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## **Human-Socialized Wolves Follow Diverse Human Gestures... And They May Not Be Alone.**

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Many studies document the domestic dogs' responsiveness to human gestures. Reports of success on human guided tasks have led to evolutionary hypotheses that set dogs' skills apart from other species, including other canids, in terms of their social cognition and comprehension of human communicative stimuli. However, until recently the range of other species tested and the availability of studies using equivalent testing methods between different species and groups have been limited, making it difficult to interpret cross-species comparisons. Here we demonstrate that human-socialized wolves are not only capable of responding to points made with the arm and hand, but are sensitive to a wide range of human gestures when given the opportunity to utilize such gestures in an object-choice task. Claims that domestic dogs are unique in their ability to respond to diverse novel stimuli may be in part due to the absence of data for the same range of gestures in other species. We also provide the first evidence that human-socialized coyotes have the capacity to utilize a human point to locate a target; further demonstrating that domestication is not a prerequisite for canid responsiveness to human actions, and that socialization and life experience are likely more important predictors of success.

The comparative study of joint attention, gesture following, and responsiveness to attentional state was at one time primarily restricted to humans and non-human primates. In recent years there has been a dramatic shift in interest to include a much broader range of species including, but not limited to, horses (McKinley & Sambrook, 2000), cats (Miklósi, Pongrácz, Lakatos, Topál & Csányi, 2005), parrots (Giret, Miklósi, Kreutzer & Bovet, 2009) bats (Hall, Udell, Dorey, Walsh, & Wynne, 2011), Jackdaws (Von Bayern & Emery, 2009), Ravens (Schloegl, Kotrschal, & Bugnyar, 2007), goats (Kaminski, Riedel, Call, & Tomasello, 2005), dolphins (Pack & Herman, 2004), and seals (Scheumann & Call, 2004). However one subspecies has drawn substantially more focus than the rest: *Canis lupus familiaris*, the domestic dog. As a result comparisons between canid species and subspecies have become an important focal point in the debate about the origins and mechanisms underlying responsiveness to social gestures, especially responsiveness to human gestures (for a review see Udell, Dorey, & Wynne, 2010b). Over the course of more than a decade of experimentation, pet domestic dogs have demonstrated that they are capable of following many different forms of human gesture to locate hidden objects (e.g., Miklósi, Polgardi, Topál, & Csányi, 1998; Soproni, Miklósi, Topál, & Csányi, 2002; Udell, Giglio, & Wynne, 2008). While substantial amounts of variation in performance exists between individuals and groups of dog, at least some have proven capable of

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following gestures as subtle as an eye shift (Miklósi et al., 1998), as challenging as a momentary distal point (where the experimenter extends her ipsilateral arm and pointer finger towards a container > 50 cm away for 2-4 seconds before returning to a neutral position) (Udell, Dorey, & Wynne, 2008), and as unusual as a far elbow cross-point (the experimenter stands behind an empty container sticking her contralateral elbow out and pointing towards the target with her finger extended in front of her body) (Soproni et al., 2002). Research has suggested that domestic dogs not only learn appropriate responses to human gestures quickly (Bentosela, Barrera, Jakovcevic, Elgier, & Mustaca, 2008; Miklosi et al., 1998; Udell, Dorey, et al. 2008; Udell, Dorey, & Wynne, 2010a) but also that some dogs follow human points from early puppyhood (Dorey, Udell, & Wynne, 2010; Hare et al., 2005; Riedel, Schumann, Kaminski, Call, & Tomasello, 2008). These findings have led to several predictions about possible evolutionary origins of this behavior, including convergent evolution with humans (Hare & Tomasello, 2002) or the development of a more human-like social cognition through domestication (Hare, Brown, Williamson, & Tomasello, 2002).

### **Why Canids?**

Much may be learned from comparing the performance of different species, subspecies, and populations of canids on human-guided tasks. The study of canines in this domain is valuable for a number of reasons including the fact that (1) both wild type and domesticated canids exist in nature and in captivity, (2) both human-socialized and unsocialized members of many species and sub-species including domestic dogs, coyotes, foxes, and wolves exist in known populations, (3) detailed information about biological changes associated with canid domestication (Trut, Plyusnina, & Oskina, 2004) and the domestic dog genome (Lindblad-Toh et al., 2005) exist, and (4) domestic dogs share a unique obligatory symbiosis' with humans that varies by population and location, and is not yet fully understood (Coppinger & Coppinger, 2001). However, more emphasis needs to be placed on consistency in the way that different species and subgroups of canids are represented and tested if a truly comparative approach is desired. Failure to account for disproportional testing of some members of the genus or even members of certain populations within a species can result in biases in the data that make generalized claims inappropriate. For example, while domestic dogs are the most common species of canid tested in human-guided object-choice tasks, pets and assistance dogs made up the entire subject pool for over ten years, neglecting domestic dogs in other niches such as strays, village dogs, and dump dogs (Udell et al., 2010a). In fact when shelter dogs were tested (Udell, Dorey, et al., 2008; Udell et al., 2010a) it was demonstrated that the majority of these dogs did not spontaneously respond to human momentary distal pointing, a standard measure of gesture responsiveness in the field. Therefore the lack of knowledge about other non-pet domestic dog populations may have helped drive evolutionary hypotheses foundationally based on the assumption that all domestic dogs would succeed on human guided tasks. This later proved not to be the case, resulting in new hypotheses stressing the importance of interactions between genetic inheritance,

socialization, and life experiences in the development of domestic dogs' responsiveness to human gestures (Reid, 2009; Udell et al., 2010b).

### **Evolving Perceptions of Wolves**

Almost in direct contrast, early studies comparing the performance of dogs and wolves on human guided tasks found that unlike dogs, wolves did not follow human gestures to a target location concealing food (Agnetta, Hare, & Tomasello, 2000; Hare et al., 2002). For example an early study by Agnetta et al. (2000) found that two captive wolves did not follow a human point with gaze or gaze alone to a target object. Likewise Hare et al. (2002) found that none of the seven wolves tested reliably followed a cross-body tap and gaze, point and gaze, or point at the individual level; however the wolves did perform above chance on the cross-body point and gaze condition as a group. However, both of these early experiments contained significant methodological confounds including the use of wolves that may not have been properly socialized to humans and the testing of wolf subjects from behind a fence while dogs were tested with no such barrier (Udell, Dorey, et al., 2008, Udell et al., 2010b; Virányi et al., 2008). Additionally the two wolves tested by Agnetta et al. (2000) were tested together at the same time within the same enclosure.

