**RUNNING HEAD: UDELL & WYNNE: Response to Hare et al. (2009)**

# Ontogeny and phylogeny both are essential to human-sensitive behavior in the genus *Canis*

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**Abstract**

In this paper we respond to Hare et al.'s (in press) critique of our prior work. We agree with Hare et al. that dogs (*Canis lupus familiaris*) have a remarkable sensitivity to human actions, and that the wolves (*C l lupus*) tested in Udell et al. (Animal Behaviour, 76, 1767-1773) were successful in following a human point because of their intensive socialization to humans. However, *contra* Hare et al. (in press) we maintain that neither a distinct co-evolutionary history of dogs and humans nor genetic domestication alone can account for the success of any canids in responding to human cues. Ontogeny is an equal partner with phylogeny in the expression of any phenotypic character. Hare et al.'s attempts to show that past studies have adequately controlled for the odor of food in the pointed-to container fail to convince. Their claims that wolves raised identically to dogs do not follow human points overlook the many procedural differences in the treatment of these two species of canid in prior studies, including the presence of a barrier between subject and experimenter and differing living conditions during adulthood. Their argument that dogs reared without human contact are still successful in following human cues are undermined by the fact that no such dogs have ever been tested. Hare et al.'s reanalysis of our data does not change the fact that more wolves were successful on the task than pet dogs, nor that dogs held at a shelter were completely unsuccessful. Hare et al.'s data from dogs held at a shelter contribute little to this debate because the dogs were tested on a simpler form of point.

In responding to Hare, Rosati, Kaminski, Bräuer, Call & Tomasello (in press), we wish to start by outlining our substantive areas of agreement. We do not disagree that pet domestic dogs (*Canis lupus familiaris*) have a remarkable sensitivity to human actions, gestures, and intentional movements. We also agree with Hare et al., that the most likely reason why the wolves tested in Udell, Dorey & Wynne (2008) were so responsive to human pointing gestures was because these animals were "highly socialized [and] [t]his socialization probably gave [these] subjects significant experience responding to actions similar to human pointing, whether the animal handler was aware of this type of exposure or not"( Hare et al. in press, p. xxx). In that paper we argued that "that environment and development affect a social animal's ability to react in situation appropriate ways to the social cues of other individuals" (Udell et al. 2008, p. 1772).

The crux of our disagreement with Hare et al. lies in our belief that socialization and experience are essential for ***all*** canids to respond to hetero- and con-specific cues. Since at least the 1920s scientists have recognized that heredity alone is insufficient to fully explain a phenotype. Phenotypes can only be characterized as the outcome of a complex interaction between heredity, development and environment (Gottlieb 2002). Unfortunately development and environment receive short shrift in the domestication hypothesis as presented by Hare et al. (in press). To be clear, we do not deny an influence of heredity or domestication on the social behavior of domestic dogs, we simply do not agree that a hypothesis based on genetic inheritance alone is viable without consideration of the interacting developmental and environmental variables that are necessary for the expression of any phenotype. Ontogeny plays just as important a role in dogs' responding to human cues as it does when dogs to respond to dog cues (or indeed when humans to respond to human cues, e.g., Behne, Carpenter, & Tomasello 2005). Pet dogs have early experience during their critical period for socialization which enables them

to accept humans as social companions, and they have ongoing exposure to humans who control access to things that are important to dogs' survival and reproduction. This relationship between humans and dogs is just as important in understanding dogs' sensitivity to humans as any considerations of phylogeny. Critical life experiences cannot be shoved aside by the brute fact of genetic domestication alone. None of the arguments marshaled by Hare et al. (in press) convince us otherwise.

Our response is organized to match Hare et al.'s commentary. First we respond to their review of the literature on dogs', wolves' and foxes' sensitivity to human cues. Second we discuss their reanalysis of our data comparing the performance of wolves and dogs in responding to a human pointing gesture (Udell et al. 2008). Third we consider the data on dogs living in a shelter reported in Hare et al. (in press). Fourth we comment briefly on Hare et al.'s response to Wynne et al.'s (2008) reanalysis of Riedel et al.'s (2008) data on the development of following human points in dog pups, before concluding with some general comments on the roles of ontogeny and phylogeny in the expression of complex interspecies social behaviors.

