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Chapter 10

A Dog's-Eye View of Canine Cognition

Monique A. R. Udell, Kathryn Lord, Erica N. Feuerbacher
and Clive D. L. Wynne

Abstract In this chapter we attempt to put the dog back at the heart of dog cognition studies. We identify that the majority of dogs are not first-world pets, dependent on their owners for the fulfillment of all essential needs, and acting as their “best friends.” Rather most dogs are scavengers on the periphery of people’s lives. These dogs are more likely to avoid human contact than seek it. The sensitivity of pet dogs to human actions and intentions that has been a major focus of recent research is unlikely to be a special adaptation or case of co-evolution, but rather is the expression of basic processes of conditioning as well as social and biological traits that domesticated and wild canids share. In individuals that have been socialized to humans and rendered completely dependent on them these processes lead to high levels of sensitivity to human actions. The fundamental differences between dog and wolf behavior lie at more basic levels: in the processes of socialization, in foraging, and in reproduction. Small but crucial intertwined changes led to an animal that is (1) more promiscuous than any other canid, (2) can reproduce more rapidly, and (3) is a much less effective hunter but (4) more efficient scavenger than other canids. The indirect consequences of these changes include the fact that we have dogs and not wolves resting at our feet. Though it may be a little less flattering to the human species, we believe this perspective on dogs is at least as fascinating and closer to the historical truth than the story that humans created dogs.

M. A. R. Udell

Department of Animal Sciences, Oregon State University, Corvallis, OR 97331, USA

K. Lord

Department of Biology, Gettysburg College, Gettysburg, PA 17325, USA

E. N. Feuerbacher

Department of Psychology, University of Florida, Gainesville, FL 32611, USA

C. D. L. Wynne (✉)

Department of Psychology, Arizona State University, Tempe, AZ 85287, USA

e-mail: clivewynne@gmail.com

10.1 Introduction

Dogs are ubiquitous in human societies. In the United States, nearly half all households include a dog (APPMA 2008). However, most of the world's dogs live in the developing world. Here pet dogs are uncommon, but feral, village, or community dogs are plentiful around humans (Coppinger and Coppinger 2001). It has been estimated that there are upwards of a billion dogs on the planet, with pet dogs in developed countries representing only 17–24 % of the total (Lord et al. 2013).

The nature of the relationships that dogs have with people is a source of fascination to many who share their homes with dogs, but also of considerable significance for the welfare of human communities. Even in the United States, where most dogs live as family pets, dogs are responsible for 12,400 bites a day (Gilchrist et al. 2008). In the third world, dogs are an even greater danger. More than 55,000 people, mainly in Asia and Africa, die each year from rabies, a disease for which dogs are the most important vector (World Health Organisation 2005).

Though the warmth of the human–dog relationship is often commented upon, even in scientific communications, the particularly rich relationship that many people enjoy with their pet dogs is both relatively recent and relatively limited to the first world and wealthier classes in the developing world. The often cited phrase, “Dog is Man’s best friend” was coined by the King of Prussia in 1789 (Laveaux and King of Prussia 1789); it didn’t enter widespread usage until the early twentieth century.

Despite claims for the novelty of the study of the human–dog relationship (Hare and Woods 2013; Miklosi 2009), the use of dogs as psychological subjects, including the study of dogs’ relationship with humans, has a history in science dating back to Pavlov at the very beginning of the twentieth century. Pavlov used dogs in a systematic behavioral research program and discovered what he termed the social reflex (Pavlov 1928), in which the presence of a certain person can increase excitatory activity in the dog (Lynch and Gantt 1968).

W. Horsley Gantt, an American who studied with Pavlov, developed Pavlov’s research into the social reflex in dogs on his return to the United States. Gantt and his students studied what he termed the ‘effect of person’ (Lynch 1987). Gantt found that a dog’s heart rate would dramatically increase (tachycardia) when a human entered the room, but would decrease (bradycardia) when petted (Gantt et al. 1966). Additionally, when dogs received unsignaled paw shocks that typically produced tachycardia, petting during shock delivery would substantially decrease this change in heart rate. Because the response to human petting could be readily conditioned to other stimuli, Gantt et al. suggested that petting was an unconditioned stimulus. However, the response also showed specificity to certain people. Those that had a “special relationship” (Gantt et al. 1966, p. 152) with the dog produced larger and more variable responses. Pavlov had also noted that the social reflex was produced by an experimenter who “played with (the dog), fed him and petted him” (Pavlov 1928, p. 368). Feuerbacher and Wynne (2011) presented a review of the extensive history of dogs as subjects in psychological research.

