 68–75.

Bergström, A., Frantz, L., Schmidt, R., Ersmark, E., Lebrasseur, O., Girdland-Flink, L., et al. (2020). Origins and genetic legacy of prehistoric dogs. *Science*, *370*(6516), 557.

Berman, M., & Dunbar, I. (1983). The social behaviour of free-ranging suburban dogs. *Applied Animal Ethology*, *10*(1), 5–17.

Bhadra, A. (2014). Preference for meat is not innate in dogs. *Journal of Ethology*, *32*(1), 15–22.

Bhattacharjee, D., Gupta, S., Sau, S., Sarkar, R., Biswas, A., Banerjee, A., et al. (2017). Free-ranging dogs show age related plasticity in their ability to follow human pointing. *PLoS One*, *12*(7), e0180643.

Bhattacharjee, D., Mandal, S., Shit, P., Varghese, M. G., Vishnoi, A., & Bhadra, A. (2020). Free-ranging dogs are capable of utilising complex human pointing cues. *Frontiers in Psychology*, *10*. https://doi.org/10.3389/fpsyg.2019.02818, 2818.

Bhattacharjee, D., Sarkar, R., Sau, S., & Bhadra, A. (2020). Sociability of Indian free-ranging dogs (Canis lupus familiaris) varies with human movement in urban areas. *Journal of Comparative Psychology*.

Bhattacharjee, D., Sau, S., & Bhadra, A. (2020). 'Bolder' together—Response to human social cues in groups of free-ranging dogs. *Behaviour*, *157*(3–4), 363–384.

Bodson, L. (2000). Motivations for pet-keeping in ancient Greece and Rome: A preliminary survey. In A. L. Podberscek, E. Paul, & J. A. Serpell (Eds.), *Companion animals and us: Exploring the relationships between people and pets* (pp. 42–60). Cambridge University Press.

Boitani, L., & Ciucci, P. (1995). Comparative social ecology of feral dogs and wolves. *Ethology Ecology and Evolution*, 7(1), 49–72.

Boitani, L., Francisci, F., Ciucci, P., & Andreoli, G. (1995). Population biology and ecology of feral dogs in central Italy. In J. A. Serpell (Ed.), *The domestic dog: Its evolution, behaviour, and interactions with people* Cambridge University Press.

Boitani, L., Ciucci, P., & Ortolani, A. (2007). Behaviour and social ecology of free-ranging dogs. In P. Jensen (Ed.), *The behavioural biology of dogs* (pp. 147–165). CAB International.

Bonanni, R., & Cafazzo, S. (2014). The Social organisation of a population of free-ranging dogs in a suburban area of Rome: A reassessment of the effects of domestication on dogs' behaviour. In J. Kaminski, & S. Marshall-Pescini (Eds.), *The social dog* (pp. 65–104). Academic Press.

Bonanni, R., Cafazzo, S., Valsecchi, P., & Natoli, E. (2010). Effect of affiliative and agonistic relationships on leadership behaviour in free-ranging dogs. *Animal Behaviour*, *79*(5), 981–991.

Bonanni, R., Cafazzo, S., Abis, A., Barillari, E., Valsecchi, P., & Natoli, E. (2017). Age-graded dominance hierarchies and social tolerance in packs of free-ranging dogs. *Behavioral Ecology*, *28*(4), 1004–1020.

Borge, K. S., Tønnessen, R., Nødtvedt, A., & Indrebø, A. (2011). Litter size at birth in purebred dogs—A retrospective study of 224 breeds. *Theriogenology*, *75*(5), 911–919.

Bowlby, J. (1958). The nature of the child's tie to his mother. *The International Journal of Psycho-Analysis*, *39*(5), 350–373.

Bradshaw, J. W. S., Blackwell, E. J., & Casey, R. A. (2009). Dominance in domestic dogs—Useful construct or bad habit? *Journal of Veterinary Behavior*, *4*(3), 135–144.

Braubach, W. (1869). *Religion, Moral & Philosophie der Darwin'sche Artlehre nach ihrer Natur und ihrem Character als kleine Parallele menschliche geistiger Entwicklung, etc*. Neuwied and Leipzig: J. H. Heuser'sche Buchhandlung.

Bräuer, J., Kaminski, J., Riedel, J., Call, J., & Tomasello, M. (2006). Making inferences about the location of hidden food: Social dog, causal ape. *Journal of Comparative Psychology*, *120*(1), 38–46.

Bräuer, J., Bös, M., Call, J., & Tomasello, M. (2013). Domestic dogs (Canis familiaris) coordinate their actions in a problem-solving task. *Animal Cognition*, *16*(2), 273–285.

Bräuer, J., Stenglein, K., & Amici, F. (2020). Dogs (Canis familiaris) and wolves (Canis lupus) coordinate with conspecifics in a social dilemma. *Journal of Comparative Psychology*, *134*(2), 211–221.

Brubaker, L., & Udell, M. A. R. (2018). The effects of past training, experience, and human behaviour on a dog's persistence at an independent task. *Applied Animal Behaviour Science*, *204*, 101–107.

Brubaker, L., Dasgupta, S., Bhattacharjee, D., Bhadra, A., & Udell, M. A. R. (2017). Differences in problem-solving between canid populations: Do domestication and lifetime experience affect persistence? *Animal Cognition*, *20*(4), 717–723.

Bugnyar, T., & Huber, L. (1997). Push or pull: An experimental study on imitation in marmosets. *Animal Behaviour*, *54*(4), 817–831.

Burgess, S. (2020 March 7). *All breeds AKC registration stats final 2019*. English Springer Spaniel Field Trial Association. https://essfta.org/wp-content/uploads/2020/03/All-Breeds-AKC-Registration-Stats-Final-2019.pdf.

Butler, J. R. A., & du Toit, J. T. (2002). Diet of free-ranging domestic dogs (Canis familiaris) in rural Zimbabwe: Implications for wild scavengers on the periphery of wildlife reserves. *Animal Conservation*, *5*(1), 29–37.

Butler, J. R. A., Du Toit, J. T., & Bingham, J. (2004). Free-ranging domestic dogs (Canis familiaris) as predators and prey in rural Zimbabwe: Threats of competition and disease to large wild carnivores. *Biological Conservation*, *115*(3), 369–378.

Cafazzo, S., Valsecchi, P., Bonanni, R., & Natoli, E. (2010). Dominance in relation to age, sex, and competitive contexts in a group of free-ranging domestic dogs. *Behavioral Ecology*, *21*(3), 443–455.

Cafazzo, S., Maragliano, L., Bonanni, R., Scholl, F., Guarducci, M., Scarcella, R., et al. (2014). Behavioural and physiological indicators of shelter dogs' welfare: Reflections on the no-kill policy on free-ranging dogs in Italy revisited on the basis of 15 years of implementation. *Physiology & Behavior*, *133*, 223–229.

Call, J., Carpenter, M., & Tomasello, M. (2005). Copying results and copying actions in the process of social learning: Chimpanzees (Pan troglodytes) and human children (Homo sapiens). *Animal Cognition*, *8*(3), 151–163.

Carney, D. R., Hall, J. A., & LeBeau, L. S. (2005). Beliefs about the nonverbal expression of social power. *Journal of Nonverbal Behavior*, *29*(2), 105–123.

Catala, A., Mang, B., Wallis, L., & Huber, L. (2017). Dogs demonstrate perspective taking based on geometrical gaze following in a Guesser–Knower task. *Animal Cognition*, *20*(4), 581–589.

Chapman, S., Cornwall, J., Righetti, J., & Sung, L. (2000). Preventing dog bites in children: Randomised controlled trial of an educational intervention. *British Medical Journal*, *320*(7248), 1512–1513.

Chawla, S. K., & Reece, J. F. (2002). *Timing of oestrus and reproductive behaviour in Indian street dogs*. British Medical Journal Publishing Group.

Chersini, N., Hall, N. J., & Wynne, C. D. L. (2018). Dog Pups' attractiveness to humans peaks at weaning age. *Anthrozoös*, *31*(3), 309–318.

Clark, H., Elsherif, M. M., & Leavens, D. A. (2019). Ontogeny vs. phylogeny in primate/canid comparisons: A meta-analysis of the object choice task. *Neuroscience & Biobehavioral Reviews*, *105*, 178–189.