## PROBLEMS WITH HARE ET AL.'S REVIEW OF THE LITERATURE

The most common form of test of a dog's ability to utilize cues given by humans involves a human pointing at one of two containers. Choice of the pointed-to container will be rewarded with a small piece of food: choice of the other container is not rewarded. In many cases the target container is pre-baited, containing the food reward before the beginning of the trial. Given that dogs are renowned for their sense of smell (e.g., Oxley & Waggoner 2009), an obvious initial question in considering the results of such studies is whether the dogs under test might not simply identify the baited container by smell alone.

Hare et al. (in press) claim that prior studies of dogs' responsiveness to human communicative behaviors have included "controls [that] rule out the use of olfactory cues; Cooper et al. 2003; Hare & Tomasello 2005; Miklosi & Soproni 2006)" (p. xxx). In fact, none of the three studies cited, just like the vast majority of other studies on this issue, report any controls for olfactory cues. Hare and Tomasello (2005) and Miklosi and Soproni (2006) are both review papers that report no original experiments or results. Miklosi and Soproni do not discuss the issue of possible olfactory cueing, and Hare and Tomasello simply state that prior studies had controlled for odor cues. Cooper et al. (2003) reported two experiments in which dogs selected between humans in order to obtain food rewards. Neither experiment includes report of any odor controls. Indeed even the new data presented by Hare et al. (in press) in their commentary include no controls for odor cuing. The absence of controls for the possibility that canids are identifying the baited container in these experiments by smell is especially worrisome in light of the fact that Szetei, Miklosi, Topal, and Csanyi (2003) demonstrated that dogs rely on odor cues when they are available in tasks of this type. We previously found that a wolf could locate an accessible piece of food in one container by odor, consistently approaching the container with accessible food, even if another container was present that contained the same amount of food buried under several cm of stones (Udell et al. 2008).

Hare et al. (in press) argue that wolves can only follow human communicative gestures if they are explicitly trained to do so, whereas dogs have a spontaneous ability to follow points, and they cite Agnetta et al. (2000), Hare et al. (2002) and Viranyi et al. (2008) to support that claim. Furthermore they claim that this dependency of wolves but not dogs on explicit training has been demonstrated in wolves "reared in identical conditions with a group of dogs for the purpose of comparing their social skills with humans" (p. xxx). We do not accept this as an accurate

summary of the prior studies on wolves. Both Agnetta et al. (2000) and Hare et al., (2002) tested the ability of adult wolves to follow the pointing gesture of a human towards a baited food container where the human stayed outside the animal's enclosure. To further add to the difficulty of the task, the wolves tested in Agnetta et al. had to move between three cages to get to the locations of the containers. In both studies the wolves were on average not successful in following the human point to find food, though individual results were not presented. We have already demonstrated (Udell et al. 2008) that having to follow a point through a fence substantially limits the abilities of dogs. Thus it is reasonable to assume that the presence of the fence barrier - which is never deployed by these authors in their studies on dogs - accounts for the poor performance of the wolves on these tests.

Viranyi et al. (2008) come closer to achieving a balanced comparison of dogs and wolves. Viranyi et al., unlike Agnetta et al. (2000) and Hare et al. (2002), reared their wolf and dog pups from birth, and they tested the animals before maturity (four months) as well as at seven months of age. While dogs followed a momentary distal point at four months of age, wolf pups performed at chance levels. At seven months, and after extensive experience with the task, wolves began to perform at the level of naive dogs. Unfortunately for an effective comparison however, the wolf pups, but not the dogs, were removed from human homes between two and four months of age and thereafter reared at a private "wolf farm" where they were visited by their human rearers for only half a day, twice per week. The fact that the experiences of the wolves involved considerably less human contact after two months of age than the dogs, means that this study cannot achieve its purpose of a direct comparison of wolf and dog pups raised under identical conditions.

We do not doubt that there are wolves - the vast majority of wolves in fact - which do not follow human points. Our demonstration that a subgroup of wolves can follow human points without explicit training - recently replicated by Gacsi et al. (2009) - demonstrates that the potential to develop responsiveness to human cues exists in non-domesticated canids. No number of demonstrations of wolves that fail to follow human points would contradict this finding.