Another wave of research on wolves' ability to utilize human gestures began in 2001 when researchers in Hungary hand-reared their first litter of wolf pups (Virányi et al., 2008). During a series of experiments taking place over several years, individuals selected from a total of nine socialized wolves were exposed to the following gestures: Dynamic touch & gaze, touch, momentary proximal point, momentary distal point, dynamic distal point, and standing behind the correct container or local enhancement. The success of individual wolves across different point types, and even the average performance of the wolves varied substantially. The most challenging point for wolves to reliably follow in these studies, however, was undoubtedly the momentary distal point. The authors of these studies suggested that while domestication or evolutionary explanations might not rule out the possibility of wolves successfully following simpler forms of human pointing, such as touching a target, proximal pointing, and local enhancement, evolutionary predispositions may have inhibited them from spontaneously following a wide range of gestures including more challenging forms of human point, such as the momentary distal point (Miklósi et al., 2003; Virányi et al., 2008). In other words domestic dogs may be unique not because they can follow a human point, but because of the wide range of human gestures that they appear to spontaneously utilize in object-choice tasks (Agnetta et al., 2000; Miklósi et al., 2003; Virányi et al., 2008).

In 2008 it was demonstrated for the first time that a group of human-socialized wolves were capable of spontaneously utilizing a momentary distal point in an object-choice task (Udell, Dorey, et al., 2008). Not only were these wolves successful as a group, matching the performance of pet dogs tested under ideal conditions, but six of the eight wolves were successful at the individual level outperforming the four groups of domestic dogs tested. These findings were quickly followed by another study conducted by a different group of researchers

showing again that adult wolves were capable of spontaneously succeeding on tasks requiring the use of a human momentary distal point (Gácsi, Gyori et al., 2009). While it is difficult to determine exactly why previous experiments failed to obtain these results, predictions regarding testing methods, socialization, and a reduction in human interaction prior to the time of testing have been made (Udell et al., 2010b). It is also important to note that Virányi et al. (2008) found that wolves that had previously failed to follow a momentary distal point could learn to do so given additional experience. Regardless of the reasons for previous failures, the successes reported by Udell, Dorey, et al. (2008) and Gácsi, Gyori, et al. (2009) provided the first solid evidence that non-domesticated wolves possessed the capacity to utilize more complex human gestures without explicit training to do so. Whether a specific individual or group of wolves will be successful likely depends on a multitude of variables including early and recent life experiences.

These progressive changes – from the view that wolves should be considered incapable of following human gestures, to the view that wolves are only successful in following simple proximal gestures, to the most recent findings that wolves are capable of spontaneously following even the more challenging momentary distal point – illustrate the importance of interpreting negative results, or even the absence of results, with caution. This is especially true when only small numbers of a species have been tested and some under considerable methodological constraints. The changes in knowledge about wolves' ability to utilize human gestures over the past eight years represent the evolution, not of the canid subspecies under test, but of the science behind those findings. Improved methods have allowed for more careful and analogous comparisons between individuals and subspecies, quality and timing of socialization have been considered, and importantly, a larger number of subjects have been tested. Demonstrating that some populations of socialized wolves are capable of spontaneously following a momentary distal point is nonetheless only the beginning. Wolves and dogs are different. This is an unarguable fact. The question is how are they different, and do these differences have any influence on their ability to respond to the gestures of their social companions, be it a conspecific or human being? Although the most recent literature suggests that wolves do not differ in their *capacity* for responsiveness to human gestures, it has been proposed that an individual wolf's ability to follow such gestures may be strongly influenced by its acceptance of humans as social companions (Udell et al., 2010b). Acceptance depends on regular interactions with humans during the critical period for socialization and as a result wolves must be intensely socialized by humans from the second week of life (Klinghammer & Goodman, 1987). One important biological consequence of domestication is a slowing of developmental processes; in domestic dogs this includes the extension of the critical period for socialization in comparison to wolves. In fact the window for socialization extends up to 16 weeks of age in some breeds of domestic dog, making them much easier to socialize and placing a more lenient time restriction on the beginning of this process (Coppinger & Coppinger, 2001; Scott & Fuller, 1965) (for review see Udell et al., 2010b). While it is possible to socialize both dogs and wolves to humans, developmental differences may play an important role in the prevalence of truly socialized members of each group available for test.

## **Range of Stimuli and Canids Under Investigation**

It is also possible that domestic dogs truly are unique in their ability to spontaneously utilize a large range of novel human gestures in comparison to their wolf relatives. While evidence in favor of such a difference may appear to exist already, many of the current distinctions made between the performance of domestic dogs and other species and subspecies, especially wolves, may be artifacts of a scientific literature that contains much more data on pet domestic dogs than most other comparison species. Pet dogs living in human homes have been the primary subject animals in studies of this type for over a decade, far outnumbering studies with wolves or any other non-primate species (Miklósi & Soproni, 2006; Udell et al., 2010a, b). Therefore the likelihood of at least a single pet-dog subject succeeding on a given gesture type in any of the many studies conducted with this population has been greatly enhanced in comparison to members of other species, where only a few individuals have been tested in a single study, utilizing a limited number of gestures. This discrepancy between absolute and relative success on human-guided tasks may create the impression that some species possess the capacity to respond to a wider range of human gestures or succeed more often than others, even when such differences may stem from a disjunct in the amount of data available for each group. The dog-wolf comparison is no exception. Only 35 wolf subjects have been tested across the last decade (2 in Agnetta et al., 2000; 7 in Hare et al., 2002; 9 in Miklósi et al., 2003, and Virányi et al., 2008; 8 in Udell, Dorey, et al., 2008; 9 in Gácsi, Gyori, et al., 2009) in experiments utilizing a total of only nine different gesture types as stimuli in object-choice tasks. With the exception of gaze and local enhancement, all stimuli have been small variations on points made with the human arm and hand and each group of wolves was only tested on a small subset of these nine gestures. While the limited number of wolves tested is likely due to the restricted availability of socialized wolves in comparison to domestic dogs, it is still an important factor to take into account when interpreting scientific results. In contrast more than 35 pet domestic dogs are often found in a single study investigating responsiveness to human gestures (e.g., 180 dogs in Gácsi, Kara, Belényi, Topál & Miklósi, 2009; 38 dogs in Udell, Dorey, et al., 2008). Dogs have also been presented with a much wider range of gesture types. In fact, more novel stimuli can often be found in one domestic dog study (e.g. 16 stimuli in Udell, Giglio, et al., 2008; 9 stimuli in Soproni et al., 2002) than the total number of gestures utilized across all six studies conducted with wolves. Therefore, it is difficult to assess the range of gestures wolves would be capable of responding to if presented with the opportunity.

Interestingly, wolves have demonstrated success, either at the individual or group level, in spontaneously following six of the nine human stimuli with which they have been tested to a target. This speaks well for breadth of performance possible given the constraints of the current literature. Therefore claims that dogs are more responsive to a diverse array of human gestures may have nothing to do with differences in species or subspecies ability or capacity but could simply be a construct of the currently available empirical literature on the topic. In Experiment

1 we address this issue, testing the responsiveness of wolves to a wide range of human gestures.