Cooper, J. J., Ashton, C., Bishop, S., West, R., Mills, D. S., & Young, R. J. (2003). Clever hounds: Social cognition in the domestic dog (Canis familiaris). *Applied Animal Behaviour Science*, *81*(3), 229–244.

Coppinger, R., & Coppinger, L. (2001). *Dogs: A new understanding of canine origin, behavior and evolution*. University of Chicago Press.

Coppinger, R., & Coppinger, L. (2016). *What is a dog?*. Chicago, IL: University of Chicago Press.

Coppinger, L., & Coppinger, R. (2014). Dogs for herding and guarding livestock. In T. Grandin (Ed.), *Livestock handling and transport* (4th ed., pp. 245–260). CABI.

Custance, D. M., Whiten, A., & Bard, K. A. (1995). Can young chimpanzees (Pan troglodytes) imitate arbitrary actions? Hayes & Hayes (1952) revisited. *Journal of the Experimental Analysis of Behavior*, *132*, 837–859.

Dale, R., Quervel-Chaumette, M., Huber, L., Range, F., & Marshall-Pescini, S. (2016). Task differences and prosociality; investigating pet dogs' prosocial preferences in a token choice paradigm. *PLoS One*, *11*(12), e0167750.

Daniels, T. J. (1983). The social organization of free-ranging urban dogs. II. Estrous groups and the mating system. *Applied Animal Ethology*, *10*(4), 365–373.

Daniels, T. J., & Bekoff, M. (1989a). Population and social biology of free-ranging dogs, canis familiaris. *Journal of Mammalogy*, *70*(4), 754–762.

Daniels, T., & Bekoff, M. (1989b). Feralization: The making of wild domestic animals. *Behavioural Processes*, *19*(1–3), 79–94.

Darwin, C. (1871). *The descent of man, and selection in relation to sex*. John Murray.

de Planhol, X. (1969). Le chien de berger; développement et signification géographique d'une technique pastorale. *Bulletin de l'Association de géographes français*, *370*, 355–368. 46e année.

Dorey, N. R., Conover, A. M., & Udell, M. A. R. (2014). Interspecific communication from people to horses (Equus ferus caballus) is influenced by different horsemanship training styles. *Journal of Comparative Psychology*, *128*(4), 337–342.

Dorrance, B. R., & Zentall, T. R. (2001). Imitative learning in Japanese Quail (Coturnix japonica) depends on the motivational state of the observer quail at the time of observation. *Journal of Comparative Psychology*, *115*, 62–67.

D'Aniello, B., & Scandurra, A. (2016). Ontogenetic effects on gazing behaviour: A case study of kennel dogs (Labrador Retrievers) in the impossible task paradigm. *Animal Cognition*, *19*(3), 565–570.

D'Aniello, B., Alterisio, A., Scandurra, A., Petremolo, E., Iommelli, M. R., & Aria, M. (2017). What's the point? Golden and Labrador retrievers living in kennels do not understand human pointing gestures. *Animal Cognition*, *20*(4), 777–787.

Dugatkin, L. A. (2020). *Principles of animal behavior* (4th ed.). University of Chicago Press.

Dwyer, C., & Cole, M. R. (2018). Domesticated dogs (Canis familiaris) tend to follow repeated deceptive human cues even when food is visible. *Learning & Behavior*, *46*(4), 442–448.

Eibl-Eibesfeldt, I. (1997). Human ethology. In A. Schmitt, K. Atzwanger, K. Grammer, & K. Schäfer (Eds.), *New aspects of human ethology* (pp. 1–23). Springer US.

Engle, E. T. (1946). No seasonal breeding cycle in dogs. *Journal of Mammalogy*, *27*(1), 79–81.

Epstein, R. (1984). Spontaneous and deferred imitation in the pigeon. *Behavioural Processes*, *9*(4), 347–354.

Feddersen-Petersen, D. (1991). The ontogeny of social play and agonistic behaviour in selected canid species. *Bonner Zoologische Beitäge*, *42*, 97–114.

Feddersen-Petersen, D. (2004). *Hundepsychologie: Sozialverhalten und Wesen, Emotionen und Individualität* (4th ed.). Kosmos Verlag.

Feddersen-Petersen, D. (2007). Social behaviour of dogs and related canids. In P. Jensen (Ed.), *The behavioural biology of dogs* (pp. 105–119). CAB International.

Ferrari, P. F., Visalberghi, E., Paukner, A., Fogassi, L., Ruggiero, A., & Suomi, S. J. (2006). Neonatal imitation in rhesus macaques. *PLoS Biology*, *4*(9), 1501.

Feuerbacher, E. N., & Wynne, C. D. L. (2011). A history of dogs as subjects in North American experimental psychological research. *Comparative Cognition and Behavior Reviews*, *6*, 46–71.

Feuerbacher, E. N., & Wynne, C. D. L. (2017). Dogs don't always prefer their owners and can quickly form strong preferences for certain strangers over others. *Journal of the Experimental Analysis of Behavior*, *108*(3), 305–317.

Fielding, W. J., & Mather, J. (2001). Dog ownership in the West Indies: A case study from the Bahamas. *Anthrozoös*, *14*(2), 72–80.

Fielding, W. J., Gall, M., Green, D., & Eller, W. S. (2012). Care of dogs and attitudes of dog owners in port-au-prince, the Republic of Haiti. *Journal of Applied Animal Welfare Science*, *15*(3), 236–253.

Filiâtre, J. C., Millot, J. L., & Montagner, H. (1986). New data on communication behaviour between the young child and his pet dog. *Behavioural Processes*, *12*(1), 33–44.

Filiâtre, J. C., Millot, J. L., & Eckerlin, A. (1990). Relations intraspecifiques et interspecifiques chez le chien familier: Aspects analogiques et differentiels des comportements d'exploration. *Behavioural Processes*, *22*, 133–150.

Flack, J, & De Waal, F. (2004). Dominance style, social power, and conflict management in macaque societies: A conceptual framework. In B Thierry, B Chapais, W Kaumanns, & M Singh (Eds.), *Macaque societies: A model for the study of social organization* (pp. 157–181). Cambridge University Press.

Flack, J. C., & De Waal, F. B. M. (2010). Dominance styles, social power, and conflict management: A conceptual framework. In *Macaque societies: A model for the study of social organization* (pp. 157–185). Cambridge University Press.

Font, E. (1987). Spacing and social organization: Urban stray dogs revisited. *Applied Animal Behaviour Science*, *17*(3), 319–328.

Fox, M. W. (1964). Behaviour and socialization of the wild timber-wolf. *Journal of Small Animal Practice*, *5*(3), 249–253.

Fox, M. (1978). *The dog*. Dogwise Publishing.

Frank, H. (1980). Evolution of canine information processing under conditions of natural and artificial selection. *Zeitschrift für Tierpsychologie*, *53*(4), 389–399.

Frank, H., & Frank, M. G. (1982). On the effects of domestication on canine social development and behavior. *Applied Animal Ethology*, *8*(6), 507–525.

Frank, H., & Frank, M. (1987). The University of Michigan canine information-processing project (1979-1981). In *Man and wolf: advances, issues, and problems in captive wolf research* (pp. 143–167). Dr. W. Junk Publishers.

Frank, H., Frank, M. G., Hasselbach, L. M., & Littleton, D. M. (1989). Motivation and insight in wolf (Canis lupus) and Alaskan malamute (Canis familiaris): Visual discrimination learning. *Bulletin of the Psychonomic Society*, *27*(5), 455–458.

Frantz, L, Mullin, V, Pionnier-Capitan, M, Lebrasseur, O, Ollivier, M, & Perri, A, et al. (2016). Genomic and archaeological evidence suggest a dual origin of domestic dogs. *Science*, *352*(6290), 1228–1231. https://doi.org/10.1126/science.aaf3161.

Fredericson, E. (1952). Perceptual homeostasis and distress vocalization in puppies. *Journal of Personality*, *20*(4), 472–477.

Freedman, D. G., King, J. A., & Elliot, O. (1961). Critical period in the social development of dogs. *Science*, *133*(3457), 1016–1017.

Fugazza, C., Pogány, Á., & Miklósi, Á. (2016). Recall of others' actions after incidental encoding reveals episodic-like memory in dogs. *Current Biology*, *26*(23), 3209–3213.

