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COMMENTARY

Response to Hansen Wheat et al.: Additional analysis further supports the early emergence of cooperative communication in dogs compared to wolves raised with more human exposure

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Abstract

Here, we address Hansen Wheat et al.'s commentary in this journal in response to Salomons et al. *Current Biology, 31*(14), 3137–3144.E11, (2021). We conduct additional analyses in response to Hansen Wheat et al.'s two main questions. First, we examine the claim that it was the move to a human home environment which enabled the dog puppies to outperform the wolf puppies in gesture comprehension tasks. We show that the youngest dog puppies who had not yet been individually placed in raisers' homes were still highly skilled, and outperformed similar-aged wolf puppies who had higher levels of human interaction. Second, we address the claim that willingness to approach a stranger can explain the difference between dog and wolf pups' ability to succeed in gesture comprehension tasks. We explain the various controls in the original study that render this explanation insufficient, and demonstrate via model comparison that the covariance of species and temperament also make this parsing impossible. Overall, our additional analyses and considerations support the domestication hypothesis as laid out by Salomons et al. *Current Biology, 31*(14), 3137–3144.E11, (2021).

Hansen Wheat et al.'s response to Salomons et al. (2021) addressed two main questions: (1) Are the dog puppies outperforming the wolf puppies at gesture comprehension before they go to their individual human raiser's homes (aged <9 weeks)? and (2) is the tendency to approach a stranger a better explanatory variable than species to predict success at gesture comprehension?

To address the first question, we start by comparing puppies still living with littermates (L puppies), who had not yet been sent individually to raisers' homes, to

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same-age wolf pups with more human exposure (see Supplemental Information). L puppies (≤9 weeks, mean age 7.6 weeks, $N = 13$) performed significantly above chance on the pointing task as a group (70.5% correct, binomial test, $p = .0003778$) and 10 out of 13 (76%) were correct on their first trial. Wolf puppies in the same age range (≤9 weeks, mean age 8.4 weeks, $N = 5$) were not above chance (60% correct, binomial test $p = .3616$) with 3 of 5 wolves (60%) choosing correctly on their first trial. On the marker gesture the L puppies ($N = 13$) performed significantly above chance as a group (85.9% correct, binomial test $p = 6.118e-11$) and all 13 (100%) were correct on the first marker trial. The five wolf puppies in the same age range were not above chance on the marker gesture (56.7% correct, binomial test $p = .5847$) and only 2 of the 5 (40%) wolves were correct on the first trial. At an individual level, when examining combined performance with the two gesture tasks, over half of the L puppies (7 out of 13) performed above chance (i.e., got ≥10 of the 12 trials correct), while no individual wolf ($N = 26$) of any age performed above chance. Unfortunately, the small wolf sample at this age prevents a meaningful group comparison using inferential statistics. Instead, we compare our L puppies with our group of 12-week-old wolves that is the same size ($N = 13$). As predicted by the directional hypothesis in the original paper, L puppies outperformed these older wolves on the pointing gesture task (dogs: mean = 70.5% correct, $SD = 23.7\%$; wolves: mean 57.7% correct, $SD = 14.6\%$; Welch's two-sample t test, $p = .04815$, one-tailed) and the marker gesture (dogs: mean = 85.9% correct, $SD = 15.0\%$; wolves: mean = 56.4% correct, $SD = 19.9\%$; Welch's two-sample t test, $p = 1.8e-05$, one-tailed).

To further address the first question, we compare the performance of the L puppies to the older group of dog puppies already living individually in raiser's homes at the time of testing (H puppies; $N = 18$). L and H puppies did not significantly differ from each other on the pointing task when compared using a linear mixed-effects model (Correct ~ I(Weeks > 9) + (1|Name), family = binomial, β age > 9 weeks = 1.1561, $SE = 0.7251$, $p = .1109$) or a Welch's two-sample t test ($p = .54$, two-tailed). On the marker gesture, L puppies outperformed the H puppies when compared using the same linear mixed-effects model (β age > 9 weeks = −1.0028, $SE = 0.4665$, $p = .0316$) and Welch's two-sample t test ($p = .006$, two-tailed). Figure 1 illustrates how puppies do not show significant increases in skill with age on either gesture task. Finally, Bray et al. (2021) tested 375 L puppies (mean age = 8.5 weeks) from the same population studied in Salomons et al. (2021) with a similar pointing task. A significant portion of these subjects, many of whom had never lived in human homes, used a human pointing gesture on their very first trial (70%).

Taken together, these multiple new analyses in response to Hansen Wheat et al.'s first question further support the hypothesis that the youngest dogs with the least amount of human exposure were already skilled at using human gestures—indeed, they were more highly skilled than similar aged wolves raised with far more human exposure. While Hansen Wheat et al. call for the wolf and dog puppies to be raised in identical conditions, it is important to emphasize that we intentionally raised the wolf puppies with substantially more human exposure and interaction than the dog puppies (including the H puppies) in order to be conservative against the hypothesis (see Supplemental Information for more raising details). If the human exposure of the H dog puppies sufficiently explained their skill level, then the wolves, who had even more human exposure at all times and from a younger age, should perform similarly, but they do not. We also see no a priori rationale to justify Hansen Wheat and colleague's comparison of the L puppies subsample to the entire wolf sample. This maximally confounds age and species in a way that our original and new analyses do not.