Studies conducted with other canid comparison groups are sparse, despite the fact that many relatives of the domestic dog exist in the wild and can also be found in captivity. What research has been reported suggests that the capacity for responsiveness to human gestures extends beyond domestic dogs and wolves. Hare et al. (2005) found that undomesticated control foxes (*Vulpes vulpes*) could follow a human point to a target at above chance levels, despite the fact that experimentally domesticated foxes performed more accurately on the task. More recently dingoes, *Canis dingo* or *Canis lupus dingo*, have also been shown to succeed on human-guided object-choice tasks (Smith & Litchfield, 2009). To our knowledge coyotes (*Canis latrans*) have remained outside of investigations of canid responsiveness to human gestures. Unlike foxes, coyotes are firmly within the genus *Canis* and unlike dingoes there is no debate about whether or not they should be considered a sub-population of domestic dogs. This makes coyotes a unique and informative out-group. Furthermore, coyotes often reside in heavily human populated areas and thus are a species of interest for both management and conservation reasons (Lehner, 1976). In Experiment 2 we conducted the first preliminary study investigating coyote responsiveness to a human point.

### **Experiment 1. Wolf and Dog Performance on an Object-choice Task Using Diverse Human Gestures**

The primary purpose of Experiment 1 was to assess the capacity for human-socialized wolves to utilize a wide range of human gestures in an object-choice task. Seven human-socialized wolves were given the opportunity to utilize nine novel gesture types to locate a target in an object-choice task. We also tested seven pet domestic dogs as a comparison group to the wolf subjects using the same methods and same nine gesture types.

### **Method**

**Subjects.** Seven pet domestic dogs (*Canis lupus familiaris*) and seven hand-reared human-socialized gray wolves (*Canis lupus lupus*) participated in this study (see Table 1). All pet domestic dogs were living in human homes as pets at the time of testing and were volunteered by their owners for participation in the study. Every dog in this study was also enrolled in Camp Marlin Doggie Daycare, a facility where dogs are dropped off by their owners several days a week during daytime hours and engage in daily activities with other dogs and human caretakers.

All wolves in the study were from Wolf Park, located in Battle Ground Indiana, and had been hand raised by staff from 10-14 days of age. All the wolves in this study were thoroughly socialized to humans using a process similar to that described in Klinghammer and Goodmann (1987). Wolf subjects were housed in large outdoor enclosures, with Ruedi, Wolfgang, Woton, and Kalani living together in the main pack, and Marion, Ayla, and Tristan living in different enclosures located on the premise. All wolves interacted with humans daily and received food treats directly from humans on a regular basis. As such they were thoroughly habituated to the presence of humans and would readily eat from human hands.

All subjects had previously participated in a study utilizing the object-choice task paradigm, where food could be earned by approaching one of two preselected containers in the presence of a human point (see Table 1). However none of the subjects, dog or wolf, had experienced any of the gesture types utilized in this study. This was done because it was not possible

to test sufficient numbers of object-choice task naive wolves; therefore we selected dogs and wolves with equivalent experience in the testing paradigm itself to avoid unintended initial differences between the groups.

**Testing Layout and Materials.** Dogs were tested in a large indoor room within Camp Marlin’s Doggie Daycare facilities. We tested dogs on days that they were already scheduled to be at the facility, incorporating behavioural testing into their normal daily routine. Additional dogs enrolled in daycare were located in an adjacent room or in an outdoor yard separated by a door. Therefore subjects had little visual access to other dogs during testing but maintained some auditory and olfactory contact. Each dog was tested by a familiar experimenter; a caretaker at the facility who had previously been trained to conduct object-choice tasks of this type.

Wolves were tested in an outdoor holding pen where fences and vegetation separated the animal under test from conspecifics. Similarly to the pet dogs, auditory, olfactory and some visual contact with the other wolves was possible. Each wolf was tested by a familiar experimenter; a caretaker at the facility who had previously been trained to conduct object-choice tasks of this type. The experimenter was located inside the pen during testing; no barrier was present between any of the subjects and experimenter.

The testing layout is illustrated in Figure 1. The subject was led into the testing area by an assistant, E2, who travelled to a marked spot 2.5 m back from the experimenter, E1. The experimenter stood between the two response objects, which were located on the ground 0.5 m to either side of her. Two cylindrical metal empty unmarked paint cans (15 cm diameter, 22 cm tall), filled with gravel and with lids tightly fastened, served as the response choice objects. No food was present in or on either container until and unless the subject indicated a choice of the correct can by touching it or by coming within 10 cm of it with its snout. This eliminated the potential for olfactory cueing based on the location of hidden food, something that has been identified as a potential confound in prior studies (see Udell, Dorey, et al., 2008; Udell et al., 2010b for details). While smells from previous trials (food, saliva, ect.) may still linger on or near the response objects even with this procedure, unlike a prebaited container they do not accurately predict the location of food on subsequent trials and give no clues as to the correct choice on any given trial. The distribution of potential odours was equivalent for each can at the time of testing due to evenly distributed contact during the initial Pretraining procedure.

The correct container was determined pseudorandomly before sessions, subject to the constraints that no one location was designated correct more than twice in a row and each location was correct for 50% of the trials.

Food rewards included 2-cm cubes of cheese, pepperoni, Bil-Jac® Liver Treats, and Pet Botanics® dog food rolls.

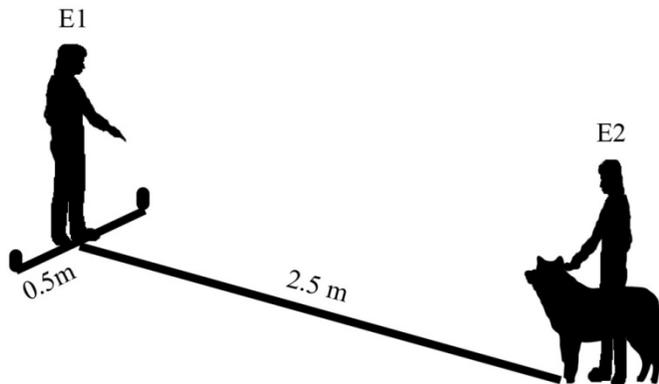


Figure 1. Testing layout for Experiments 1 and 2.