Fugazza, C., & Miklósi, Á. (2014). Should old dog trainers learn new tricks? The efficiency of the Do as I do method and shaping/clicker training method to train dogs. *Applied Animal Behaviour Science*, *153*, 53–61.

Fugazza, C., Petro, E., Miklósi, Á., & Pogány, Á. (2019). Social learning of goal-directed actions in dogs (Canis familiaris): Imitation or emulation? *Journal of Comparative Psychology*, *133*(2), 244–251.

Gácsi, M., Topál, J., Miklósi, A., Dóka, A., & Csányi, V. (2001). Attachment behavior of adult dogs (Canis familiaris) living at rescue centers: Forming new bonds. *Journal of Comparative Psychology*, *115*(4), 423–431.

Gácsi, M., Miklósi, Á., Varga, O., Topál, J., & Csányi, V. (2004). Are readers of our face readers of our minds? Dogs (Canis familiaris) show situation-dependent recognition of human's attention. *Animal Cognition*, *7*(3), 144–153.

Gácsi, M., Györi, B., Miklósi, A., Virányi, Z., Kubinyi, E., Topál, J., et al. (2005). Species-specific differences and similarities in the behavior of hand-raised dog and wolf pups in social situations with humans. *Developmental Psychobiology*, *47*(2), 111–122.

Gácsi, M., Györi, B., Virányi, Z., Kubinyi, E., Range, F., Belényi, B., et al. (2009). Explaining dog wolf differences in utilizing human pointing gestures: Selection for synergistic shifts in the development of some social skills. *PLoS One*, *4*(8), e6584.

Gácsi, M., Maros, K., Sernkvist, S., Faragó, T., & Miklósi, Á. (2013). Human analogue safe haven effect of the owner: Behavioural and heart rate response to stressful social stimuli in dogs. *PLoS One*, *8*(3), e58475.

Gaioni, S. J., Hoffman, H. S., DePaulo, P., & Stratton, V. N. (1978). Imprinting in older ducklings: Some tests of a reinforcement model. *Animal Learning & Behavior*, *6*(1), 19–26.

Germonpré, M., Sablin, M. V., Stevens, R. E., Hedges, R. E. M., Hofreiter, M., Stiller, M., et al. (2009). Fossil dogs and wolves from Palaeolithic sites in Belgium, the Ukraine and Russia: Osteometry, ancient DNA and stable isotopes. *Journal of Archaeological Science*, *36*(2), 473–490.

Germonpré, M., Lázničková-Galetová, M., & Sablin, M. V. (2011). Palaeolithic dog skulls at the Gravettian Předmostí site, the Czech Republic. *Journal of Archaeological Science*, *39*, 184–202.

Gershman, K. A., & Sacks, J. J. (1994). Which dogs bite? A case-control study of risk factors. *Pediatrics*, *93*(6), 913.

Ghosh, B., Choudhuri, D. K., & Pal, B. (1984). Some aspects of the sexual behaviour of stray dogs, canis familiaris. *Applied Animal Behaviour Science*, *13*(1), 113–127.

Gilchrist, J., Sacks, J. J., White, D., & Kresnow, M.-J. (2008). Dog bites: Still a problem? *Injury Prevention*, *14*(5), 296–301.

Gipson, P. S. (1983). Evaluation and control implications of behavior of feral dogs in interior Alaska. In D. Kaukeinen (Ed.), *Vertebrate pest control and management materials: Fourth symposium* (pp. 285–294). ASTM International.

Gipson, P. S., Gipson, I. K., & Sealander, J. A. (1975). Reproductive biology of wild Canis (Canidae) in Arkansas. *Journal of Mammalogy*, *56*(3), 605–642.

Haase, E. (2000). Comparison of reproductive biological parameters in male wolves and domestic dogs. *Zeitschrift Für Säugetierkunde*, *65*(5), 257–270.

Hall, N. J., Udell, M. A. R., Dorey, N. R., Walsh, A. L., & Wynne, C. D. L. (2011). Megachiropteran bats (Pteropus) utilize human referential stimuli to locate hidden food. *Journal of Comparative Psychology*, *125*(3), 341–346.

Hall, N. J., Lord, K., Arnold, A.-M. K., Wynne, C. D. L., & Udell, M. A. R. (2015). Assessment of attachment behaviour to human caregivers in wolf pups (Canis lupus lupus). *Behavioural Processes*, *110*, 15–21.

Hare, B. (2017). Survival of the friendliest: Homo sapiens evolved via selection for prosociality. *Annual Review of Psychology*, *68*(1), 155–186.

Hare, B., & Tomasello, M. (2005). Human-like social skills in dogs? *Trends in Cognitive Sciences*, *9*(9), 439–444.

Hare, B., Brown, M., Williamson, C., & Tomasello, M. (2002). The domestication of social cognition in dogs. *Science*, *298*, 1634–1636.

Hare, B., Rosati, A., Kaminski, J., Bräuer, J., Call, J., & Tomasello, M. (2010). The domestication hypothesis for dogs' skills with human communication: A response to and. *Animal Behaviour*, *79*(2), e1–e6.

Hare, B., Wobber, V., & Wrangham, R. (2012). The self-domestication hypothesis: Evolution of bonobo psychology is due to selection against aggression. *Animal Behaviour*, *83*(3), 573–585.

Hayes, C. (1951). *The ape in our house* (1st ed.). Harper.

Hayes, K. J., & Hayes, C. (1952). Imitation in a home-raised chimpanzee. *Journal of Comparative and Physiological Psychology*, *45*(5), 450.

Heberlein, M. T., Manser, M. B., & Turner, D. C. (2017). Deceptive-like behaviour in dogs (Canis familiaris). *Animal Cognition*, *20*(3), 511–520.

Hecht, J., & Horowitz, A. (2015). Seeing dogs: Human preferences for dog physical attributes. *Anthrozoos: A Multidisciplinary Journal of The Interactions of People & Animals*, *28*(1), 153–163.

Hess, E. H. (1959). Imprinting. *Science*, *130*(3368), 133–141.

Hess, E. H. (1973). *Imprinting; early experience and the developmental psychobiology of attachment*. Van Nostrand Reinhold Co.

Heyes, C. M. (1994). Social learning in animals: Categories and mechanisms. *Biological Reviews*, *69*, 207–231.

Heyes, C. M. (1998). Theory of mind in nonhuman primates. *Behavioral and Brain Sciences*, *21*, 101–134.

Heyes, C. M., & Dawson, G. R. (1990). A demonstration of observational learning in rats using a bidirectional control. *Quarterly Journal of Experimental Psychology. B, Comparative and Physiological Psychology*, *42*, 59–71.

Heyes, C. M., Jaldow, E., & Dawson, G. R. (1994). Imitation in rats: Conditions of cocurrence in a bidirectional control procedure. *Learning and Motivation*, *25*, 276–287.

Heyes, C. M., Jaldow, E., Nokes, T., & Dawson, G. R. (1994). Imitation in rats (Rattus norvegicus): The role of demonstrator action. *Behavioural Processes*, *32*, 173–182.

Hollinshead, F. K., Ontiveros, M., Burns, J. G., Magee, C., & Hanlon, D. W. (2020). Factors influencing parentage ratio in canine dual-sired litters. *Theriogenology*, *158*, 24–30.

Horn, L., Huber, L., & Range, F. (2013). The importance of the secure base effect for domestic dogs—Evidence from a manipulative problem-solving task. *PLoS One*, *8*(5), e65296.

Huber, L., Range, F., Voelkl, B., Szucsich, A., Virányi, Z., & Miklósi, A. (2009). The evolution of imitation: What do the capacities of non-human animals tell us about the mechanisms of imitation? *Philosophical Transactions of the Royal Society of London B: Biological Sciences*, *364*(1528), 2299–2309.

Huber, L., Range, F., & Virányi, Z. (2012). Dogs imitate selectively, not necessarily rationally: Reply to Kaminski et al. (2011). *Animal Behaviour*, *83*(6), e1–e3.

Hughes, J., & Macdonald, D. W. (2013). A review of the interactions between free-roaming domestic dogs and wildlife. *Biological Conservation*, *157*, 341–351.

Itakura, S., Das, L., & Farshid, A. (2017). Gaze processing in nonhuman primates. In R. Flom, K. Lee, & D. Muir (Eds.), *Gaze-following: Its development and significance* (pp. 297–312). Lawrence Erlbaum Associates Publishers.