10.1.1 What are Humans for Dogs?

More recent studies have continued to develop our understanding of the functions of human contact for dogs within an operant framework—asking what consequences provided by humans can influence the behavior of dogs. Dogs in Western households experience a range of human interactions, including food delivery, petting, and vocal praise. [Fonberg et al. \(1981\)](#) reported that both food and 20–30 s of petting maintained operant responding in dogs. More recently, [Feuerbacher and Wynne \(2012\)](#) found that food maintained more and faster responding in shelter dogs, pet dogs, and hand-reared captive wolves than a brief social interaction comprised of petting and vocal praise. This was true even though, in the case of the pet dogs, their owners provided the petting and praise under the direction of the lead experimenters. [Fukuzawa and Hayashi \(2013\)](#) also found that food produced shorter latencies to respond early in training compared to petting or vocal praise. Both of these studies indicate that in some cases food is a more effective reinforcer than human interaction.

That food is an important consequence for dogs is also supported by developmental evidence in which hand-fed food-deprived puppies showed more approach and fewer avoidance behaviors towards humans ([Elliott and King 1960](#)). Similarly, puppies given a choice between two fake cloth dams, one that provided food and one that did not, preferred the dam that provided food over a 20-day test period ([Igel and Calvin 1960](#)). However, when given a choice between a cloth dam that did not produce milk, and a wire one that did, dog pups, like Harlow and Zimmerman's (1959) juvenile monkeys, preferred the non-nutritive cloth mother over the nutritive wire mother ([Igel and Calvin 1960](#)).

The potency of food as a reinforcer may be instrumental in producing social interaction between humans and dogs, since in many contexts humans provide access to food for dogs. Nevertheless, [Fonberg et al.'s \(1981\)](#) finding that both food and petting maintained operant responding indicates that human interactions other than food delivery, such as petting, might also function as reinforcers. Petting was sufficient to maintain military dogs' operant responding to the cues, 'sit', 'down', 'come', 'stay', and 'heel' ([McIntire and Colley 1967](#)). Furthermore, [Feuerbacher and Wynne \(in prep.\)](#) observed that both shelter and owned dogs remained in proximity to a person providing petting, and showed no signs of satiation to that stimulus. Given a choice between a person providing food and another providing petting, some shelter and some owned dogs (which were being petted by their owner) preferred petting to food when food was readily available. Those dogs that preferred food to petting shifted their preference towards petting as the rate of food delivery was reduced ([Feuerbacher and Wynne in prep.](#)). This parallels [Gantt et al.'s \(1966\)](#) findings that petting might be an unconditioned stimulus for dogs and [Igel and Calvin's](#) research, noted above, in which puppies preferred a non-food producing cloth mother to a food-producing wire mother. Together these results support the idea that petting, or "contact comfort" ([Harlow and Zimmerman 1959](#)), is a reinforcer for dogs as it is for primates.

Unlike petting, vocal praise seems to be at best a conditioned reinforcer for dogs. Latencies to respond to basic obedience cues (such as *sit*, *down*, *come*, *stay*, and *heel*) increased when only vocal praise was provided for correct responses (McIntire and Colley 1967), and dogs spent as little time near a human providing vocal praise as when the person provided no interaction at all, even when the human was the dog's owner (Feuerbacher and Wynne in prep). Vocal praise likely has to be explicitly paired with another reinforcer to become a conditioned reinforcer and extinguishes rapidly if not backed up by a primary reinforcer.

Finally, the dog's relationship to the person providing the interaction impacts its behavior towards humans. Owned dogs showed more social approach behavior, as well as more redirected and appeasement behavior, when being petted by a familiar person than someone unfamiliar (Kuhne et al. 2012). Barrera et al. (2010) found that shelter dogs emitted more appeasement behaviors and remained closer to a stranger than did owned dogs, which more often stayed by the door of the enclosure. However, owned dogs remained in proximity to their owner just as much as shelter dogs stayed in proximity to a stranger for petting (Feuerbacher and Wynne in prep.). This suggests that humans might be a source of comfort for socialized dogs in stressful situations such as a shelter or an unfamiliar laboratory. One possible mechanism for this effect may be petting-induced increases in serum levels of hormones associated with pleasure and social bonding such as b-endorphin, oxytocin, prolactin, b-phenylethylamine, and dopamine (Odendaal and Meintjes 2003).

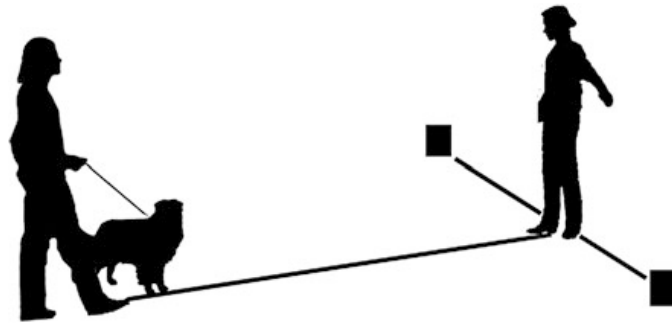
10.1.2 Dogs' 'Human-like' Social Cognition

Over the last two decades there has been a growing interest in the cognitive abilities of dogs, especially with regard to their social cognition. Much of this research has sought to elucidate the acute sensitivity to human actions of many pet dogs (Udell and Wynne 2008; Udell et al. 2010a).