Hare et al. (in press) cite Hare et al.'s (2005) study of Balyaev's foxes and control wild-type foxes as further evidence that wild-type canids are incapable of following human pointing gestures. Balyaev (see e.g., Trut 1999) bred foxes for over 40 generations for tolerance of humans (reduced flight distance to human approach). Hare et al. (2005) tested Balyaev's and wild-type control foxes for their ability to follow a human point to locate food hidden in one of two containers. Importantly *both* groups of foxes scored significantly above chance, however the Balyaev's foxes attained a higher level of performance than the wild foxes (though only on a one-tailed statistical test). We have drawn attention elsewhere (Udell et al. in press) to the fact that matching the Balyaev's and wild-type foxes by chronological age in fact introduces a confound into the comparison. One of the major impacts of the artificial selection for tameness in Balyaev's foxes is a lengthening of the critical window for socialization (Trut, Plyusnina, & Oskina 2004). Thus the finding that Balyaev's foxes follow human points at a marginally higher level than non-human-socialized wild-type foxes is probably due to their developmental trajectories, including differences in developmental stage at the time of testing, and not simply a function of their phylogenetic histories (see Udell et al. in press for a thorough review of this confound).

Hare et al. (in press) further argue that "dogs develop their ability to use human communicative cues, such as pointing cues or gaze cues, as young puppies regardless of rearing history." Hare et al. (2002) tested dog pups ranging in age from 9 to 26 weeks, some of whom had lived in human families while others, "lived their entire lives with litter-mates in a kennel and so had been exposed to humans for only a few minutes each day for husbandry purposes." (p. xxx). Hare et al. reported that even the youngest age group (9 to 13 weeks) of pups experiencing "minimal" human contact were successful at following a human pointing gesture to find food at above chance levels - scoring an average of around 15 out of 18 trials correct. However one important problem with Hare et al.'s interpretation of this data (2002) is that it is simply not the case that the kennel-reared pups had experienced only minimal human contact. The pups were obtained from Pik a Pup kennels in Holliston MA. This establishment breeds dogs for placement as pets in human homes. They describe their pups as "a new family member who will give unconditional love for years to come" (http://pikapup.com/index.php), and report that both employees and customers interact with the pups on a daily basis.

Dog pups not socialized to human company are rare in modern Western societies where the majority of dogs have a close bond to humans (New et al. 2004). Since dog pups imprint easily on humans during their long critical window for social development (up to 16 weeks: Coppinger & Coppinger 2001), and are usually around people during the first four months of life, it is actually quite difficult to rear a dog that is not socially imprinted on humans. No responsible breeder would intentionally rear such animals, and it is unlikely that rearing unsocialized dogs would be tolerated by animal experimentation ethics committees in the Western world today. Fifty years ago, Scott and Fuller (1965) reared a small number of

completely unsocialized dogs and reported that these animals "… later react toward [humans] with extreme fear and hostility" (p. 176).

We have already commented on the results obtained by Riedel et al. (2008) in Wynne et al. (2008). Since Hare et al. (in press) raise issues with our re-analysis of Riedel et al.'s data, we dedicate a separate subsection to this study below. Suffice it to say here that this study offers clear evidence that dogs' ability to follow human cues improves with age (Wynne et al. 2008).

## REANALYSIS OF UDELL ET AL. (2008): WOLVES ARE STILL MORE SKILLED THAN DOGS

Hare et al. (in press) raise several questions about the methodology by which we compared the performance of wolves and several groups of dogs in their ability to follow human points in Udell et al. (2008).

Their first criticism is that "Unlike Hare et al. (2005) and Viranyi et al. (2008), none of the subjects [in Udell et al. 2008] were reared for the purposes of the experiment." While it is true that Viranyi et al. (2008) reared their wolves for the purpose of their experimental test, this is the exception in the literature, not the rule. In a recent review, we analyzed the performance of dogs following human points from 14 published papers (Dorey et al. 2009). In not one of these papers were the dogs specially raised by the experimenters - rather they were all pets volunteered for testing by their owners.

Furthermore, the fox and dog subjects in Hare et al. (2005) and the wolf and dog subjects in Hare et al. (2002) were also not reared for the purpose of the experiments. The wolves Hare et al. (2002) utilized resided at Wolf Hollow, an educational establishment not dissimilar from Wolf Park where the wolves tested in Udell et al. (2008) were living. The wolves were reported

to be adults at the onset of the experiment and there is no evidence that they were reared specifically for Hare et al.'s experiment. The dog subjects used in the same study were pets and dogs intended to be sold as pets: none was reported to be reared by the experimenters for the purpose of the experiment. The foxes tested by Hare et al. (2005) were part of the stock of the Balyaev fox farm at the Russian Academy of Sciences, Institute for Cytology and Genetics, and were also not reared for Hare et al.'s (2005) experiments (see Hare et al. 2005, supplemental material). Despite the fact that none of the canids was reared for the purpose of these experiments, Hare et al. (in press) do not hesitate to use these data as support for the domestication hypothesis.