Table 1

*Name, Canid Type, Age, Sex, Breed, and Testing Order for Subjects in Experiment 1. All subjects had participated in a prior human-guided object choice task experiment prior to the start of this study. The point type and number of trials experienced is also listed.*

<b>Subject</b>	<b>Canid Type</b>	<b>Age (Years)</b>	<b>Sex</b>	<b>Breed</b>	<b>Testing Order</b>	<b>Prior Experiments Point Type (#) Trials</b>
Kalani	Gray Wolf	5	F	~	3	Momentary Distal (10)
Ruedi	Gray Wolf	5	M	~	2	Momentary Distal (10)
Renki	Gray Wolf	5	M	~	3	Momentary Distal (10)
Ayla	Gray Wolf	5	F	~	2	Momentary Distal (10)
Marion	Gray Wolf	9	F	~	1	Momentary Distal (10)
Woton	Gray Wolf	4	M	~	1	Momentary Distal (10)
Wolfgang	Gray Wolf	4	M	~	2	Momentary Distal (10)
Delta	Domestic Dog	7	F	Basset hound	1	Momentary Distal (10)
Jaxx	Domestic Dog	2.5	M	Labrador retriever	3	Momentary Distal (10)
Black Jack	Domestic Dog	1	M	Labrador retriever	2	Momentary Distal (10)
BJ	Domestic Dog	1.5	M	Jack Russell Mix	2	Dynamic Distal (10)
Moose	Domestic Dog	1.5	M	Labrador retriever	2	Static Touch (10)
Buster	Domestic Dog	6	M	Beagle	3	Dynamic Distal (10)
Lucky	Domestic Dog	9	F	Labrador retriever	1	Momentary Proximal (10)

**Pretraining Trials.** Once the subject was at the designated starting place in the testing area, next to the assistant E2, the experimenter called it by name until it oriented towards her. The experimenter then held up a piece of food in the subject's view and placed it on top one of the testing cans. The subject was released, allowed to approach, and eat the food. This was repeated three more times, totalling two food presentations on each can.

**Experimental Testing.** During experimental trials the subject was called back to the starting position by the assistant and was distracted with food or attention until the experimenter began the trial by calling the subject's name. Once the subject oriented towards the experimenter the condition-specific gesture was directed towards the target can and the subject was released to make a choice. If the subject approached the correct container the experimenter placed a piece of food on top for consumption while giving verbal praise. Incorrect choices, approaching the alternative can or neither can within a minute, had no direct consequences and the subject was called back to the starting position to begin the next trial.

If any individual made three incorrect responses in a row, two pretraining trials were given (one to each side) to ensure that the canid was still motivated to obtain the food if it saw the placement of the food directly. No individual ever failed a test of motivation within an experimental session.

The nine gesture types were divided over three sessions, each consisting of thirty total experimental trials, or ten trials of each of three gesture types. Breaks of at least an hour and no longer than two days were given between sessions. The duration varied based on an individual's immediate interest in food, determined by a willingness to eat the food if freely presented, and scheduling within the testing facilities. All gestures were given from a standing position, with the experimenter oriented and looking forward, and with the gesture remaining in place until the subject made a choice, unless otherwise noted. The nine gestures were defined as follows (Figure 2):

*Dynamic proximal point* – While kneeling, E1 extends her arm toward the target container and maintains a point with her finger 10 cm from the target.

*Bow* – While standing between the response objects, E1 orients and lowers her head and torso over the target container and stares at it.

*Body orient* – E1 turns and orients towards the target container.

*Asymmetric point* – E1 steps behind the incorrect container but points to the target container with her ipsilateral arm and hand (distal point, > 50 cm from target).

*Head turn* – E1 turns her head only and stares at the target container (also sometimes referred to as *gaze* in the broader literature).

*Back-turn distal point* – With her back turned to the subject, E1 extends her ipsilateral arm toward the correct container and maintains a point with her finger more than 50 cm from the target.

*Cross-body distal point* – E1 extends her arm across her body toward the cross-lateral target container. She maintains a point with her finger more than 50 cm from the target.

*Foot point* – E1 stands on one foot while pointing at the target container with her ipsilateral foot.

*Elbow point* – E1 tucks her fist against her chest — near her armpit — while sticking her elbow out towards the ipsilateral target container.

To reduce the potential for order effects across gesture types, different gesture orders were created and each point type was assigned a number. Gestures were divided into three session groups A, B, C. Session group A consisted of the dynamic proximal point (1), bow (2), and body orient (3). Session group B consisted of the asymmetric point (4), head turn (5), back-turn distal point (6). Session group C consisted of cross-body distal point (7), foot point (8), and elbow point (9). Gesture Orders were as follows, Order 1: B 4, 6, 5; C 7, 9, 8; A 1, 3, 2; Order 2: C 8, 9, 7; B 5, 6, 4; A 1, 3, 2;

Order 3: A 1, 3, 2; B 4, 6, 5; C 9, 7, 8. Order 1 was randomly generated and orders 2 and 3 were pseudorandomly generated to ensure counterbalancing of gesture order. Subjects were randomly assigned to a gesture order group (Table 1) with matching numbers of dogs and wolves experiencing each order type.

**Control Trials.** For each session the tenth and twentieth experimental trials were followed by one control trial and the thirtieth trial was followed by two control trials. This resulted in four control trials per experimental session, and twelve control trials total for each dog and wolf over the full three sessions of testing. On control trials a to-be-rewarded container was still determined, but the experimenter remained in a neutral position throughout the subject's approach and indication of choice. The presentation of food still followed a correct choice just as in experimental trials. This was done to assess whether other extraneous cues could explain above chance performance in addition to, or in the absence of, the intended gesture. Wolves averaged 5.57 (range 4:7) control trials correct out of 12, and dogs averaged six control trials correct out of 12 (range 4:8). No individual performed greater than would be expected by chance on control trials (Binomial test  $p \geq 0.19$ ), suggesting that success on the task during experimental trials could be attributed to the gesture under test and not to possible extraneous cues that might present in the absence of the gesture.

**Statistical Analysis.** One sample  $t$ -tests were used to determine if dogs or wolves as a group performed significantly better than would be expected by chance on a particular gesture type. To determine if an individual subject performed above chance when using a particular gesture binomial tests were conducted; success was measured as eight or more trials correct out of ten ( $p \leq 0.05$ ).

A two-factor ANOVA was used to compare the mean performance of dogs and wolves across gesture types and the performance of subjects when presented with the different forms of gestures. This test was followed up with  $t$ -tests, using a corrected alpha, to determine where significant differences existed when applicable. To determine if differences existed in the number of individual dogs and wolves meeting success criterion on the task, Fishers exact tests were conducted for each gesture type. All tests were two-tailed and had an alpha of 0.05 unless otherwise noted.

Session	Gesture Types		
A	 <p data-bbox="443 548 720 578">Dynamic proximal point (1)</p>	 <p data-bbox="1037 557 1129 586">Bow (2)</p>	 <p data-bbox="1507 561 1661 591">Body orient (3)</p>
B	 <p data-bbox="474 886 688 915">Asymmetric point (4)</p>	 <p data-bbox="1016 898 1148 927">Head turn (5)</p>	 <p data-bbox="1461 902 1713 932">Back-turn distal point (6)</p>
C	 <p data-bbox="447 1230 716 1260">Cross-body distal point (7)</p>	 <p data-bbox="1016 1239 1148 1268">Foot point (8)</p>	 <p data-bbox="1503 1235 1665 1265">Elbow point (9)</p>

Figure 2. Images of each of the nine gesture types used in Experiment 1, along with session and number designation.