One task that has become axiomatic for the responsiveness of dogs to humans is the human-guided choice task, also known as the pointing task (see Fig. 10.1) (see also Rossi et al. this volume). In this test, an experimenter points at one of two or more locations where food can be found if the dog approaches that location first. Typically, dogs living in human homes excel on this type of problem (Miklósi and Soproni 2006; Udell et al. 2010a). Although points are often made with the experimenter's arm and hand, research shows that many pet dogs can also follow a wide range of other gesture types, including those made with other body parts like a human leg or head, those made from a greater distance, or even after a short delay (Miklósi et al. 1998; Soproni et al. 2001, 2002; Udell et al. 2008b, 2011).

Pet dogs have also proven responsive to human attentional state, at least under some conditions. In situations in which a dog can beg from a human looking at it or from a human with her back turned—simple begging tasks—dogs typically choose the person looking at them (Cooper et al. 2003; Gácsi et al. 2004; Udell et al. 2011). However this ability likely has more to do with dogs' experiences in their home

Fig. 10.1 Sketch of the typical layout of a human-guided choice task, also known as a pointing task. The person on the right points at one of two containers on the ground before the dog is released to make its choice



environment where they experience the consequences of begging from people who have different levels of attentiveness than with true perspective-taking, as dogs do not appear to recognize that a human wearing a bucket over her head and eyes is inattentive (Cooper et al. 2003; Udell et al. 2011). Furthermore, only pet dogs recognize that a human reading (with a book covering her face) is inattentive; in our study, dogs living in a shelter and hand-reared wolves which had less opportunity to experience this scenario in their current environment, begged equally from a person who was reading and a person looking at them (Udell et al. 2011).

Dogs also appear to respond to human attentional state in a related problem: the forbidden food task. Here dogs again have to determine whether a human is attentive or inattentive, only this time the goal is not cooperative in nature. In forbidden food tasks, a piece of food is placed on the floor in front of the dog, which is then instructed by the owner or experimenter not to eat it. While dogs may obey, and leave the food untouched when the human is present and attentive, they are increasingly likely to disobey if the human's eyes are closed, her back is turned, she leaves the room, or if a barrier blocks the human's view of the food and the dog's approach (Bräuer et al. 2004; Call et al. 2003).

Dogs have also been reported to use their gaze to guide the attention of humans towards desired objects that are out of reach (Miklósi et al. 2000), to succeed in human-guided detour tasks (Pongracz et al. 2001), and some have even proven capable of emulating human actions (Topál et al. 2006) or responded to large numbers of human words with extensive training. So far the record for words understood rests with Chaser—a Border Collie from South Carolina which has learned names for around 1,200 items (Pilley and Reid 2011).

These findings have led to evolving hypotheses about canine cognition, beginning with the proposal that wolves might be more oriented towards physical (means-end type) cues and thus better at problem solving tasks such as maze and barrier tasks (see Frank et al. 1987, for an overview). Dogs, on the other hand, might be more socially oriented and thus better on training tasks (such as leash training and coming when called) (Frank and Frank 1987). These differences between dogs and wolves were explained primarily as a byproduct of dogs' neoteny (particularly the slowing of social and physical development, making young dogs easier to handle and thus socialize), as well as a long history of human provisioning of dogs, weakening the selection pressure for physical problem solving competence. Later it was proposed by Hare et al. (2002) that dogs

could have evolved a human-like form of social cognition during domestication resulting in a higher level of sensitivity to human actions than seen in wolves. Proponents of this hypothesis suggested that domestic dogs were uniquely prepared to respond to human actions, arguing that "...dogs' ability to follow human communicative cues is a skill present in dogs before exposure to humans can have ontogenetically major influences on dogs' behaviour... this skill therefore represents a special adaptation in dogs which is present from early (sic) age" (Riedel et al. 2008, p. 10).

Despite earlier claims that dogs show more human-like social cognition than wolves (Hare et al. 2002, 2005; Miklósi et al. 2003), several recent studies have demonstrated that if wolves are properly socialized to humans and have the opportunity to interact with humans regularly, then they too can succeed on some human-guided cognitive tasks (Gácsi 2009a; Range and Virányi 2011; Udell et al. 2008b, 2011, 2012), in some cases outperforming dogs at the individual level (Udell et al. 2008b). Like dogs, wolves have also proven capable of following more complex point types made with body parts other than the human arm and hand and after a short delay (Udell et al. 2012). It is also important to note, that even though the earlier reports suggested that dogs outperformed wolves and foxes on human-guided tasks, they did not claim that wild-type canids were universally unsuccessful; rather, the wild-type individuals performed above chance on some of the human-guided tasks (or gesture types) under test in every study (Hare et al. 2002, 2005; Miklósi et al. 2003; Virányi et al. 2008).