If what Hare et al. (in press) really meant was that the foxes and wolves tested by Hare et al (2002; 2005) were reared in a research facility that raised their animals in a specific and known way, although *not actually* reared for the *purpose* of the experiment, then the same is true of the wolf subjects used in Udell et al. (2008).

It appears that the crux of this critique is not really about special rearing of animals for testing but rather with the amount of socialization and experience with humans our wolf subjects may have received in comparison to previously tested undomesticated canids. Hare et al. state: "In fact, we suspect that, given their use in public education programs, the wolves that Udell and colleagues tested probably had received previous training and were highly socialized. **This socialization probably gave their subjects significant experience responding to actions similar to human pointing, whether the animal handler was aware of this type of exposure or not.** Udell et al. (2008) cannot rule out this type of simple exposure explanation for the success of their adult wolves based on the current data." (p. xxx emphasis added).

We do not disagree that the wolves we tested were more successful than those tested in prior studies because they had been more effectively socialized to humans. This was precisely our point in Udell et al. (2008). Discussions with the wolves' caregivers assured us that the wolves tested had not experienced explicit training on following points, but we consider it highly likely that their daily experiences with humans had led them to attend to the movement of human hands in anticipation of food and other rewards. We also agree that this attentiveness to human limb movements is likely to occur in environments where canids have daily interactions with humans - whether the handler is aware of it or not. Research and education facilities where wolves are effectively socialized to humans and continue to receive daily interaction with humans throughout their lives, just like dogs living in human homes, are candidates for such exposure.

Hare et al. (in press) are also concerned about our use of response objects (closed paint cans), that did not conceal food prior to the subject making a choice. As we stated in Udell et al. (2008): "This method was adopted because preliminary studies with wolves indicated that they could detect even small pieces of pre-hidden food in a container by smell alone" (Udell et al. 2008, p. 1769). We have already discussed the paucity of controls for odor cuing in the extant literature. Since our methodology was consistent across all groups, differences in performance between canid types cannot be explained by our use of this methodology.

Two other criticisms were raised about our methodology: 1. The use of a clicker and 2. The use of warm-up trials. A clicker is a device that simply makes a consistent "click" sound, much like the sound of opening a soda can. This sound was a tool to reduce the effects of reinforcer delay since food was not immediately accessible as it is in the traditional

methodology. None of the subjects in our experiment received prior training on the experimental task with or without the use of a clicker. Our use of the term "naive" was intended to convey that no such training had taken place.

Second, our use of warm-up trials to familiarize the subjects with the response objects and to test for motivation is not "unlike all previous studies" (Hare et al. in press, p. xxx). Such warm up trials have been used since the first experiment of this type conducted with dogs (Miklosi et al 1998). The experiment on shelter dogs reported in Hare et al.'s critique (in press) itself includes similar warm-up trials. The only identifiable difference from our warm-up procedure and that of other researchers is that we placed food on top of the response objects during warm-up trials rather than in or under the response object. Since the purpose of warm-up trials is simply to test for food motivation and to familiarize subjects with the condition of eating food from the experimental containers, we can see no reason to place food inside the containers during warm-up trials if food is never going to be found inside the containers during testing.

Hare et al. (in press) raise several issues concerning our data analysis. In Udell et al. (2008) we defined a correct choice as the subject "touching or coming within 10 cm of [the correct can] with its snout" (p. 1769). Failure to make a correct response during an experimental trial was scored as an incorrect response. Hare et al. (in press) argue that the only valid incorrect response is touching the opposite can, all other responses they code as non-participation and do not include in statistical analyses. We were fully aware of the possibility of non-participation when designing our study. In fact, as Hare et al. (in press) mention, unlike most studies, we included a specific test of motivation in our methodology to ensure that, irregardless of point following performance, subjects were motivated to participate in the task. None of the subjects

reported in Udell et al. (2008) failed a test of motivation at any point in the study. When a participating subject did not approach either can during a trial, it often performed an alternative behavior used to solicit food in their home environment, such as begging from the experimenter or barking at her. However, when we report that each subject experienced ten trials and got some number of those trials correct, we mean what we say: The stimulus (the human's hand movement) was presented ten times; the subject had ten opportunities to respond; on some number of those opportunities the subject responded to the container pointed to and was reinforced. All of our statistical analyses were performed on the basis of the number of correct responses out of a total of 10 trials per subject; there were no "do-overs," selectively dropped trials, or any other variations from our stated procedure.