## Results

As a group, wolves were able to successfully utilize six of the nine gesture types to locate the target object reliably (one-sample  $t$  tests,  $t(6) \geq 2.40$ ,  $p \leq 0.05$ ); these were the dynamic proximal point, bow, body orient, asymmetric point, back-turned distal point, and foot point. Dogs as a group utilized five of the nine gesture types (one-sample  $t$ -tests,  $t(6) \geq 2.91$ ,  $p < 0.05$ ); dynamic proximal point, bow, body orient, back-turned distal point, and cross-body distal point. In each of the gesture conditions at least one individual wolf and one individual dog was successful in using the gesture at above chance levels (binomial tests,  $p \leq 0.05$ ) with the exception of the head turn and elbow pointing gestures. For these conditions no individual wolf reliably located the target using the provided stimulus (binomial tests,  $p > 0.05$ ), however two out of seven dogs were able to utilize the head turn and three were able to use the elbow point. Average performances and number of individual successes for each gesture type can be found in Figure 3.

Overall there was no significant difference between the performance of the socialized wolves and pet domestic dogs on the human guided task (Two-factor ANOVA,  $F(1,12) = 3.73$ ,  $p = 0.08$ ), there was however a strong effect of gesture type (Two-factor ANOVA,  $F(8, 96) = 8.29$ ,  $p < 0.0001$ ) and the interaction between gesture and canid type (Two-factor ANOVA,  $F(8, 96) = 2.95$ ,  $p < 0.005$ ) on performance. As a group dogs outperformed wolves on two of the nine gesture types: Cross-body distal ( $t$ -test, Bonferroni-corrected alpha = 0.006,  $t(12) = 3.55$ ,  $p = 0.004$ ) and back-turned distal ( $t(12) = 3.47$ ,  $p = 0.005$ ). At the individual level, however, dogs only significantly outperformed wolves in the back-turned distal condition (Fishers exact test,  $p = 0.03$ ).

To test for generalization across gesture types the average number of trials correct was compared to the total number of trials experienced prior to the session regardless of gesture type. There was a moderate correlation between experience and performance on the task (Pearson correlation,  $r = 0.71$ ,  $p = 0.03$ ) however since performance was generally high across the board this likely limited the degree of improvement possible over trials.

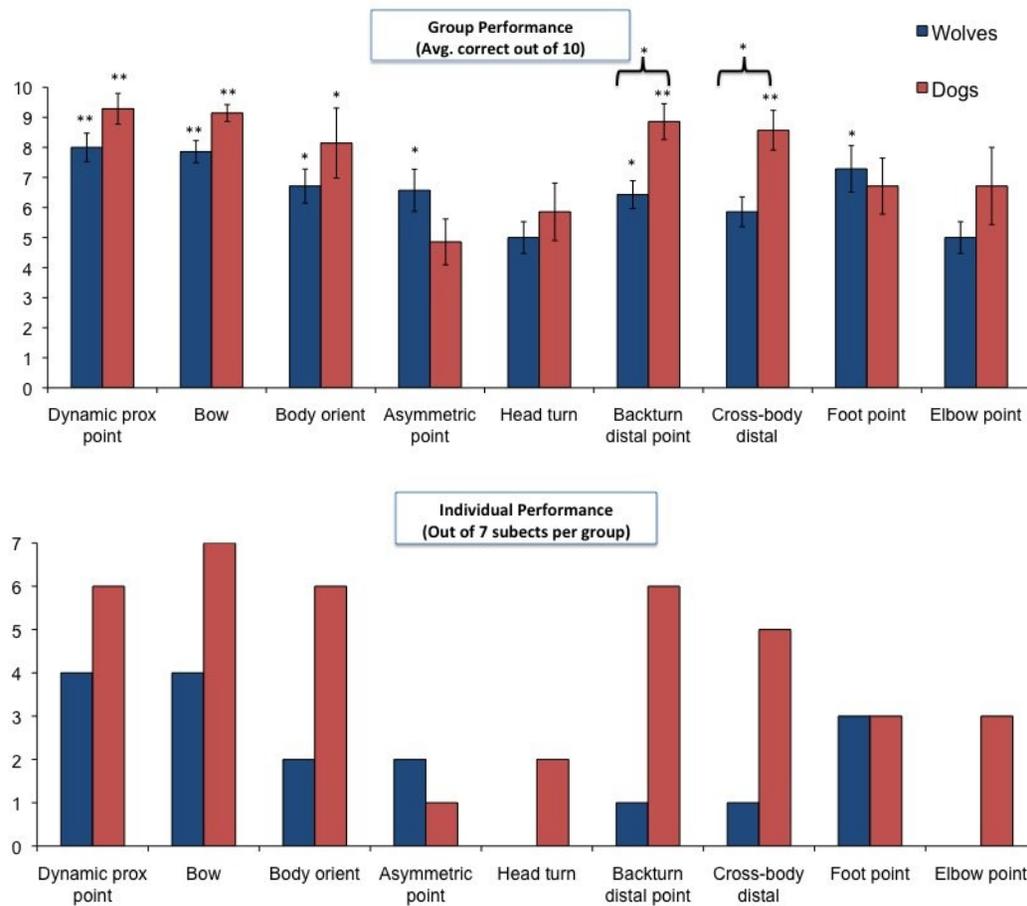


Figure 3. Mean performance and individual successes on the human-guided object-choice task across the nine gesture types utilized in Experiment 1. Top Panel: The average number of trials correct (out of ten) for each gesture is indicated by blue bars for wolves and red bars for dogs. Bottom Panel: The number of individuals in each group (out of 7) to successfully utilize a given gesture is illustrated by blue bars for wolves and red bars for dogs. An individual success was measured as eight or more trials correct out of ten (binomial test,  $p \leq 0.05$ ). Testblocks were as follows: A (dynamic proximal point, bow, body orient) B (asymmetric point, head turn, back-turn distal point) C (cross-body distal point, foot point, and elbow point).

\*  $p \leq 0.05$

\*\*  $p \leq 0.001$

A \* over a bracket represents a significant difference between dogs and wolves on a gesture type ( $t$ -test, Bonferroni-corrected,  $p < 0.005$ ).

## Discussion

The findings of this study unequivocally demonstrate that human-socialized wolves have the capacity to succeed on a wide range of gesture types beyond traditional points made with the human arm and hand. This is consistent with the recent findings that non-domesticated species of animal including canids are responsive to the gestures of humans given early socialization and regular interactions with humans (Gácsi, Gyori, et al., 2009; Udell, Dorey, et al., 2008; Von Bayern & Emery, 2009).