Various explanations have been offered for why tame wolves may sometimes fail to perform as well as dogs on some versions of a human-guided point-following task. For example, Hare et al. (2002) tested wolves with multiple individuals in the enclosure during testing and from behind a fence, while dogs were tested individually, indoors, with no barrier between them and the experimenter. Udell et al. (2008b) demonstrated that the presence of a fence barrier, like the one that the wolves (but not dogs) had to contend with in Hare et al. (2002), could lead to a similar decrement in performance in domestic dogs when tested under the same conditions. Frank and Frank (1987) had earlier noted that insufficient socialization can lead to poorer performance by wolves on social tasks: "Insofar as socialization to humans might involve sensitization to human behavioral cues, therefore, the incompletely socialized wolf pups may have been operating at a comparative disadvantage in the training situation, much like a nearsighted child trying to learn to read" (p. 35). Frank and Frank (1987) demonstrated this point by rearing a new litter of wolf pups with the socialization procedure established by Klinghammer and Goodman (1987), resulting in wolves with a substantially improved level of responsiveness towards humans. With properly socialized wolves, social interaction with humans could be used as reinforcement, performance on social tasks increased, and handling became easier as these wolves could be called by name.

Whatever the reasons for the failures of some wolves on human-guided tasks, it is just as important to acknowledge that many pet dogs also fail to perform above chance on these tasks. In fact in some studies more than half of the dog subjects

did not reliably follow human points (Udell et al. 2008b; Gácsi et al. 2009b). Even those individuals that did follow some gestures or point types often failed to follow others (Udell et al. 2008a, 2010a, b, 2011, 2013), a finding that parallels the results of early studies with wolves. However, the much larger number of dogs tested in these studies can lead to an outcome where a group of dogs can perform above chance on average, even when such an interpretation is inconsistent with the behavior of the majority of the dogs. Given the much larger number of human-socialized pet dogs available for test, it is not surprising that the total number of dogs succeeding on these tasks is greater than wolves. This may be deceptive, however, because the individual success rate for wolves is actually quite high. Furthermore, as previously noted, pet dogs only make up a small percentage of the total domestic dog population and there is little evidence to suggest that the behavior of most dogs world-wide is accurately represented by those living in human homes as pets.

The suggestion that pet dogs perform well on human-guided tasks because of a newly evolved human-like social cognition (Hare et al. 2002) fails to account for the diversity of human-directed behaviors across the broader dog population, as well as successful performances on human-guided tasks not only by wolves, but a wide range of human-socialized non-domesticated species including parrots (Giret et al. 2009), bats (Hall et al. 2011), jackdaws (Von Bayern and Emery 2009), ravens (Schloegl et al. 2008), dolphins (Pack and Herman 2004), elephants (Smet and Byrne 2013), and seals (Scheumann and Call 2004), suggesting that the domestication hypothesis is no longer compatible with current scientific knowledge.

In sum, sometimes dogs may perform better than wolves on human-guided tasks, at other times wolves may perform better than dogs; some individuals from both groups have proven skilled at responding to human gestures, while some individuals from both groups fail. Thus both dogs and wolves have the cognitive capacity for this level of prosocial behavior towards humans, however it is not guaranteed for either subspecies. In the absence of appropriate life experiences, or outside certain contexts, both dogs and wolves may fail. These observations led to the development of a new hypothesis, which takes both phylogeny and ontogeny into account when predicting the social behavior of dogs (and other species) towards humans: the Two Stage Hypothesis (Udell et al. 2010a).

The Two Stage Hypothesis predicts that for canids to perform well on traditional human-guided tasks (like following a human point) both relevant lifetime experiences with humans, including socialization to humans during the critical period for social development, and opportunities to associate human body parts with certain outcomes (such as food being provided by human hands, a human throwing or kicking a ball, etc.) are required.

The Two-Stage hypothesis is not an alternative to an evolutionary approach; instead its predictions focus on the interactions between evolutionary and lifetime factors that contribute to the rich diversity of social behavior in canids (Udell et al. 2010a; Udell and Wynne 2010). While a mechanism for a new heritable form of cognition in dogs is lacking, there are still known heritable biological and

developmental traits associated with domestication (like the timing of perceptual and social development—see below) that when combined with the unique environment and experiences of pet dogs would likely be very conducive to success on socio-cognitive tasks. This hypothesis is also more consistent with evidence that environmental and life experience do play a significant role in a dog's response to human actions, and thus provides predictions that can account for the behavior of all dogs, not just pet dogs.

In addition to the fact that many individual pet dogs do not perform above chance on human-guided tasks (Gácsi et al. 2009a, b), there is also evidence that dogs are constantly learning about human actions (Bentosela et al. 2008; Horowitz 2012), gestures (Elgier et al. 2009; Miklósi et al. 1998; Udell et al. 2008a, 2010b, 2013), and attentional state (Udell et al. 2011), and adjust their behavior accordingly. In fact, pet dogs sometimes continue to learn about human gestures over the course of experimental testing, resulting in above chance performance on challenging tasks that may appear spontaneous, but is actually a byproduct of experimental experience. For example, Udell et al. (2013) found that pet dogs which were tested on a series of nine point types (ten trials per point) in order of increasing difficulty performed significantly better on the most difficult point types such as the momentary distal point, where the point is only held in place for a few seconds (returning to a neutral position before the dog is allowed to approach) and the target is located further than 50 cm away from the experimenter's extended arm and hand when compared with naive dogs.