While Hare et al. assert that their reanalysis of our data utilized a "more conventional method of examining separately (1) participation (making a choice or not) and (2) the level of correct choices (choosing the cup indicated by a point instead of the one ignored)" (Hare et al. in press, p. xxx), they provide no references for prior use of this method and we are not aware that it has ever been previously deployed. Furthermore this is not the method they use for scoring or analyzing *their own experimental data* in the shelter dog study provided within their critique. Instead the method Hare et al. use is selective repetition of trials when their subject fails to make one of two desired responses. According to Hare et al. (in press, p. xxx) "If a dog did not clearly touch one of the two cups within 25 s (i.e. the dog became distracted or unmotivated), the trial was repeated." No behavioral definitions or tests for distraction or lack of motivation are provided. Thus it seems the experimenter had the option of deciding, 25 seconds into a trial, whether the dog was responding in a desirable way. If not, the data were removed from the analysis and the dog was given another chance to view the human point before making a choice.

While an overall percentage of these *redo* trials is given, the authors provide no indication of which trials for which individuals were redone, or what circumstances justified the selective removal of data beyond the failure to obtain a desired response from the dog. Yet according to Hare et al. (in press, p. xxx) "in previous studies the exclusion or repetition of no-choice trials has been the standard." Again no citations are offered, but one can only assume that this is the standard method used by Hare and colleagues in prior experiments even though published methods do not mention it.

The analysis presented in Udell et al. (2008) accurately summarized the full data set collected in that study. Even after Hare et al.'s (in press) reanalysis, wolves and pet dogs tested indoors still performed significantly above chance on an object choice task using a momentary distal point without the use of additional smell cues or the repetition of trials during testing. Furthermore, Hare et al.'s reanalysis also leaves untouched our finding that shelter dogs did not succeed on the human-guided object choice task. Thus our conclusion that "domestication alone cannot account for canids' sensitivity to human social cues involved in following a point" (Udell et al. 2008. p. xxx) is not impacted by Hare et al.'s reanalysis.

While Hare et al. argue that their reanalysis demonstrates that "there is no evidence from the data of Udell et al. (2008) that adult wolves outperform adult dogs using a human pointing gesture" (Hare et al. in press, p. xxx), that is simply because they chose to avoid all mention of individual performance. Udell et al. (2008, p.1770) reported that "more individual wolves (six out of eight subjects) followed the point on eight or more out of 10 trials (binomial test: $P = 0.05$) more often than did domestic dogs [home unfamiliar group] (three out of eight subjects)." According to Hare et al.'s *participation* reanalysis "Post hoc comparisons (Bonferroni tests)

revealed that the dog home unfamiliar group participated significantly more often than the other three dog groups, but did not differ from the wolf group ($P < 0.05$ for all significant tests)." Therefore individual comparisons between the dog home unfamiliar group and wolves remain valid even under this new criterion. Despite equal levels of contact with the two response objects, more individual wolves used a human point to perform above chance on the human guided task than did pet domestic dogs. In fact, even adding the number of successful individuals from *all* of the domestic dog groups in Udell et al. (2008) together (N = 32), only seven domestic dogs were individually successful on the task (22%). Out of only eight wolves, six were individually successful using the same point (75%). Thus our overall conclusion that "wolves outperform dogs in following human social cues" remains an accurate portrayal of the findings presented in Udell et al. (2008).

Lastly, Hare et al. (in press) suggest that dogs tested in a more distracting environment (e.g. outdoors or in an unfamiliar location) may perform worse on an object choice task than they would in a familiar environment. We agree entirely. In fact we said so in our original article: "Pet dogs reared in comparable conditions can perform differently from each other in different testing environments (indoors versus outdoors and fence versus no fence)" (Udell et al. 2008, p. 1771). No prior study had considered testing environment as an important variable. We suggested in Udell et al. that environmental considerations were likely relevant considerations in prior research conducted with wolves and dogs: "Wolves in the study by Hare et al. (2002) and in the studies by Viranyi et al. (2008) were tested under different conditions from their own domestic dog comparison groups and thus interfering or distracting aspects of the wolves' testing environment may not been accounted for." (Udell et al. 2008, p. 1772). It is gratifying to find other researchers taking an interest in this important variable.