Dogs were also successful in utilizing most of the nine gesture types in the object-choice task. While their average performance was moderately better than that of the wolves on two-thirds of the point types, they only performed significantly better than wolves as a group when the gesture type was a back-turned distal point or cross-body distal point. Since wolves have been shown to match and even outperform domestic dogs on tasks requiring the use of a distal point in some cases (Udell, Dorey, et al., 2008), it would be interesting to further assess the importance of an experimenter turning her back or crossing her arm over her body in this type of task. More investigation into why some gestures are more salient than others for both dogs and wolves would also be useful. The variation in responsiveness to different gesture types seen in this study is consistent with the current literature (Gasci, Kara, et al., 2009; Miklosi et al., 2008; Udell, Dorey, et al., 2008) and factors ranging from development to prior experience to gesture size have been implicated as potential sources. However, more systematic study is necessary to identify which individual factors or combination of factors are most predictive of canid success in using specific gesture types. The important finding here, however, is that that human-socialized wolves and pet domestic dogs can share the same range of responsiveness across a variety of human gestures when both are provided equal opportunity and experience.

While testing conditions for both subspecies were kept as similar as possible, it is important to note two potential relevant factors in this study that may have influenced performance: (1) Wolves were necessarily tested outdoors, whereas dogs were tested indoors. (2) Since the dogs were pets and also enrolled in a doggie daycare their total exposure to humans on a daily basis was much greater than that of the wolves. In fact it was likely greater than that of many dogs tested in previous studies as well. The outdoor-indoor difference in testing location was chosen for this study because Udell, Dorey, et al. (2008) found that pet dogs tested outdoors showed a substantial decrement in performance in comparison to those tested indoors. When Udell, Dorey, et al. (2008) tested dogs and wolves with a momentary distal point the most comparable groups were the pet dogs tested indoors and wolves tested outdoors. This may be because the majority of pet dogs tested live and interact with humans primarily indoors, whereas the wolves live and interact with humans primarily outdoors. Therefore while it is possible that distractions inherent to an outdoor testing environment could lead to a decrement in performance for wolves, these two testing locations promised to provide the most functionally equivalent starting point for comparing performance across gesture types in this study based on past findings.

It should also be noted that the population of dogs utilized in this study, while denoted as pets, could in fact represent a distinct subgroup of pet dogs. Many pet dogs spend hours of each day alone while their owners go to work, run errands, or engage in other dogless activities. However the dogs in this study were regulars at a doggie daycare that provided around the clock contact and supervision by humans. It is possible that these dogs are even more prepared to succeed on human guided tasks given this additional exposure. Differences of this type may account for some of the variation between individual dogs on human guided tasks. They might also account for a proportion of the differences in performance seen between wolves and dogs in this study, and possibly previous studies, as different durations and types of interaction experienced with human caregivers prior to testing might be an important variable in such experiments.

While the current study demonstrated that individual human-socialized wolves, known to respond to some human-gestures, were capable of responding to diverse human stimuli, another important question remains: Do other non-domesticated human-socialized canid species demonstrate proficiency in utilizing human gestures to locate a target?

## **Experiment 2. A Preliminary Test of Coyote (*Canis latrans*) Performance on a Human-Guided Object-Choice Task**

Experiment 1 demonstrated that the range of gestures that may be utilized by a subspecies of non-domesticated canid, specifically socialized wolves, is wider than previously thought. In Experiment 2 we asked if the range of non-domesticated canids with the capacity to utilize human gestures might be broader than previously established as well. To our knowledge coyotes have never served as subjects in a human-guided object-choice task. Therefore a preliminary test was conducted with two human-socialized coyotes using a momentary distal point as the stimulus.

### **Method**

**Subjects.** Two coyotes (*Canis latrans*) served as subjects in this experiment. Willow was a 1.5-year-old female, and Twister was a 1.5-year-old male at the time of testing. Both coyotes had been hand raised at Wolf Park where they were socialized to humans in the same manner as the wolves in Experiment 1, using the methods established by Klinghammer and Goodmann (1987). Willow and Twister lived together in an outdoor enclosure, and were exposed to humans daily. They were able to engage in direct interactions with familiar caretakers inside their enclosure and would readily eat food from their hands.

**Testing Layout and Materials.** A familiar experimenter, who had been trained to conduct an object-choice task prior to testing, served as the demonstrator for each coyote. The experimenter was located inside the coyotes' home enclosure during testing; no barrier was present between subject and experimenter. To allow each subject to be tested individually in its home cage, the coyote not under test was temporarily relocated to a separate holding area until it was its turn to be tested. The testing layout was the same as in Experiment 1 (see Figure 1). As in Experiment 1 the subject was led into the testing area by an assistant, E2, who walked to a marked spot 2.5 m back from the experimenter, E1. The experimenter stood between the two response objects, which were located on the ground 0.5 m to either side of him. Two cylindrical metal empty unmarked paint cans (15 cm diameter, 22 cm tall), filled with gravel and with lids tightly fastened, served as the response

choice objects. No food was present in or on either container until and unless the subject indicated a choice of the correct can by touching or coming within 10 cm of it with its snout. The correct container was determined pseudorandomly before sessions, subject to the constraints that no one location was designated correct more than twice in a row and each location was correct for 50% of the trials.

Food rewards included 2-cm cubes of cheese, pepperoni, Bil-Jac® Liver Treats, and Pet Botanics® dog food rolls.

**Pretraining and Experimental Trials.** Pretraining and experimental trials were conducted in the same manner as described in Experiment 1, with the exception that each subject only received ten trials of a single gesture type: A momentary distal point. In an object-choice task utilizing a momentary distal point, the experimenter extends his arm toward the target container while the subject watches and maintains a point with his finger 50 cm from the container for 4 s. The experimenter then returns to a neutral position and the subject is released to make its choice. This point type is typically considered a standard in the field, and is recognized as a challenging stimulus that can be used to discriminate between individuals and species that differ in responsiveness to human cues (Miklósi et al., 2003; Udell, Dorey, et al., 2008).

**Control Trials.** Each coyote was presented with six control trials total. A single control trial was presented after experimental trials one, two, four, six, eight, and ten. During control trials a to-be-rewarded container was still determined, but the experimenter remained in a neutral position throughout the subject's approach and indication of choice. The presentation of food still followed a correct choice just as in experimental trials.

**Statistical Analysis.** Due to the small number of subjects available for this preliminary study, the performance of each subject was analyzed independently. Binomial tests were used to determine if each coyote scored above chance on the task. Success was measured as eight or more trials correct out of ten ( $p \leq 0.05$ ).

## Results

Willow followed the experimenter's point to the target container during seven out of the ten experimental trials she was presented with. During trials one, nine, and ten she failed to make a choice within one minute, therefore those trials had to be scored as incorrect. While her performance was not statistically above chance (binomial test,  $p = 0.17$ ) she showed a definite trend towards point following, especially given that she never actively approached the incorrect container during an experimental trial.

Twister's performance was statistically better than would be expected by chance. He approached the correct container on nine out of ten experimental trials (binomial test,  $p = 0.01$ ), demonstrating a clear and spontaneous mastery of the task.