Thus, while it is entirely possible that canines have a predisposition to attend to the actions of their social companions, it appears that individuals (be they dog or wolf) must first learn to recognize that humans are indeed companions worth watching, and then continue to learn about the relationship between human actions and salient outcomes throughout their lives. While in some cases this learning may be a product of experimental setup or explicit training, much of what canines learn about human actions occurs naturally within their home environment without conscious effort by people (Reid 2009; Udell and Wynne 2008). Feral dogs likely also learn about, and respond to, human actions. As obligatory symbiotes even dogs that do not live as pets typically live near and benefit from the presence of humans and human waste (Coppinger and Coppinger 2001; Udell et al. 2010a). However the specific behavioral responses of feral dogs to human actions may not look like the responses one would expect from a pet dog; each would be expected to behave in ways consistent with its environment and life experiences.

10.1.3 So What do we Mean by Dogs?

One important consideration when interpreting research on canine cognition is the exact nature of the population under test: are the dogs succeeding on these tasks a good model for all domestic dogs, or are they unique in significant ways, including

lifetime experience or environment, that might provide alternative explanations for their performance than subspecies membership itself? When reading scientific reports about 'dog' cognition, it may seem reasonable to assume that the information presented is representative of the entire subspecies, the domestic dog (*Canis lupus familiaris*). Unfortunately this is often not the case. The great majority of modern research on dog cognition has focused on pet dogs living in human homes (Udell et al. 2010a). Working dogs (search and rescue, guide dogs for the blind, sniffer dogs) have also garnered increasing scientific attention in recent years (e.g., Bensky et al. 2013). However other groups, such as stray dogs or dogs living in shelters, have been vastly underrepresented in canine cognition research, despite the fact that in the US alone roughly 10 % of the domestic dog population lives in shelters (Udell et al. 2010b).

Yet even these three populations combined constitute a minority of dogs worldwide. As mentioned previously, the great majority of dogs (as much as three-quarters of the world dog population) live outside the first world as scavengers. These dogs have never been, and likely never will be, owned by a human, and even those who are owned lead considerably different lives than Westernized pets (Coppinger and Coppinger 2001; Lord et al. 2013). This population has been almost entirely neglected in experimental studies on canine cognition.

Such populations have received some attention from scientists using less intrusive methods, however, and this work has shed light on the general behavior patterns of these populations (e.g., Beck 1973; Berman and Dunbar 1983; Boitani and Ciucci 1995; Daniels 1983; Daniels and Bekoff 1989; Ortolani et al. 2009; Pal 2008; Pal et al. 1998). Some of these studies also illustrate why it has been difficult to include feral dogs in traditional socio-cognitive experiments. For example, Ortolani et al. (2009) looked at the social response of feral village dogs in four Ethiopian villages when approached by a human. They found that the most common response of these dogs was to run away (52 %); another 11 % responded to the approaching human with aggression. Only 4 % of the surveyed population reciprocated the approach in a non-aggressive manner.

Given, first, that pet dogs represent a small minority of the domestic dog population, and, second, that many domestic dogs from other populations (such as free-living and shelter dogs) may show quantifiably different behavior towards humans (including fear and aggression), it seems very unlikely that the social behavior or cognition of pet dogs can be explained as a product or byproduct of domestication alone. What little we know about these free-ranging populations of dogs adds to the ample evidence that domestication does not guarantee excessively social, or even prosocial, behavior in dogs towards humans in the absence of appropriate life experience. In fact, in one of the most comprehensive laboratory studies on the social behavior of dogs to date, Scott and Fuller (1965), demonstrated that domesticated dog puppies raised entirely apart from humans "may later react toward them with extreme fear and hostility" (p. 176). This work was among the first to define a timeline for, and emphasize the importance of, the critical period for social development in dogs: a sensitive period early in a puppy's

		Phylogeny/ Domestication Status	
		Domesticated	Non-domesticated
Ontogeny/ Developmental Experience	Human-socialized	Pet dogs & village dogs raised with early human contact	Hand-reared wolves and other captive canids in research facilities and zoos
	Non-human-socialized	Village and other feral dogs raised outside of early human contact	Wild-living wolves and other wild canids

Fig. 10.2 Examples of canids occupying all four of the logically possible intersections of domestication status and human socialization

life where social interaction has a much greater effect on the development of future social behavior than at any other time.

Domestication has made it easier to tame, or socialize, dogs in comparison to their wild counterparts, primarily due to changes in the timing of development (a topic to which we will return). However it is worth noting that domestication on the one hand and taming or socialization on the other are different processes; the first is a genetic or evolutionary process, the latter a lifetime process (for a review see Udell et al. 2010a). Domestication and socialization/taming can be thought of as occurring on two interacting continua, resulting in four possible canid types illustrated in Fig. 10.2: (1) domesticated and tame; (2) domesticated and not socialized to humans (feral or untame); (3) undomesticated (genetically wild) and tame; (4) undomesticated and not socialized to humans. While in the Western world we most often encounter domesticated dogs that are also tame (category 1) and, less often, undomesticated canines (wolves, coyotes, foxes) that are not socialized to humans (category 4), the other combinations are possible as well. Feral dogs and socialized wolves in research facilities or zoos serve as examples of these two cases respectively.