**ENVIRONMENT, EXPERIENCE, AND METHODOLOGY MATTER**

Hare et al. (in press) present additional data on the ability of dogs at a shelter to follow human points. The implication seems to be that that by presenting data on shelter-housed dogs that *do* follow human points Hare et al. (in press) can thereby correct the impression created by the eight shelter-living dogs that we showed in Udell et al. (2008) *did not* following points.

Unfortunately, Hare et al. tested their shelter dogs on a substantially simpler form of point than that utilized by Udell et al. (2008). In the dynamic proximal point deployed by Hare et al., the human pointing gesture was repeated four times 20 cm from the target container. While the resting place of the human hand was not specified by Hare et al., dynamic proximal points are typically left in place until the subject makes its choice. The momentary distal point used in Udell et al. involved the experimenter gesturing only once, her hand came no closer than 50 cm to the pointed to container and returned to her midline before the canid was released to make its choice. (For point type definitions and the importance of carefully defining stimuli used in object choice tasks see Miklósi and Soproni 2006 and Udell et al. in press). Thus we see no inherent contradiction between around one third of Hare et al.'s subjects being successful on a dynamic proximal point and none of our subjects achieving success in following the more challenging momentary distal point. We have re-analyzed Hare et al.'s data from trials on which the human point was presented, and find that 7 of the 22 subjects followed the human gesture at above chance levels (binomial, $p < 0.05$). Our own results (M. A. R. Udell, N. R. Dorey & C. D. L. Wynne, unpublished data) indicate an even higher success rate of shelter dogs on the dynamic proximal point (six out of seven subjects performed above chance in the first ten trials, binomial $p < 0.05$). These are different types of point and success and failure of different groups of canids will vary correspondingly. In any case, our purpose was not to claim that *all* dogs cannot follow

points: not even that all dogs living in shelters cannot follow points. Instead we predict that canids may or may not follow points depending on their developmental experiences and current environments resulting in varied levels of responsiveness in different individuals raised and living under different conditions.

An additional concern with Hare et al.'s shelter dog comparison is that of the four "human communicative cue" conditions presented, only one was in fact human based: the human point and gaze cue just discussed. The other three cues were i) a block of wood placed on top of the cup containing food, ii) shaking the cup containing food to produce an audible noise, and iii) shaking the empty cup to produce no noise. As defined in a paper authored by the last four authors of Hare et al. (in press), (Bräuer et al. 2006) these are considered *causal* cues, not *human communicative* cues. If unconventional methodology was thought to explain the poor performance of shelter dog's in Udell et al. (2008) this question could have been addressed by a comparison of the specific methodological differences criticized by Hare et al. (in press). This was not done, however, and it is difficult to see how any comparison can be made on the basis of a study utilizing not only different methodology but completely different stimuli.

## SPECIFIC EXPERIENCES WITH HUMANS MATTER

Hare et al. (in press) revisit our previous critique of the developmental study by Riedel et al. (2008): Wynne et al. (2008). We are reluctant to simply repeat remarks we have previously published, so we focus instead on a few broader issues in assessing the development of this behavior.

First, it is important to recognize that demonstrating the absence of a developmental change in behavior amounts statistically to affirming the null hypothesis. Statistical hypothesis testing is only suited for analyses designed to reject a null hypothesis. A failure to reject the null hypothesis cannot be used as evidence that the null hypothesis is true because null hypothesis testing assumes the truth of the null hypothesis *a priori*.

When Riedel et al. (2008) carried out their main analysis of an effect of age on all pointing types, they included the control condition. Since age would not be expected to impact performance on the control trials, this meant that in the analysis of variance, the effect of age enters as an interaction. Interactions necessarily have fewer degrees of freedom than main effects on the same dataset, thereby reducing the statistical power of the test. When Riedel et al. (2008) analyzed each point type separately they likewise reduced the number of observations per cell compared to the analysis that pools across all point types, and thereby again reduced the power of the statistical test. Even so, Hare et al. (in press) and Riedel et al. (2008) concede that one point type showed a definite effect of age, and the other is close to customary levels of statistical significance ($P = 0.094$). Though a probability of rejecting the null hypothesis of around 9% would not normally be considered sufficient to actually reject the null hypothesis, it is far from what can be considered strong support *in favor* of the null hypothesis. The bottom line for the analysis of dog pups' ability to follow points in Riedel et al.'s (2008) experiment 1 is that their figure 2 shows very obvious improvements with age.