Both coyotes performed below chance on control trials making it unlikely that extraneous cues, or stimuli beyond the experimental stimulus, would have aided performance during experimental testing. Willow only chose correctly in one of her six control trials, and refused to approach either container within one minute during three control trials. Twister selected the correct container during two of his six control trials, and refused to choose during one. It is not surprising that both individuals did not make a choice on some control trials, as no programmed stimulus was present to direct their behaviour to the correct container. Dogs often show a similar response when the stimulus is absent or unclear (e.g., Udell et al., 2010a).

## **Discussion**

While human-socialized coyotes may not be as common or as easily accessible as socialized dogs or wolves, our current data suggest that they provide another potential out-group for understanding the evolution and development of success on human-guided tasks. Both individuals performed well, and one clearly exceeded chance performance on the task, even in the presence of what is considered a challenging stimulus type, the momentary distal point. Willow's failure to make a choice during three of the ten experimental trials may have been due to her failure to comprehend the stimulus; on the other hand, in working with coyotes it quickly became clear that they are high energy and become distracted more quickly than wolves and dogs under the same conditions. Therefore it is also possible that environmental distractions inherent to an outdoor testing environment played a greater role for this species. Future studies need to be conducted using coyotes to determine what factors contribute to success or failure across individuals within the species, such as socialization, experience, testing environment, and even methodology. However, here we provide the first evidence that coyotes represent yet another non-domesticated canid species with the capacity to respond to human gestures given socialization to humans early in life.

## **General Discussion**

In any comparative endeavour there is a chance that some species or groups will receive more attention from the scientific community than others, possibly resulting in larger subject numbers, a greater diversity of stimuli, or wider range of methods tested and utilized. When this occurs it is often tempting to point towards the many examples of success found in a focal species to support predictions of unique capabilities or diverged cognitive skills. Resulting comparisons rest on the assumption that all other animals/outgroups were equally represented when in practice this is often not the case. For canines this has resulted in claims that dogs are more like humans than are wolves in terms of certain social skills (Hare et al., 2002; Miklósi et al., 2003). However when wolves are human-socialized (Gácsi, Gyori, et al., 2009; Udell, Dorey, et al., 2008; Virányi et al., 2008) and are tested in a more equivalent manner to pet dogs (e.g., Udell, Dorey, et al., 2008) they often perform well on human guided tasks (Gácsi, Giglio, et al., 2009; Udell, Dorey, et al., 2008a). Furthermore, domestic dogs' spontaneous success on human guided tasks does not appear to extend to all populations of domestic dog (Udell et al., 2010a). The findings of our current study demonstrate that canid responsiveness to human stimuli is less restricted than previously thought: wolves have the capacity to respond to a wide range of human gestures and human-socialized coyotes demonstrate some level of responsiveness as well. While these findings might contradict previous thought about canid responsiveness to human gestures they do not clash with previous data; instead this study provides new data on a wider range of stimuli and a species previously lacking from the literature. Other holes critical for phylogenetic analysis (with regard to species proficiency or range of sensitivity) may still exist. Work

demonstrating successful point following in dingoes (Smith & Litchfield, 2009) and non-domesticated foxes (Hare et al., 2005) lends additional support to the idea that there is more to be learned about the behavior of domestic dogs' genetic relatives before solid claims about the evolutionary origins of social responsiveness in pet dogs can be made.

Another important consideration is the large amount of variability in performance; not only within and between subspecies, but within and between individual subjects as well. While a species' or subspecies' capacity to utilize a particular gesture can be demonstrated by a single individual's success on the task, this is not in practice sufficient to reliably predict the performance of other individuals in the presence of the same stimulus, or the same individual in the presence of a different human stimulus. While both dogs and wolves demonstrated the capacity to successfully utilize most gesture types in Experiment 1, there was at least one individual dog and wolf for each gesture type that failed to locate the target at above chance levels. Previous studies have shown that individual responsiveness to human gestures is readily modified by life experience (Bentosela et al., 2008; Elgier, Jakovcevic, Mustaca, & Bentosela, 2009; Udell et al., 2010a) therefore it is likely that much of this variation is due to prior individual experience and learning history. Previous studies have also suggested that physical properties of the gestures themselves, such as size and animation, may influence performance (Udell, Dorey, et al., 2008). However, even in studies using standard human point types, such as the momentary distal point, focusing on average scores alone may give a deceiving impression of a species' or group's spontaneous success on a task. Recently Gácsi, Kara, et al. (2009) showed that out of 180 dogs tested on a human guided object-choice task utilizing a momentary distal point as a stimulus, fewer than half of the dogs were individually successful in following the point. The group's average performance, however, was above chance demonstrating the stark dichotomy that often exists between mean data and the behavior of individual members of the group. In fact many individual dogs fail to spontaneously follow a momentary distal point (e.g., Udell, Dorey, et al., 2008; Udell et al., 2010a). However Udell et al. (2010a) demonstrated that a failure to spontaneously utilize a particular gesture does not imply an inherent socio-cognitive deficit or the absence of the capacity to utilize that gesture. Instead dogs from populations that routinely fail to utilize the momentary distal pointing gesture, such as shelter dogs, can often learn to utilize the point rapidly if reinforcement is made contingent on a specific response. In fact half the dogs in that study began following the point reliably after only 15 additional presentations of the stimulus (25 pointing demonstrations total). Thus demonstrating that individuals from different populations and species are capable of responding to different gestures or stimuli is just the first step, albeit an important one. Environmental factors and the life experiences of the individuals under test are also significant variables that require consideration.

The findings demonstrated here may hold true for other species outside the Canidae family as well; only time and more comparative investigations will tell. Therefore, when animals cannot be treated equally, in terms of method, number, or range, comparative interpretations should be made carefully (1) allowing for the possibility that a wider range of individuals or species might match the cognitive or behavioural capacities of the target species under more comparable conditions,

and (2) that the testing of new individuals or conditions might result in the expression of behaviour in a species for which an untapped capacity existed all along.