In other words, dogs may be pets, workers, stray or free living, but all of these individuals are ‘domesticated’ and belong to the same subspecies. Designations like ‘pet’ or ‘feral’ refer to an individual’s home environment, lifestyle or current niche, but do not imply significant genetic differences. Domestication, on the other hand, implies genetic change in comparison to wild-type counterparts. While this process may change the probability of tame behavior, it does not determine it (Scott and Fuller 1965; Udell et al. 2010a). Although some dogs (many pets and working dogs) have shown remarkable sensitivity to people, so too have some human socialized wolves. Unsocialized individuals from both groups have been difficult to test, however tame wolves with more intensive socialization have been found to perform better on social tasks than inadequately socialized wolves (Frank et al. 1987).

10.1.4 What is different about the Behavior of Dogs Compared to their Wild Relatives?

Having outlined areas in which the behavior of pet dogs and human-socialized wolves is more alike than some previous authors have claimed, and in full cognizance that dogs and wolves are extremely similar genetically, we nonetheless recognize that there are important behavioral differences between these two species—differences that make dogs widespread pets, whereas socialized wolves are rare. The purpose of this section is to review what we consider the essential behavioral differences between dogs and wolves (see also Fugazza and Miklósi, this volume).

10.1.4.1 Social Imprinting

The first major difference in the behavior of dogs and wolves has already been alluded to. While it is possible to tame a wolf, the process is much more intensive than that required to produce a tame dog.

Dogs require as little as ninety minutes of contact with humans during their 'critical period' of socialization—one of the critical periods of development (see also Fiset et al., this volume)—to form a social attachment (Freedman et al. 1960). This is the minimum requirement and will not result in a highly social pet dog, but it will create a dog that will solicit human attention.

Wolves require twenty-four hours contact a day starting before three weeks of age (Klinghammer and Goodman 1987; Zimen 1987). The standard protocol is to remove pups from the den at about ten days of age. They are then kept in constant contact with humans until they are around four weeks old. At this point they begin to bite their sleeping human companions and thus co-sleeping with humans ends, but the pups still spend all their waking hours in the presence of people. This socialization process continues until the pups are four months old at which point they can live with other captive wolves and will maintain their socialization with humans as long as they continue to get daily human contact (Klinghammer and Goodman 1987).

Despite this intensive process, a well-socialized wolf still behaves very differently from a well-socialized dog. Taming a wolf does not eliminate any of its species-typical behaviors (Gácsi et al. 2005). Tamed wolves still display species-typical hunting and reproductive behaviors, but they will display them in closer proximity to humans (Fentress 1967; Klinghammer and Goodmann 1987). This means it is more likely that they will also display them towards humans. For example, if wolves are not raised with other wolves while being socialized with humans they will direct reproductive behaviors towards humans. During breeding season they may become territorial and compete with human caretakers over perceived potential (human) mates.

Well-socialized wolves do not generalize their socialization to all humans in the same manner as a well socialized dog and are more fearful of novelty in general than socialized dogs (Fentress 1967; Klinghammer and Goodmann 1987; Zimen 1987).

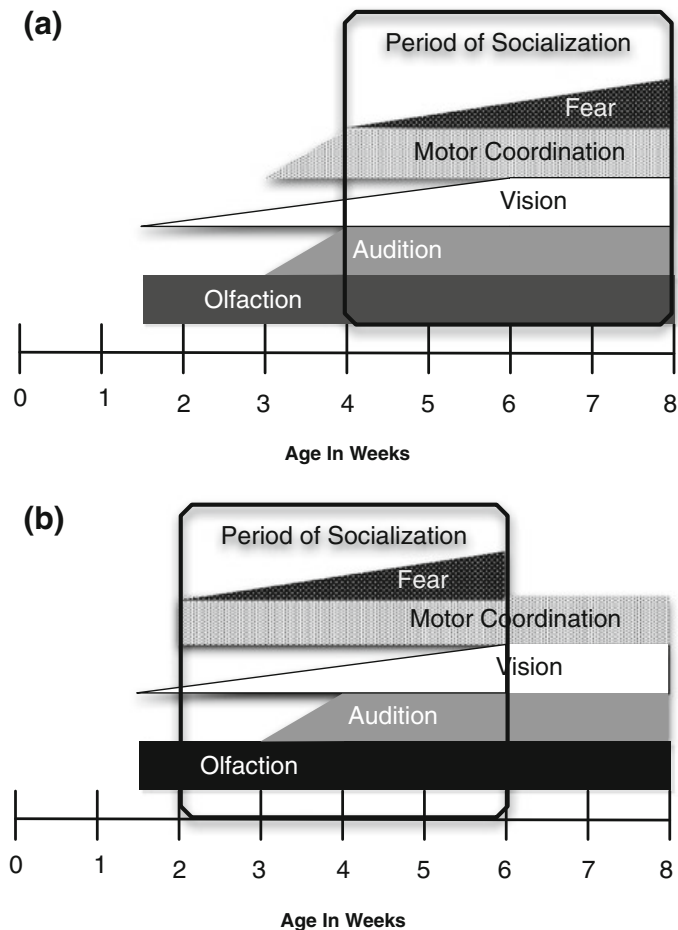
It has long been thought that these differences are due to a change in the timing of the critical period of socialization in dogs and wolves, since this is the time period when social bonds are formed both within an animal's own species and between species.

