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Ontogeny and phylogeny: both are essential to human-sensitive behaviour in the genus *Canis*

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In responding to Hare et al. (2010), we wish to start by outlining our substantive areas of agreement. We do not disagree that pet domestic dogs 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 et al. (2008a) 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. 2010, page e6). 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. 2008a, page 1772).

The crux of our disagreement with Hare et al. (2010) is our belief that socialization and experience are essential for all canids to respond to hetero- and conspecific 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. (2010). To be clear, we do not deny an influence of heredity or domestication on the social behaviour 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. Our response is organized to match Hare et al.'s (2010) commentary. First, we respond to their review of the literature on the sensitivity of dogs, wolves and foxes 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. 2008a). Third, we consider the data on dogs living in a shelter reported in Hare et al. (2010). 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 behaviours.

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

The most common form of test of a dog's ability to use cues given by humans involves a human pointing at one of two

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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. (2010) claim that prior studies of dogs' responsiveness to human communicative behaviours have included 'controls [that] rule out the use of olfactory cues; (Cooper et al. 2003; Hare & Tomasello 2005; Miklósi & Soproni 2006)' (page e1). In fact, none of the three studies, nor the vast majority of other studies on this issue, have reported controls for olfactory cues. Indeed, even the new data presented by Hare et al. (2010) in their commentary included no controls for odour 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 et al. (2003) demonstrated that dogs can utilize odour 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 odour, consistently approaching the container with accessible food, even if another container was present that contained the same amount of food buried under several centimetres of stones (Udell et al. 2008a).

Hare et al. (2010) argue that wolves can only follow human communicative gestures when 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 Virányi et al. (2008) to support that claim. Furthermore, they claim that this dependency of wolves but not of 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' (page e1). 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, on average, were not successful in following the human point to find food, although individual results were not presented. We have already demonstrated (Udell et al. 2008a) that the ability of dogs to follow a human point through a fence is substantially limited. Thus, it is reasonable to assume that the presence of the fence barrier, which was not used by Agnetta et al. (2000) and Hare et al. (2002) in their studies on dogs, accounts for the poor performance of the wolves on these tests.

Virányi et al. (2008) come closer to achieving a balanced comparison of dogs and wolves. Virányi et al. (2008), 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 (at 4 months old) as well as at 7 months old. While dogs followed a momentary distal point at 4 months of age, wolf pups performed at chance levels. At 7 months, and after extensive experience with the task, wolves began to perform at the level of naïve dogs. Unfortunately, the wolf pups, but not the dog pups, were removed from human homes between 2 and 4 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 2 months of age than did those of 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 the vast majority of wolves do not follow human points. Our demonstration that a subgroup of wolves can follow human points without explicit training, recently replicated by Gácsi et al. (2009), demonstrates that the potential to develop responsiveness to human cues exists in nondomesticated canids. No number of demonstrations of wolves that fail to follow human points would contradict this finding.

Hare et al. (2010) 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's foxes were bred for over 40 generations for tolerance of humans, including reduced flight distance to human approach (Trut 1999). 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 (although 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 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 et al. 2004). Thus, the finding that Balyaev's foxes follow human points at a marginally higher level than do nonhuman-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 (for a thorough review of this confound see Udell et al., in press).

Hare et al. (2010) 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' (page e1). Hare et al. (2002) tested dog pups ranging in age from 9 to 26 weeks, some of which had lived in human families, while others had 'lived their entire lives with littermates in a kennel and so had been exposed to humans for only a few minutes each day for husbandry purposes' (page 1635). Hare et al. (2010) reported that even the youngest age group (9–13 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 15 of 18 trials correct. However, one important problem with Hare et al.'s (2010) interpretation of these data is that it was 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, Massachusetts, U.S.A. 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 exposed to people during their first 4 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 & Fuller (1965) reared a small number of completely unsocialized dogs and reported that these animals '… later react toward [humans] with extreme fear and hostility' (page 176).

We have already commented on the results obtained by Riedel et al. (2008) in Wynne et al. (2008). Since Hare et al. (2010) raise issues with our reanalysis of Riedel et al.'s (2008) data, we dedicate