Jaakkola, K., Guarino, E., & Rodriguez, M. (2010). Blindfolded imitation in a bottlenose dolphin (Tursiops truncatus). *International Journal of Comparative Psychology*, *23*(4), 671–688.

Jakovcevic, A., Mustaca, A., & Bentosela, M. (2012). Do more sociable dogs gaze longer to the human face than less sociable ones? *Behavioural Processes*, *90*(2), 217–222.

Jarvis, T., & Hall, N. J. (2020). Development of point following behaviors in shelter dogs. *Learning & Behavior*, *48*(3), 335–343.

Johnston, A. M., Huang, Y., & Santos, L. R. (2018). Dogs do not demonstrate a human-like bias to defer to communicative cues. *Learning & Behavior*, *46*(4), 449–461.

Jones, A. C., & Gosling, S. D. (2005). Temperament and personality in dogs (Canis familiaris): A review and evaluation of past research. *Applied Animal Behaviour Science*, *95*(1), 1–53.

Kaiser, D. H., Zentall, T. R., & Galef, B. G., Jr. (1997). Can imitation in pigeons be explained by local enhancement together with trial-and-error learning? *Psychological Science*, *8*, 459–460.

Kalma, A. (1991). Hierarchisation and dominance assessment at first glance. *European Journal of Social Psychology*, *21*(2), 165–181.

Kaminski, J., & Nitzschner, M. (2013). Do dogs get the point? A review of dog–human communication ability. *Learning and Motivation*, *44*(4), 294–302.

Kaminski, J., Riedel, J., Call, J., & Tomasello, M. (2005). Domestic goats, Capra hircus, follow gaze direction and use social cues in an object choice task. *Animal Behaviour*, *69*(1), 11–18.

Kaminski, J., Tomasello, M., Call, J., & Bräuer, J. (2009). Domestic dogs are sensitive to a human's perspective. *Behaviour*, *146*(7), 979–998.

Kaminski, J., Nitzschner, M., Wobber, V., Tennie, C., Bräuer, J., Call, J., et al. (2011). Do dogs distinguish rational from irrational acts? *Animal Behaviour*, *81*(1), 195–203.

Kaminski, J., Pitsch, A., & Tomasello, M. (2013). Dogs steal in the dark. *Animal Cognition*, *16*(3), 385–394.

Karlsson, J., Eriksson, M., & Liberg, O. (2007). At what distance do wolves move away from an approaching human? *Canadian Journal of Zoology*, *85*(11), 1193–1197.

Kellogg, W. N., & Kellogg, L. A. (1933). *The ape and the child*. Hafner Publishing Company.

Kirchhofer, K. C., Zimmermann, F., Kaminski, J., & Tomasello, M. (2012). Dogs (Canis familiaris), but not chimpanzees (Pan troglodytes), understand imperative pointing. *PLoS One*, 7(2), e30913.

Kleiman, D. G., & Eisenberg, J. F. (1973). Comparisons of canid and felid social systems from an evolutionary perspective. *Animal Behaviour*, *21*(4), 637–659.

Kleiman, D. G., & Malcolm, J. R. (1981). The evolution of male parental investment in mammals. In D. J. Gubernick, & P. H. Kopfer (Eds.), *Parental care in mammals* (pp. 347–387). Springer.

Klinghammer, E., & Goodmann, P. A. (1987). Socialization and management of wolves in captivity. In H. Frank (Ed.), *Man and wolf: Advances, issues and problems in captive wolf research* (pp. 31–60). W. Junk.

Konno, A., Romero, T., Inoue-Murayama, M., Saito, A., & Hasegawa, T. (2016). Dog breed differences in visual communication with humans. *PLoS One*, *11*(10), e0164760.

Krause, M. A., Udell, M. A., Leavens, D. A., & Skopos, L. (2018). Animal pointing: Changing trends and findings from 30 years of research. *Journal of Comparative Psychology*, *132*(3), 326.

Kubinyi, E., Topal, J., Miklósi, A., & Csanyi, V. (2003). Dogs (Canis familiaris) learn from their owners via observation in a manipulation task. *Journal of Comparative Psychology*, *117*, 156–165.

Kundey, S. M. A., De Los Reyes, A., Taglang, C., Allen, R., Molina, S., Royer, E., et al. (2010). Domesticated dogs (Canis familiaris) react to what others can and cannot hear. *Applied Animal Behaviour Science*, *126*(1–2), 45–50.

Lakatos, G., Soproni, K., Dóka, A., & Miklósi, A. (2009). A comparative approach to dogs'(Canis familiaris) and human infants' comprehension of various forms of pointing gestures. *Animal Cognition*, *12*(4), 621–631.

Langbein, J., & Puppe, B. (2004). Analysing dominance relationships by sociometric methods—A plea for a more standardised and precise approach in farm animals. *Applied Animal Behaviour Science*, *87*(3), 293–315.

Larson, G., Karlsson, E. K., Perri, A., Webster, M. T., Ho, S. Y. W., Peters, J., et al. (2012). Rethinking dog domestication by integrating genetics, archeology, and biogeography. *Proceedings of the National Academy of Sciences of the United States of America*, *109*(23), 8878–8883.

Lazarowski, L., & Dorman, D. C. (2015). A comparison of pet and purpose-bred research dog (Canis familiaris) performance on human-guided object-choice tasks. *Behavioural Processes*, *110*, 60–67.

Lazzaroni, M., Range, F., Bernasconi, L., Darc, L., Holtsch, M., Massimei, R., et al. (2019). The role of life experience in affecting persistence: A comparative study between free-ranging dogs, pet dogs and captive pack dogs. *PLoS One*, *14*(4), e0214806.

Lazzaroni, M., Marshall-Pescini, S., Manzenreiter, H., Gosch, S., Přibilová, L., Darc, L., et al. (2020). Why do dogs look back at the human in an impossible task? Looking back behaviour may be over-interpreted. *Animal Cognition*, *23*(3), 427–441.

Lea, S. E. G., & Osthaus, B. (2018). In what sense are dogs special? Canine cognition in comparative context. *Learning & Behavior*, *46*(4), 335–363.

Lenkei, R., Újváry, D., Bakos, V., & Faragó, T. (2020). Adult, intensively socialized wolves show features of attachment behaviour to their handler. *Scientific Reports*, *10*(1), 17296.

Lord, K. (2013). A comparison of the sensory development of wolves (Canis lupus lupus) and dogs (Canis lupus familiaris). *Ethology*, *119*(2), 110–120.

Lord, K., Feinstein, M., Smith, B., & Coppinger, R. (2013). Variation in reproductive traits of members of the genus Canis with special attention to the domestic dog (Canis familiaris). *Behavioural Processes*, *92*, 131–142.

Lorenz, K. (1937). The companion in the bird's world. *Auk*, *54*(3), 245–273.

Lorenz, K. (1943). Die angeborenen Formen möglicher Erfahrung. *Zeitschrift für Tierpsychologie*, *5*(2), 235–409.

Lorenz, K. (1954). *Man meets dog* (M. K. Wilson, Trans.) (1st ed.). London: Methuen.

Lundberg, P., Hartmann, E., & Roth, L. S. V. (2020). Does training style affect the human-horse relationship? Asking the horse in a separation–reunion experiment with the owner and a stranger. *Applied Animal Behaviour Science*, *233*, 105144.

Macdonald, D, & Moehlman, P. (1982). Cooperation, Altruism, and Restraint in the Reproduction of Carnivores. In P Bateson, & P Klopfer (Eds.), *Ontogeny* (pp. 433–467). Springer.

Macdonald, D. W., & Carr, G. M. (1995). Variation in dog society: Between resource dispersion and social flux. In J. A. Serpell (Ed.), *The domestic dog: Its its evolution, behavior and interactions with people* (1st ed., pp. 199–216). Cambridge University Press.

Macdonald, D. W., & Carr, G. M. (2016). Variation in dog society: Between resource dispersion and social flux. In *The domestic dog: Its evolution, behavior and interactions with people* (2nd ed., pp. 319–341). Cambridge University Press.

Maginnity, M. E., & Grace, R. C. (2014). Visual perspective taking by dogs (Canis familiaris) in a guesser–Knower task: Evidence for a canine theory of mind? *Animal Cognition*, *17*(6), 1375–1392.