The critical period for socialization begins with the ability to walk and explore the environment (see Lord 2013, for discussion). Wolves begin to walk and explore at two weeks of age (Frank and Frank 1982; Packard 2003). Dogs do not start to walk and explore until four weeks (Rheingold 1963; Fox 1964). The critical period of socialization closes with the avoidance of novelty, when an animal runs away from, rather than approaching and exploring, novel objects. This threshold has previously been referred to as the onset of fear, but fear actually starts well before the avoidance of novelty. In dogs, fear gradually increases from four weeks, when they show little to no fear of novelty, until around eight weeks when they will run away from a truly novel stimulus (a stimulus having no familiar characteristics). Figure 10.3 shows the development of fear and sensory capacities in dogs and wolves based on Lord (2013)'s study.

It has been hypothesized that wolves reach the end of the critical period for socialization at three weeks (see review in Miklosi 2009). This is based on the fact that it is not possible to socialize a wolf after three weeks of age (Klinghammer and Goodman 1987; Zimen 1987). Wolves also show the first appearance of fear in the form of a startle response to sound at three weeks of age (Zimen 1987). This hypothesis would imply that wolves have a one week critical period of socialization (since socialization begins at two weeks when the wolf pups start to explore), and could thus explain neatly the difference between the ability of dogs and wolves to form interspecies social bonds. However, this hypothesis is based on a confusion concerning the use of the term "onset of fear." The startle response is an altogether different phenomenon from fear and the avoidance of novelty. In fact, dogs, just like wolves, also show their first startle responses to sound at around three weeks of age. And wolves don't show the avoidance of novelty—the true "onset of fear"—until six weeks of age. Thus wolves and dogs both have a four-week critical period for socialization—wolves just go through it two weeks earlier than dogs do.

In itself, the earlier progress of wolves than dogs through the critical period for socialization does not explain the behavioral differences between dogs and wolves. However, Lord (2013) recently found that, despite this two-week difference in the timing of the ability to walk and explore, the dogs and wolves in her study developed the ability to see, hear, and smell at the same time. The consequence of this is that dogs began to explore the world around them at four weeks of age with the senses of sight, hearing, and smell available to them, while wolves began to explore the world at two weeks of age when they had the ability to smell but while functionally blind and deaf (see Fig. 10.3). This change in the interaction between

Fig. 10.3 Early sensory development in relationship to critical period for socialization in dogs (*top*) and wolves (*bottom*). The beginning of a bar marks the first appearance of a behavior or sensory capacity, and the full width of a bar indicates mature capacity. From Lord (2013); used by permission



the developing senses and the critical period for socialization means that dogs can generalize familiarity using all of their senses, while wolves must rely primarily on their sense of smell, making more things novel and frightening as adults.

10.1.4.2 Reproductive Behavior

Reproduction is another domain of behavior where wolves and dogs differ importantly. Wolves, and in fact all of the wild members of the genus *Canis*, display complex coordinated parental behaviors. Wolf pups are cared for primarily by their mother for their first three weeks of life (Mech 1970). During this time she remains in the den with them while they rely on her milk for sustenance and her presence for protection from predators. Because of this she cannot spend much time away from them, and the father brings the mother food during this period. Once the pups come out of the den and have enough teeth to chew, the father, mother as well as some pups from previous years, begin to regurgitate food to the pups (Mech et al. 1999). Wolf pups become independent by five to eight months, although they often stay with their parents for years (see Lord et al. 2013 for further discussion).

Dogs, on the other hand, show greatly reduced parental behavior. Pups are still cared for by the mother. They rely on her for milk and protection just like wolves. However, unlike wolves, the mother gets no help from any other dogs during this time. There is no paternal care, let alone help from older siblings. Once pups are weaned at around 10–11 weeks they are independent and receive no further maternal care (see review in [Lord et al. 2013](#)).

[Lord et al. \(2013\)](#) reviewed several important differences between dog reproductive behavior and that of the wild canids. Dogs have lost seasonality of reproduction: in other words they do not reproduce solely at a particular time of year ([Gipson et al. 1975](#); [Lord et al. 2013](#)). Dogs also reach sexual maturity faster than wolves and can reproduce during their first year of life ([Boitani et al. 1995](#), [Ghosh et al. 1984/85](#)). Furthermore, dogs are polygamous, in contrast to wolves, which are generally monogamous ([Ghosh et al. 1984/85](#); [Harrington et al. 1982](#)). Thus dogs show no pair bonding and protection of a single mate, but rather have multiple mates in a year.