## 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*, 107-112. doi:10.1007/s100710000070
- Bentosela, M., Barrera, G., Jakovcevic, A., Elgier, A. M., & Mustaca, A. E. (2008). Effect of reinforcement, reinforcer omission and extinction on a communicative response in domestic dogs (*Canis familiaris*). *Behavioural Processes*, *78*, 464-469. doi:10.1016/j.beproc.2008.03.004
- Coppinger, R., & Coppinger, L. (2001). *Dogs: A startling new understanding of canine origin, behavior & evolution* (1st ed.). New York, NY: Scribner.
- Dorey, N. R., Udell, M. A. R., & Wynne, C. D. L. (2010). When do domestic dogs, *Canis familiaris*, start to understand human pointing? The role of ontogeny in the development of interspecies communication. *Animal Behaviour*, *79*, 37-41. doi:10.1016/j.anbehav.2009.09.032
- Elgier, A. M., Jakovcevic, A., Mustaca, A. E., & Bentosela, M. (2009). Learning and owner-stranger effects on interspecific communication in domestic dogs (*Canis familiaris*). *Behavioural Processes*, *81*, 44-49. doi:10.1016/j.beproc.2008.12.023
- Gácsi, M., Gyori, B., Virányi, Z., Kubinyi, E., Range, F., Belenyi, B., & Miklósi, A. (2009). Explaining dog wolf differences in utilizing human pointing gestures: Selection for synergistic shifts in the development of some social skills. *PLOS One*, *4*, e6584. doi:10.1371/journal.pone.0006584
- Gácsi, M., Kara, E., Belenyi, B., Topal, J., & Miklósi, A. (2009). The effect of development and individual differences in pointing comprehension of dogs. *Animal Cognition*, *12*, 471-479. doi:10.1007/s10071-008-0208-6
- Giret, N., Miklósi, A., Kreutzer, M., & Bovet, D. (2008). Use of experimenter-given cues by African gray parrots (*Psittacus erithacus*). *Animal Cognition*, *12*, 1-10. doi:10.1007/s10071-008-0163-2
- 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*, 341-346.
- Hare, B., Brown, M., Williamson, C., & Tomasello, M. (2002). The domestication of social cognition in dogs. *Science*, *298*, 1634-1636. doi:10.1126/science.1072702
- Hare, B., Plyusnina, I., Ignacio, N., Schepina, O., Stepika, A., Wrangham, R., & Trut, L. (2005). Social cognitive evolution in captive foxes is a correlated by-product of experimental domestication. *Current Biology*, *15*, 226-230.
- Hare, B., & Tomasello, M. (2005). Human-like social skills in dogs? *Trends in Cognitive Sciences*, *9*, 439-444. doi:10.1016/j.tics.2005.07.003
- 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*, 11-18. doi:10.1016/j.anbehav.2004.05.008
- 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. 31-61). Dordrecht, The Netherlands: W. Junk
- Lehner, P. N. (1976). Coyote behavior: Implications for management. *Wildlife Society Bulletin*, *4*, 120-126.

- Lindblad-Toh, K., Wade, C. M., Mikkelsen, T. S., Karlsson, E. K., Jaffe, D. B., Kamal, M., Clamp, M., ...Lander, E. S. (2005). Genome sequence, comparative analysis and haplotype structure of the domestic dog. *Nature*, *438*, 803-819. doi:10.1038/nature04338
- McKinley, J., & Sambrook, T. D. (2000). Use of human-given cues by domestic dogs (*Canis familiaris*) and horses (*Equus caballus*). *Animal Cognition*, *3*, 13-22. doi:10.1007/s100710050046
- Miklósi, Á., Kubinyi, E., Topál, J., Gácsi, M., Virányi, 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. doi:10.1016/S0960-9822(03)00263-X
- Miklósi, Á., Polgardi, R., Topál, J., & Csányi, V. (1998). Use of experimenter-given cues in dogs. *Animal Cognition*, *1*, 113-121. doi:10.1007/s100710050016
- Miklósi, Á., Pongrácz, P., Lakatos, G., Topál, J., & Csányi, V. (2005). A comparative study of the use of visual communicative signals in interactions between dogs (*Canis familiaris*) and humans and cats (*Felis catus*) and humans. *Journal of Comparative Psychology*, *119*, 179-186. doi:10.1037/0735-7036.119.2.179
- Miklósi, Á., & Soproni, K. (2006). A comparative analysis of animals' understanding of the human pointing gesture. *Animal Cognition*, *9*, 81-93. doi:10.1007/s10071-005-0008-1
- 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*, 160-171.
- Reid, P. J. (2009). Adapting to the human world: Dogs' responsiveness to our social cues. *Behavioural Processes*, *80*, 325-333. doi:10.1016/j.beproc.2008.11.002
- Riedel, J., Schumann, K., Kaminski, J., Call, J., & Tomasello, M. (2008). The early ontogeny of human-dog communication. *Animal Behaviour*, *75*, 1003-1014.
- Scheumann, M., & Call, J. (2004). The use of experimenter-given cues by South African fur seals (*Arctocephalus pusillus*). *Animal Cognition*, *7*, 224-230. doi:10.1007/s10071-004-0216-0
- Schloegl, C., Kotrschal, K., & Bugnyar, T. (2007). Do common ravens (*Corvus corax*) rely on human or conspecific gaze cues to detect hidden food? *Animal Cognition*, *11*, 231-241. doi:10.1007/s10071-007-0105-4
- Scott, J. P., & Fuller, J. L. (1965). *Genetics and the social behavior of the dog* (1st ed.). Chicago, IL: University Of Chicago Press.
- Smith, B. P., & Litchfield, C. A. (2009). Dingoes (*Canis dingo*) can use human social cues to locate hidden food. *Animal Cognition*, *13*, 367-376. doi:10.1007/s10071-009-0287-z
- Soproni, K., Miklósi, A., Topál, J., & Csányi, V. (2002). Dogs' (*Canis familiaris*) responsiveness to human pointing gestures. *Journal of Comparative Psychology*, *116*, 27-34.
- Trut, L. N., Plyusnina, I. Z., & Oskina, I. N. (2004). An experiment on fox domestication and debatable issues of evolution of the dog. *Russian Journal of Genetics*, *40*, 644-655. doi:10.1023/B:RUGE.0000033312.92773.c1
- 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. doi:10.1016/j.anbehav.2008.07.028
- Udell, M. A. R., Dorey, N. R., & Wynne, C. D. L. (2010a). The performance of stray dogs (*Canis familiaris*) living in a shelter on human-guided object-choice tasks. *Animal Behaviour*, *79*, 717-725. doi:10.1016/j.anbehav.2009.12.027

- Udell, M. A. R., Dorey, N. R., & Wynne, C. D. L. (2010b). What did domestication do to dogs? A new account of dogs' sensitivity to human actions. *Biological Reviews*, 85, 327-345. doi:10.1111/j.1469-185X.2009.00104.x
- Udell, M. A. R., Giglio, R. F., & Wynne, C. D. L. (2008). Domestic dogs (*Canis familiaris*) use human gestures but not nonhuman tokens to find hidden food. *Journal of Comparative Psychology*, 122, 84-93. doi:10.1037/0735-7036.122.1.84
- Virányi, Z., Gácsi, M., Kubinyi, E., Topál, J., Belényi, B., Ujfalussy, D., & Miklósi, Á. (2008). Comprehension of human pointing gestures in young human-reared wolves (*Canis lupus*) and dogs (*Canis familiaris*). *Animal Cognition*, 11, 373-387. doi:10.1007/s10071-007-0127-y
- von Bayern, A. M. P., & Emery, N. J. (2009). Jackdaws respond to human attentional states and communicative cues in different contexts. *Current Biology*, 19, 602-606. doi:10.1016/j.cub.2009.02.062