Hare et al. (in press) draw attention to the fact that in Wynne et al. (2008) we did not comment on experiments 2 and 3 in Riedel et al. (2008). We refrained from commenting on these other experiments because the performance of the dogs tested was at such uniformly low

levels that they contribute nothing to a discussion of the importance of ontogeny to this ability. If a task is too easy or too difficult, developmental trends will not be identifiable. This says nothing important, however, about the contribution of ontogeny to these behaviors.

## GENERAL DISCUSSION

Behavior develops: This is an uncontroversial statement. Human behavior develops; wolf behavior develops; fox behavior develops and dog behavior develops. The development of adult social behavior of humans with other humans is dependent on interactions with humans during childhood (see for example Harwood, Miller & Vasta 2008). An extensive literature documents how the development of conspecific social behavior in dogs and wolves is dependent on appropriate interactions with other members of their species during development (for a review see Udell et al. in press). Thus we would consider it at least anomalous if dogs had an ability to comprehend human social cues such as pointing gestures that was present at the earliest testable ages and did not depend on particular environmental experiences. After all, no such ability exists in human infants. Ample evidence exists, some by co-authors to the commentary by Hare et al. (in press), that clearly shows that children do not develop the ability to follow human pointing gestures until their second year of life (Behne, et al. 2005; Lakatos, Soproni, Doka, & Miklósi 2009; Lempers, 1979; Murphy & Messer 1977).

Although the domestication hypothesis posits that learning does not have an effect on domestic dogs' performance in object choice tasks, there is ample evidence to the contrary. For example, Bentosela et al. (2008), showed that dogs can learn to attend to human gaze in as few as three trials; Udell, Giglio & Wynne (2008), showed that dogs learn to follow unfamiliar human cues in fewer than ten trials (see Udell et al. in press, for a more thorough review). The

selective deletion of incorrect responses, which Hare et al. (in press) state is customary in this literature, implies that subjects have more opportunities to learn to follow human gestures than the published studies indicate. The rapidity with which dogs can learn new human cues combined with the apparently customary incomplete data reporting in the literature, means that it is unclear how any claims about changes in performance across trials can be made by these authors.

Of course something happened during domestication. We are not for a moment suggesting that a dog cannot be distinguished from a wolf. The question is not *if* something happened during domestication but *what*. There is a substantial literature on how domestication affects development and socialization in canids (for a review see Udell et al. in press). Our assertion that domestication *in itself* cannot explain domestic dogs' responsiveness to human cues, calls for an acknowledgement that neither phylogeny nor ontogeny occur in isolation. It is the interaction that counts. Domestic dogs are interesting specifically because their evolutionary history *and* their daily life experiences are uniquely tied to human society; their behavior is always a product of both. We suggest that the phylogenetic prerequisites for responding to the bodily gestures of companions are present in both wolves and domestic dogs. Socialization to humans during early development allows humans to be viewed as companions, and experience throughout life allows for flexible associations between specific bodily movements of companions and important environmental events. These are the predictions of the two-stage hypothesis (Udell et al. in press). According to this hypothesis domestication changes the timeframe, and subsequently socialization intensity, during which primary socialization to companions, including humans, needs to take place to have the greatest effect. For non-

438 domesticated canids, such as wolves, this period is shorter and ends earlier than in domesticated
439 canids such as dogs.

440 In this commentary we have restricted our comments solely to those aspects of the
441 literature on canids' abilities to respond to human cues raised by Hare et al. For a more thorough
442 analysis of the reasons why the Domestication hypothesis is untenable see Udell et al. 2009.

443 In conclusion we are gratified to see our raw data put to interesting use by other
444 researchers. Such fresh analysis can move a field forward much more rapidly than if different
445 groups of researchers have to collect equivalent data sets. Our trial-by-trial raw data are available
446 to all interested parties on our website, www.caninecognition.com. We could wish other
447 researchers would return the courtesy (Dorey et al. 2009).

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