Malassis, R., & Delfour, F. (2015). Sea lions' (Zalophus californianus) use of human pointing gestures as referential cues. *Learning & Behavior*, *43*(2), 101–112.

Malavasi, R., & Huber, L. (2016). Evidence of heterospecific referential communication from domestic horses (Equus caballus) to humans. *Animal Cognition*, *19*(5), 899–909.

Malm, K. (1995). Regurgitation in relation to weaning in the domestic dog: A questionnaire study. *Applied Animal Behaviour Science*, *43*(2), 111–122.

Mariti, C, Carlone, B, Borgognini-Tarli, S, Presciuttini, S, Pierantoni, L, & Gazzano, A. (2011). Considering the dog as part of the system: Studying the attachment bond of dogs toward all members of the fostering family. *Journal of Veterinary Behavior*, *6*(1), 90–91.

Mariti, C., Carlone, B., Ricci, E., Sighieri, C., & Gazzano, A. (2014). Intraspecific attachment in adult domestic dogs (Canis familiaris): Preliminary results. *Applied Animal Behaviour Science*, *152*, 64–72.

Marshall-Pescini, S., Schwarz, J. F., Kostelnik, I., Virányi, Z., & Range, F. (2017). Importance of a species' socioecology: Wolves outperform dogs in a conspecific cooperation task. *Proceedings of the National Academy of Sciences of the United States of America*, *114*, 11793–11798. 201709027.

Marshall-Pescini, S., Valsecchi, P., Petak, I., Accorsi, P. A., & Previde, E. P. (2009). Does training make you smarter? The effects of training on dogs' performance (Canis familiaris) in a problem solving task. *Behavioural Processes*, *81*(3), 17–22.

Marshall-Pescini, S., Colombo, E., Passalacqua, C., Merola, I., & Prato-Previde, E. (2013). Gaze alternation in dogs and toddlers in an unsolvable task: Evidence of an audience effect. *Animal Cognition*, *16*(6), 933–943.

Martins, T. (1949). Disgorging of food to the puppies by the lactating dog. *Physiological Zoology*, *22*(2), 169–172.

McConnell, P. (2007). *For the love of a dog: Understanding emotion in you and your best friend*. Ballantine Books.

McGreevy, P. D., Starling, M., Branson, N. J., Cobb, M. L., & Calnon, D. (2012). An overview of the dog–human dyad and ethograms within it. *Journal of Veterinary Behavior*, 7(2), 103–117.

Mech, L. (1970). *The Wolf: The Ecology and Behavior of an Endangered Species*. American Museum of Natural History.

Mech, L. D. (1981). *The wolf: The ecology and behavior of an endangered species*. University of Minnesota Press.

Mech, L. D. (2002). Breeding season of Wolves, Canis lupus, in relation to latitude. *Canadian Field-Naturalist*, *116*(1), 139–140.

Mech, L. D., & Boitani, L. (2003). Wolf social ecology. In L. D. Mech, & L. Boitani (Eds.), *Wolves: Behavior, ecology, and conservation* (pp. 1–34). University of Chicago Press.

Mersmann, D., Tomasello, M., Call, J., Kaminski, J., & Taborsky, M. (2011). Simple mechanisms can explain social learning in domestic dogs (Canis familiaris). *Ethology*, *117*(8), 675–690.

Met, A., Miklósi, Á., & Lakatos, G. (2014). Gaze-following behind barriers in domestic dogs. *Animal Cognition*, *17*(6), 1401–1405.

Mignault, A., & Chaudhuri, A. (2003). The many faces of a neutral face: Head tilt and perception of dominance and emotion. *Journal of Nonverbal Behavior*, *27*(2), 111–132.

Miklósi, A. (2015). *Dog behaviour, evolution, and cognition*. Oxford University Press.

Miklósi, Á., & Topál, J. (2013). What does it take to become 'best friends'? Evolutionary changes in canine social competence. *Trends in Cognitive Sciences*, *17*(6), 287–294.

Miklósi, A., Polgárdi, R., Topál, J., & Csányi, V. (2000). Intentional behaviour in dog-human communication: An experimental analysis of "showing" behaviour in the dog. *Animal Cognition*, *3*(3), 159–166.

Miklósi, A., Kubinyi, E., Topál, J., Gacsi, M., Viranyi, Z., & Csányi, V. (2003). A simple reason for a big difference: Wolves do not look back at humans, but dogs do. *Current Biology*, *13*, 763–766.

Millan, C., & Peltier, M. J. (2007). *Cesar's way: The natural, everyday guide to understanding & correcting common dog problems*. Three Rivers Press.

Miller, G. A. (1962). *Psychology, the science of mental life*. Harper & Row.

Miller, H. C., Rayburn-Reeves, R., & Zentall, T. R. (2009). Imitation and emulation by dogs using a bidirectional control procedure. *Behavioural Processes*, *80*(2), 109–114.

Millot, J. L. (1994). Olfactory and visual cues in the interaction systems between dogs and children. *Behavioural Processes*, *33*(1), 177–188.

Millot, J. L., Filiâtre, J. C., Gagnon, A. C., Eckerlin, A., & Montagner, H. (1988). Children and their pet dogs: How they communicate. *Behavioural Processes*, *17*(1), 1–15.

Mitchell, C. J., Heyes, C. M., Gardner, M. R., & Dawson, G. R. (1999). Limitations of a bidirectional control procedure for the investigation of imitation in rats: Odour cues on the manipulandum. *Quarterly Journal of Experimental Psychology. B, Comparative and Physiological Psychology*, *52*, 193–202.

Mitchell, N., Strohbach, M. W., Pratt, R., Finn, W. C., & Strauss, E. G. (2015). Space use by resident and transient coyotes in an urban–rural landscape mosaic. *Wildlife Research*, *42*(6), 461–469.

Mongillo, P., Pitteri, E., Carnier, P., Gabai, G., Adamelli, S., & Marinelli, L. (2013). Does the attachment system towards owners change in aged dogs? *Physiology & Behavior*, *120*, 64–69.

Monks of New Skete. (2002). *How to be your dog's best friend: The classic training manual for dog owners* (revised, updated edition). Little, Brown and Company.

Moore, B. R. (1992). Avian movement imitation and a new form of mimicry: Tracing the evolution of a complex form of learning. *Behaviour*, *122*(3–4), 231–263.

Morey, D. F. (2014). In search of Paleolithic dogs: A quest with mixed results. *Journal of Archaeological Science*, *52*, 300–307.

Morissette, P., Ricard, M., & Décarie, T. G. (1995). Joint visual attention and pointing in infancy: A longitudinal study of comprehension. *British Journal of Developmental Psychology*, *13*(2), 163–175.

Mui, R., Haselgrove, M., Pearce, J., & Heyes, C. (2008). Automatic imitation in budgerigars. *Proceedings of the Royal Society B: Biological Sciences*, *275*(1651), 2547–2553.

Muro, C., Escobedo, R., Spector, L., & Coppinger, R. P. (2011). Wolf-pack (Canis lupus) hunting strategies emerge from simple rules in computational simulations. *Behavioural Processes*, *88*(3), 192–197.

Musil, A. (1928). *The manners and customs of the Rwala Bedouins*. American Geographical Society.

Myowa-Yamakoshi, M., & Matsuzawa, T. (1999). Factors influencing imitation of manipulatory actions in chimpanzees (Pan troglodytes). *Journal of Comparative Psychology*, *113*, 128–136.

Myowa-Yamakoshi, M., & Matsuzawa, T. (2000). Imitation of intentional manipulatory actions in chimpanzees (Pan troglodytes). *Journal of Comparative Psychology*, *114*, 381–391.

Nawroth, C., Ebersbach, M., & von Borell, E. (2014). Juvenile domestic pigs (Sus scrofa domestica) use human-given cues in an object choice task. *Animal Cognition*, *17*(3), 701–713.

New, J. C., Jr., Kelch, W. J., Hutchison, J. M., Salman, M. D., King, M., Scarlett, J. M., et al. (2004). Birth and death rate estimates of cats and dogs in U. S. Households and related factors. *Journal of Applied Animal Welfare Science*, 7(4), 229–241.