It is easy to look at these differences in reproductive behavior between dogs and wild canids and assume they are the result of artificial selection by humans or relaxed selection for parental care for pups, as humans intervene to assure pup survival. This hypothesis was proposed by Darwin (1859) among others. It should be kept in mind however that, as noted above, on a global scale, most dogs are not under the direct care of humans. An alternative hypothesis, proposed by [Lord et al. \(2013\)](#), is that reduced parental care in dogs may be an adaptive strategy for a particular niche.

[Lord et al. \(2013\)](#) proposed that these differences in parenting behavior amount to an alternative breeding strategy, one adapted to a life of scavenging instead of hunting. Whereas wolves are constrained to a maximum of one litter a year starting at two years of age, female dogs start reproduction in their first year and can recycle and have another litter as soon as eight months postpartum. The male dog, by not caring for pups or their mother and being unconstrained by seasonality, is free to continue to mate all year long with as many receptive females as he can find. The consequence of this is that whereas wolves put a lot of energy into a few pups, dogs maximize the production of pups. This higher pup production rate enables dogs to maintain or even increase their population with a lower pup survival rate than wolves. It also means that dogs would have a greater capacity than wolves to grow their population after a population crash or when entering a new habitat.

Dogs are only able to adopt this strategy because they no longer have to spend as much energy and ingenuity foraging. Rather than hunting prey, dogs can rely on human refuse, which is more predictably located and available year round. Foraging on garbage is a less complex behavior pattern than hunting and dog pups can forage even before they are entirely weaned. Thus, by the time they are ten weeks old they are perfectly capable of finding their own food ([Macdonald and Carr 1995](#); [Pal 2008](#)).

The changes in dog reproductive behaviors and behavioral development that we have noted here are not a consequence of direct human action in the form of people

adopting pups on a widespread scale. The role of humans in supporting dogs is indirect. Humans provide a food source, in the form of their garbage, that is easier to find and exploit than live prey. The canids that became dogs adapted to this new niche in several ways. They became more fertile, through earlier onset of reproduction, year-round fecundity, and reduced parental care. Dog parents are able to reduce their investment in each pup because foraging on trash requires less strength and skill than does hunting live prey. This increased fertility enables dogs to more rapidly colonize new niches, and allows more rapid rebound of populations after disease outbreak or other catastrophic population loss.

The changes in behavioral development we note here are likely also adaptations to scavenging on human trash dumps instead of hunting live prey. Whereas wolves go through the critical period for socialization with only olfaction fully functional, dogs have their senses at close to adult levels of functionality during this important phase. This makes it easier for dogs to generalize across sensory dimensions and increases the range of objects to which they can readily be socialized. This is also an adaptation to foraging close to human settlements as it increases the probability that dogs tolerate human proximity.

10.2 Conclusions

We have attempted in this chapter to put the dog back in the center of discussions on dog cognition and behavior (see also Coppinger and Coppinger 2001). Not the dog as viewed by first-world pet owners (among whom we count ourselves), but the dog viewed as a biological object with psychological properties. This is an animal that not only lies at its master's feet as he types, but the dog that scavenges on the fringes of human settlements well away from National Geographic documentaries; the dog that nobody considers their "best friend." This form of dog is still the most common on the planet; it does not come when called, on the contrary, it scurries away when an unfamiliar person appears (Ortolani et al. 2009).

There is little evidence that the particular sensitivity to human actions and intentions that has become a major focus of cognitive studies on dogs in the last two decades is a special adaptation or a case of co-evolution (Hare et al. 2002; Schleidt and Schalter 2003). Indeed, such sensitivity is not widespread among the world's billion-strong dog population, nor is it, as we have summarized above, absent from wolves, in those rare cases where wolves have been effectively socialized to humans. Rather the ability of a few dogs and fewer wolves to respond to human behavior is more likely an expression of basic processes of conditioning operating on animals that have been socialized to and made completely dependent on human beings (Udell et al. 2010a, b), in concert with social and biological traits shared by both wild and domesticated canines.

The real differences between dog and wolf behavior lie at more basic levels: in the process of socialization, in foraging, and in reproduction. The intertwined changes that led to an animal that is (1) more promiscuous than any other member

of the genus *Canis*, (2) can reproduce more rapidly, and (3) is a much less effective hunter but (4) more efficient scavenger on human refuse than other members of its genus are small but they have massive downstream effects. These indirect consequences include the fact that we have dogs resting at our feet and not wolves.

We have attempted here to demystify dogs, in the sense that we have sought explanations for their behavior that do not assume special processes or unique relationships, but we submit that a deeper and richer understanding of these fascinating animals will flow from a recognition that they are not human creations, nor co-evolved to be our companions. Rather, dogs are canids that have come to occupy a new niche through natural selection. Though it may be a little less flattering to the human species, we believe this perspective on dogs is at least as fascinating and closer to the historical truth.

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