Nobis, G. (1981). Aus Bonn: Das älteste Haustier des Menschen. Unterkiefer eines Hundes aus dem Magdaleniengrab von Bonn-Oberkassel. *Das Rheinische Landesmuseum Bonn: Berichte Aus Der Arbeit Des Museums*, *4/81*, 49–50.

Oppenheimer, E. C., & Oppenheimer, J. R. (1975). Certain behavioral features in the pariah dog (Canis familiaris) in West Bengal. *Applied Animal Ethology*, *2*(1), 81–92.

Ortolani, A., Vernooij, H., & Coppinger, R. (2009). Ethiopian village dogs: Behavioural responses to a stranger's approach. *Applied Animal Behaviour Science*, *119*, 210–218.

Ostojić, L., & Clayton, N. S. (2014). Behavioural coordination of dogs in a cooperative problem-solving task with a conspecific and a human partner. *Animal Cognition*, *17*(2), 445–459.

Pack, A. A., & Herman, L. M. (2004). Bottlenosed dolphins (Tursiops truncatus) comprehend the referent of both static and dynamic human gazing and pointing in an object-choice task. *Journal of Comparative Psychology*, *118*(2), 160.

Packard, J. (2003). Wolf behavior: Reproductive, social and intelligent. In L. D. Mech, & L. Boitani (Eds.), *Wolves: Behavior, ecology and conservation* (pp. 35–65). University of Chicago Press.

Pal, S. K. (2001). Population ecology of free-ranging urban dogs in West Bengal, India. *Acta Theriologica*, *46*(1), 69–78.

Pal, S. K. (2003). Reproductive behaviour of free-ranging rural dogs in West Bengal, India. *Acta Theriologica*, *48*(2), 271–281.

Pal, S. K. (2005). Parental care in free-ranging dogs, Canis familiaris. *Applied Animal Behaviour Science*, *90*(1), 31–47.

Pal, S. K. (2008). Maturation and development of social behaviour during early ontogeny in free-ranging dog puppies in West Bengal, India. *Applied Animal Behaviour Science*, *111*(1–2), 95–107.

Pal, S. K., Ghosh, B., & Roy, S. (1998). Agonistic behaviour of free-ranging dogs (Canis familiaris) in relation to season, sex and age. *Applied Animal Behaviour Science*, *59*(4), 331–348.

Pal, S. K., Ghosh, B., & Roy, S. (1999). Inter- and intra-sexual behaviour of free-ranging dogs (Canis familiaris). *Applied Animal Behaviour Science*, *62*(2), 267–278.

Panova, E. M., & Agafonov, A. V. (2017). A beluga whale socialized with bottlenose dolphins imitates their whistles. *Animal Cognition*, *20*(6), 1153–1160.

Parker, H. G., Dreger, D. L., Rimbault, M., Davis, B. W., Mullen, A. B., Carpintero-Ramirez, G., et al. (2017). Genomic analyses reveal the influence of geographic origin, migration, and hybridization on modern dog breed development. *Cell Reports*, *19*(4), 697–708.

Passalacqua, C., Marshall-Pescini, S., Barnard, S., Lakatos, G., Valsecchi, P., & Prato Previde, E. (2011). Human-directed gazing behaviour in puppies and adult dogs, Canis lupus familiaris. *Animal Behaviour*, *82*(5), 1043–1050.

Paul, M., Sen Majumder, S., & Bhadra, A. (2014). Selfish mothers? An empirical test of parent-offspring conflict over extended parental care. *Behavioural Processes*, *103*, 17–22. https://doi.org/10.1016/j.beproc.2013.10.006.

Paul, M., Sen Majumder, S., Sau, S., Nandi, A. K., & Bhadra, A. (2016). High early life mortality in free-ranging dogs is largely influenced by humans. *Scientific Reports*, *6*(1), 19641.

Pearce, J. M. (2008). *Animal learning and cognition, 3rd Edition: An introduction* (3rd ed.). Psychology Press.

Pemberton, N., & Worboys, M. (2015). The invention of the basset hound: Breed, blood and the late Victorian dog fancy, 1865–1900. *European Review of History: Revue Européenne d'histoire*, *22*(5), 726–740.

Perri, A. (2013). *Global hunting adaptations to early holocene temperate forests: Intentional dog burials as evidence of hunting strategies*. PhD Thesis, Durham University https://www.researchgate.net/profile/Angela_Perri/publication/270508753_Global_Hunting_Adaptations_to_Early_Holocene_Temperate_Forests_Intentional_Dog_Burials_as_Evidence_of_Hunting_Strategies/links/54c4ec820cf2911c7a511570.pdf.

Perri, A. (2016). A wolf in dog's clothing: Initial dog domestication and Pleistocene wolf variation. *Journal of Archaeological Science*, *68*, 1–4.

Perri, A. R., Feuerborn, T. R., Frantz, L. A. F., Larson, G., Malhi, R. S., Meltzer, D. J., et al. (2021). Dog domestication and the dual dispersal of people and dogs into the Americas. *Proceedings of the National Academy of Sciences of the United States of America*, *118*(6), e2010083118. https://doi.org/10.1073/pnas.2010083118.

Persson, M. E., Wright, D., Roth, L. S., Batakis, P., & Jensen, P. (2016). Genomic regions associated with interspecies communication in dogs contain genes related to human social disorders. *Scientific Reports*, *6*, 33439.

Persson, M. E., Trottier, A. J., Bélteky, J., Roth, L. S. V., & Jensen, P. (2017). Intranasal oxytocin and a polymorphism in the oxytocin receptor gene are associated with human-directed social behavior in golden retriever dogs. *Hormones and Behavior*, *95*(Suppl. C), 85–93.

Persson, M. E., Sundman, A.-S., Halldén, L.-L., Trottier, A. J., & Jensen, P. (2018). Sociality genes are associated with human-directed social behaviour in golden and Labrador retriever dogs. *PeerJ*, *6*, e5889.

Peterson, R. O., Woolington, J. D., & Bailey, T. N. (1984). Wolves of the Kenai Peninsula, Alaska. *Wildlife Monographs*, *88*, 3–52.

Petter, M., Musolino, E., Roberts, W. A., & Cole, M. (2009). Can dogs (Canis familiaris) detect human deception? *Behavioural Processes*, *82*(2), 109–118.

Pettijohn, T. F., Wong, T. W., Ebert, P. D., & Scott, J. P. (1977). Alleviation of separation distress in 3 breeds of young dogs. *Developmental Psychobiology*, *10*(4), 373–381.

Pilot, M., Greco, C., Jędrzejewska, B., Randi, E., Jędrzejewski, W., Sidorovich, V. E., et al. (2014). Genome-wide signatures of population bottlenecks and diversifying selection in European wolves. *Heredity*, *112*(4), 428–442.

Pongrácz, P., Hegedüs, D., Sanjurjo, B., Kővári, A., & Miklosi, A. (2013). "We will work for you"—Social influence may suppress individual food preferences in a communicative situation in dogs. *Learning and Motivation*, *44*(4), 270–281.

Povinelli, D. J., & Eddy, T. J. (1996). What young chimpanzees know about seeing. *Monographs of the Society for Research in Child Development*, *61*, i–vi. 1-152.

Povinelli, D. J., & Vonk, J. (2003). Chimpanzee minds: Suspiciously human? *Trends in Cognitive Sciences*, 7(4), 157–160.

Povinelli, D. J., Nelson, K. E., & Boysen, S. T. (1990). Inferences about guessing and knowing by chimpanzees (Pan troglodytes). *Journal of Comparative Psychology*, *104*, 203–210.

Protopopova, A., & Wynne, C. D. L. (2014). Adopter-dog interactions at the shelter: Behavioral and contextual predictors of adoption. *Applied Animal Behaviour Science*, *157*, 109–116.

Range, F., & Virányi, Z. (2014). Wolves are better imitators of conspecifics than dogs. *PLoS One*, *9*(1), e86559.

Range, F., & Virányi, Z. (2015). Tracking the evolutionary origins of dog-human cooperation: The "Canine Cooperation Hypothesis". *Frontiers in Psychology*, *5*, 1582.

Range, F., Virányi, Z., & Huber, L. (2007). Selective imitation in domestic dogs. *Current Biology*, *17*(10), 868–872.

Range, F., Ritter, C., & Virányi, Z. (2015). Testing the myth: Tolerant dogs and aggressive wolves. *Proceedings of the Royal Society B: Biological Sciences*, *282*, 20150220.

Rausch, R. A. (1967). Some aspects of the population ecology of Wolves, Alaska. *American Zoologist*, 7(2), 253–265.

Rehn, T., McGowan, R. T. S., & Keeling, L. J. (2013). Evaluating the strange situation procedure (SSP) to assess the bond between dogs and humans. *PLoS One*, *8*(2), e56938.

Rehn, T., Lindholm, U., Keeling, L., & Forkman, B. (2014). I like my dog, does my dog like me? *Applied Animal Behaviour Science*, *150*, 65–73.

Rehn, T., Handlin, L., Uvnäs-Moberg, K., & Keeling, L. J. (2014). Dogs' endocrine and behavioural responses at reunion are affected by how the human initiates contact. *Physiology & Behavior*, *124*, 45–53.

Rendell, L., & Whitehead, H. (2001). Culture in whales and dolphins. *Behavioral and Brain Sciences*, *24*, 309–382.

Rheingold, H. L. (1963). *Maternal behavior in mammals*. Wiley.

Richards, D. G., Wolz, J. P., & Herman, L. M. (1984). Vocal mimicry of computer-generated sounds and vocal labeling of objects by a bottlenosed dolphin, Tursiops truncatus. *Journal of Comparative Psychology*, *98*(1), 10–28.

Riedel, J., Schumann, K., Kaminski, J., Call, J., & Tomasello, M. (2008). The early ontogeny of human-dog communication. *Animal Behaviour*, *75*(3), 1003–1014.

Ritvo, H. (1987). *The animal estate: The english and other creatures in Victorian England*. Harvard University Press.

Ritvo, H. (2010). *Noble cows and hybrid zebras: Essays on animals and history*. University of Virginia Press.

Rodriguez, K. E., Greer, J., Yatcilla, J. K., Beck, A. M., & O'Haire, M. E. (2020). The effects of assistance dogs on psychosocial health and wellbeing: A systematic literature review. *PLoS One*, *15*(12), e0243302.

Rosa, E., & Mazur, A. (1979). Incipient status in small groups. *Social Forces*, *58*(1), 18–37.

Rowan, A. (2020, May). *Global dog populations*. https://wellbeingintl.org/global-dog-populations-2/.

Rubin, H. D., & Beck, A. M. (1982). Ecological behavior of free-ranging urban pet dogs. *Applied Animal Ethology*, *8*(1), 161–168.

Russell, N. (2011). *Social zooarcheology: Human and animals in prehistory*. Cambridge University Press.

Russell, E. (2018). *Greyhound nation: A coevolutionary history of England, 1200–1900*. Cambridge University Press.

Russon, A. E., & Galdikas, B. M. (1993). Imitation in free-ranging rehabilitant orangutans (Pongo pygmaeus). *Journal of Comparative Psychology*, *107*, 147–161.

Schilder, M. B. H., Vinke, C. M., & van der Borg, J. A. M. (2014). Dominance in domestic dogs revisited: Useful habit and useful construct? *Journal of Veterinary Behavior: Clinical Applications and Research*, *9*(4), 184–191.

Schleidt, W., & Schalter, M. (2003). Co-evolution of humans and canids: An alternative view of dog domestication: Homo homini lupus? *Evolution and Cognition*, *9*(1), 57–72.

Schwartz, B., Tesser, A., & Powell, E. (1982). Dominance cues in nonverbal behavior. *Social Psychology Quarterly*, *45*(2), 114–120.

Scott, J. P., & Fuller, J. L. (1974). *Genetics and the social behaviour of the dog*. Chicago: University of Chicago Press.

Scott, J. P., & Marston, M. V. (1950). Critical periods affecting the development of normal and mal-adjustive social behavior of puppies. *The Journal of Genetic Psychology*, 77(1), 25.

Sen Majumder, S., Bhadra, A., Ghosh, A., Mitra, S., Bhattacharjee, D., Chatterjee, J., et al. (2014). To be or not to be social: Foraging associations of free-ranging dogs in an urban ecosystem. *Acta Ethologica*, *17*(1), 1–8.

Sen Majumder, S., Paul, M., Sau, S., & Bhadra, A. (2016). Denning habits of free-ranging dogs reveal preference for human proximity. *Scientific Reports*, *6*(1), 32014.

Serpell, J. (2004). Factors influencing human attitudes to animals and their welfare. *Animal Welfare*, *13*(1), 145–151.

Shapiro, A. D., Janik, V. M., & Slater, P. J. (2003). A gray seal's (Halichoerus grypus) responses to experimenter-given pointing and directional cues. *Journal of Comparative Psychology*, *117*(4), 355.

Shipman, P. (2017). *The invaders: How humans and their dogs drove neanderthals to extinction* (reprint edition). Belknap Press: An Imprint of Harvard University Press.

Silk, M. J., Cant, M. A., Cafazzo, S., Natoli, E., & McDonald, R. A. (2019). Elevated aggression is associated with uncertainty in a network of dog dominance interactions. *Proceedings of the Royal Society B: Biological Sciences*, *286*(1906), 20190536.

Siniscalchi, M., d'Ingeo, S., Fornelli, S., & Quaranta, A. (2017). Are dogs red–green colour blind? *Royal Society Open Science*, *4*(11), 170869.

Stoinski, T. S., & Whiten, A. (2003). Social learning by orangutans (Pongo abelii and Pongo pygmaeus) in a simulated food-processing task. *Journal of Comparative Psychology*, *117*(3), 272.

Stronen, A. V., Jedrzejewska, B., Pertoldi, C., Demontis, D., Randi, E., Niedzialkowska, M., et al. (2013). North-south differentiation and a region of high diversity in European wolves (Canis lupus). *PLoS One*, *8*(10), e76454.

Subiaul, F., Cantlon, J. F., Holloway, R. L., & Terrace, H. S. (2004). Cognitive imitation in rhesus macaques. *Science*, *305*(5682), 407.

Sumner, K. (2004-2016). Dog whisperer with Cesar Millan (TV Series 2004–2016). In *MPH entertainment productions* National Geographic Channel.

Svartberg, K, & Forkman, B. (2002). Personality traits in the domestic dog (Canis familiaris). *Applied Animal Behaviour Science*, *79*(2), 133–156. https://doi.org/10.1016/S0168-1591(02)00121-1.

Svartberg, K. (2005). A comparison of behaviour in test and in everyday life: Evidence of three consistent boldness-related personality traits in dogs. *Applied Animal Behaviour Science*, *91*(1–2), 103–128. https://doi.org/10.1016/j.applanim.2004.08.030.

Szetei, V., Miklósi, Á., Topál, J., & Csányi, V. (2003). When dogs seem to lose their nose: an investigation on the use of visual and olfactory cues in communicative context between dog and owner. *Applied Animal Behaviour Science*, *83*(2), 141–152.

Téglás, E., Gergely, A., Kupán, K., Miklósi, Á., & Topál, J. (2012). Dogs' gaze following is tuned to human communicative signals. *Current Biology*, *22*(3), 209–212.

Tennie, C., Glabsch, E., Tempelmann, S., Bräuer, J., Kaminski, J., & Call, J. (2009). Dogs, Canis familiaris, fail to copy intransitive actions in third-party contextual imitation tasks. *Animal Behaviour*, 77(6), 1491–1499.

Thielke, L. E., & Udell, M. A. R. (2019). Evaluating cognitive and behavioral outcomes in conjunction with the secure base effect for dogs in shelter and foster environments. *Animals*, *9*(11), 932.

Thielke, L. E., & Udell, M. A. R. (2020). Characterizing human–dog attachment relationships in foster and shelter environments as a potential mechanism for achieving mutual wellbeing and success. *Animals*, *10*(1), 67.

Tinbergen, N. (1969). *The study of instinct*. Oxford University Press.

Topál, J., Miklósi, Á., Csányi, V., & Dóka, A. (1998). Attachment behavior in dogs (Canis familiaris): A new application of Ainsworth's (1969) Strange Situation Test. *Journal of Comparative Psychology*, *112*(3), 219–229.

Topál, J., Gácsi, M., Miklósi, Á., Virányi, Z., Kubinyi, E., & Csányi, V. (2005). Attachment to humans: A comparative study on hand-reared wolves and differently socialized dog puppies. *Animal Behaviour*, *70*(6), 1367–1375.

Topál, J., Erdõhegyi, Á., Mányik, R., & Miklósi, Á. (2006). Mindreading in a dog: An adaptation of a primate'mental attribution'study. *International Journal of Psychology and Psychological Therapy*, *6*(3), 365–379.

Topál, J., Byrne, R., Miklósi, Á., & Csányi, V. (2006). Reproducing human actions and action sequences: "Do as I Do!" in a dog. *Animal Cognition*, *9*(4), 355–367.

Trisko, R. K., & Smuts, B. B. (2015). Dominance relationships in a group of domestic dogs (Canis lupus familiaris). *Behaviour*, *152*(5), 677–704.

Tuber, D. S., Sanders, S., Hennessy, M. B., & Miller, J. A. (1996). Behavioral and glucocorticoid responses of adult domestic dogs (Canis familiaris) to companionship and social separation. *Journal of Comparative Psychology*, *110*(1), 103–108.

Udell, M. A. R. (2015). When dogs look back: Inhibition of independent problem-solving behaviour in domestic dogs (Canis lupus familiaris) compared with wolves (Canis lupus). *Biology Letters*, *11*(9), 20150489.

Udell, M. A. R., Dorey, N. R., & Wynne, C. D. L. (2008). Wolves outperform dogs in following human social cues. *Animal Behaviour*, *76*, 1767–1773.

Udell, M. A. R., Dorey, N. R., & Wynne, C. D. L. (2010). The performance of stray dogs (Canis familiaris) living in a shelter on human-guided object-choice tasks. *Animal Behaviour*, *79*(3), 717–725.

Udell, M. A. R., Dorey, N. R., & Wynne, C. D. L. (2011). Can your dog read your mind? Understanding the causes of canine perspective taking. *Learning & Behavior*, *39*(4), 289–302.

Udell, M. A. R., Dorey, N. R., & Wynne, C. D. L. (2012). Inter-species social learning in dogs: The inextricable roles of phylogeny and ontogeny. In T. R. Zentall, & E. A. Wasserman (Eds.), *The Oxford handbook of comparative cognition* (2nd ed., pp. 819–831). Oxford University Press.

Udell, M., Hall, N. J., Morrison, J., Dorey, N. R., & Wynne, C. D. (2013). Point topography and within-session learning are important predictors of pet dogs' (Canis lupus familiaris) performance on human guided tasks. *Revista Argentina de Ciencias Del Comportamiento*, *5*(2), 3–20.

Udell, M, Brubaker, L, Thielke, L, Wanser, S, Rosenlicht, G, & Vitale, K. (2021). Dog-Human Attachment as an Aspect of Social Cognition: Evaluating the Secure Base Test. In J Anderson, & H Kuroshima (Eds.), *Comparative cognition: Commonalities and diversity* Springer. In press.

van Kerkhove, W. (2004). A fresh look at the wolf-pack theory of companion-animal dog social behavior. *Journal of Applied Animal Welfare Science*, 7(4), 279–285.

van der Borg, J. A. M., Schilder, M. B. H., Vinke, C. M., & de Vries, H. (2015). Dominance in domestic dogs: A quantitative analysis of its behavioural measures. *PLoS One*, *10*(8), e0133978.

Vanak, A. T., & Gompper, M. E. (2009). Dietary niche separation between sympatric free-ranging domestic dogs and Indian foxes in central India. *Journal of Mammalogy*, *90*(5), 1058–1065.

Vitale, K. R., & Udell, M. A. (2019). The quality of being sociable: The influence of human attentional state, population, and human familiarity on domestic cat sociability. *Behavioural Processes*, *158*, 11–17.

Voelkl, B., & Huber, L. (2000). True imitation in marmosets. *Animal Behaviour*, *60*(2), 195–202.

Voelkl, B., & Huber, L. (2007). Imitation as faithful copying of a novel technique in marmoset monkeys. *PLoS One*, *2*(7), e611.

Voith, V. L. (1985). Attachment of people to companion animals. *The Veterinary Clinics of North America. Small Animal Practice*, *15*(2), 289–295.

Voltaire. (1764/1824). *A philosophical dictionary: From the french*. J. and H. L. Hunt.

vonHoldt, B. M., Shuldiner, E., Koch, I. J., Kartzinel, R. Y., Hogan, A., Brubaker, L., et al. (2017). Structural variants in genes associated with human Williams-Beuren syndrome underlie stereotypical hypersociability in domestic dogs. *Science Advances*, *3*(7), e1700398.

VonHoldt, B. M., Ji, S. S., Aardema, M. L., Stahler, D. R., Udell, M. A. R., & Sinsheimer, J. S. (2018). Activity of genes with functions in human Williams-Beuren syndrome is impacted by mobile element insertions in the gray wolf genome. *Genome Biology and Evolution*, *10*(6), 1546–1553.

Wallis, L. J., Range, F., Müller, C. A., Serisier, S., Huber, L., & Virányi, Z. (2015). Training for eye contact modulates gaze following in dogs. *Animal Behaviour*, *106*, 27–35.

Wandeler, A. I., Matter, H. C., Kappeler, A., & Budde, A. (1993). The ecology of dogs and canine rabies: A selective review. *Revue Scientifique et Technique*, *12*(1), 51–71.

Wanser, S. H., Simpson, A. C., MacDonald, M., & Udell, M. A. R. (2020). Considering family dog attachment bonds: Do dog-parent attachments predict dog-child attachment outcomes in animal-assisted interventions? *Frontiers in Psychology*, *11*, 566910.

Wanser, S. H., & Udell, M. A. R. (2019). Does attachment security to a human handler influence the behavior of dogs who engage in animal assisted activities? *Applied Animal Behaviour Science*, *210*, 88–94.

Wayne, R. K. (2012). Evolutionary genomics of dog domestication. *Mammalian Genome*, *23*(1–2), 3–18.

Wayne, R. K., & Ostrander, E. A. (2007). Lessons learned from the dog genome. *Trends in Genetics*, *23*(11), 557–567.

Whiten, A., & Custance, D. (1996). Studies of imitation in chimpanzees and children. In C. M. Heyes, & B. G. Galef Jr., (Eds.), *Social learning in animals: The roots of culture* (pp. 291–318). Academic Press.

Woolpy, J. H., & Ginsburg, B. E. (1967). Wolf socialization: A study of temperament in a wild social species. *American Zoologist*, 7(2), 357–363.

Worboys, M. (2018). Inventing dog breeds: Jack russell terriers. *Humanimalia*, *10*(1), 44–73.

Worboys, M., Strange, J.-M., & Pemberton, N. (2018). *The invention of the modern dog: Breed and blood in Victorian Britain* (1 ed.). Johns Hopkins University Press.

World Health Organization. (2013). *WHO Expert Consultation on Rabies: Second Report*. World Health Organization.

Wynne, C. D. L. (2019). *Dog is love: Why and how your dog loves you*. Houghton Mifflin Harcourt.

Wynne, C. D. L., & Udell, M. A. R. (2020). *Animal cognition: Evolution, behavior and cognition* (third, revised edition). Red Globe Press.

Xitco, M. J., Gory, J. D., & Kuczaj, S. A. (2001). Spontaneous pointing by bottlenose dolphins (Tursiops truncatus). *Animal Cognition*, *4*(2), 115–123.

Yin, S. (2007). Dominance versus leadership in dog training. *Compendium: Continuing Education for Veterinarians*, *414–417*, 432.

Zentall, T. R. (2006). Imitation: Definitions, evidence, and mechanisms. *Animal Cognition*, *9*(4), 335–353.

Zentall, T. R. (2013). Observational learning in animals. In K. Clark (Ed.), *Social learning theory: Phylogenetic considerations across animal, plant, and microbial Taxa* (pp. 1–34). Nova Science Publishers.

Zimen, E. (1987). Ontogeny of approach and flight behavior towards humans in wolves, poodles and wolf-poodle hybrids. In H. Frank (Ed.), *Man and wolf: Advances, issues, and problems in captive wolf research* (pp. 275–292). Springer Science & Business Media.

Zivin, G. (1977). Facial gestures predict preschoolers' encounter outcomes. *Social Science Information*, *16*(6), 715–729.