In regard to Hansen Wheat et al.'s second question, they state, "since gesture-following in an experimental context necessarily also involves approaching a stranger, this large difference in willingness to approach could account for the difference . . . between the two species." Several design features in the original study argue against this interpretation. First, unlike the go/no-go tasks used to assess temperament (e.g., stranger approach), both a correct or incorrect choice in the two-way object choice paradigm (used to test memory, gesture comprehension, and controls) requires a subject to approach one of two bowls that are equidistant from the experimenter. Second, all subjects passed the memory test as a prerequisite to participating in the gesture tasks, which required the same approach behavior as the gesture tasks and on which the two species performed the same. Third, the body versus point control was designed as another test of this. In this control, subjects would have been most successful by avoiding the bowl closest to the experimenter. However, wolves did not avoid the experimenter and did not differ from dogs in their performance. Regarding the model comparisons, the variables of "species" and "willingness to approach stranger" strongly co-vary (as demonstrated by the results of the temperament test), and the models including these variables are indistinguishable using AIC scores (see Supplemental Information). Therefore, any separate contributions to the overall effect cannot be determined using model comparison with the current dataset.

Finally, as a supplemental measure to address Wheat et al.'s supposition that human attraction sufficiently explains dogs' success in gesture following, and in response to the previously published suggestion that dogs are simply attracted to human hands and things they touch (Wynne et al., 2008), we coded whether our L puppies were attracted

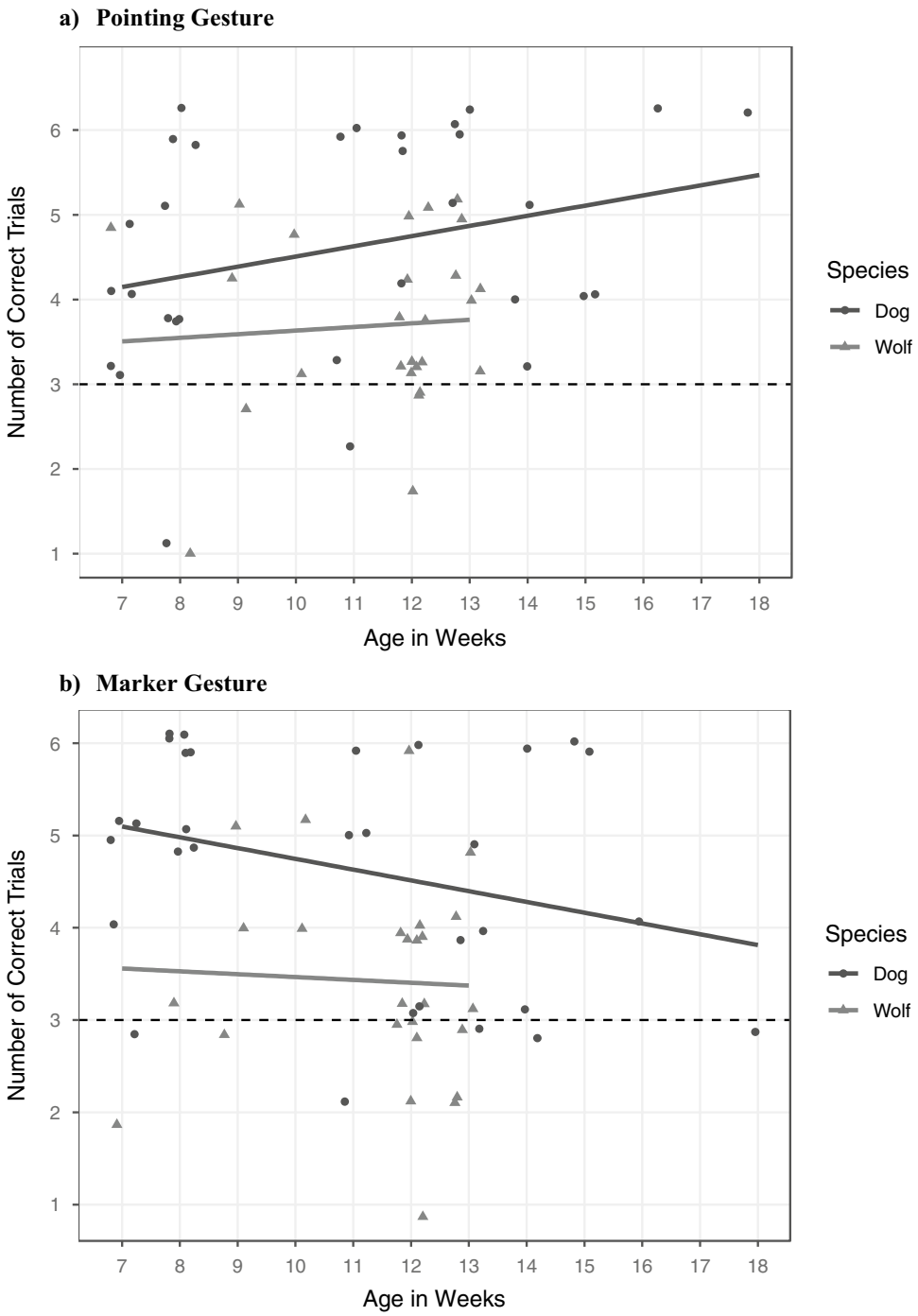

Fig. 1 Number of correct choices made by the different aged subjects. Performance does not significantly increase with age on either of the gesture comprehension tasks. Dashed line represents chance performance (50% correct). All points are jittered for visibility (see Supplemental Information for table of points). **a)** Pointing gesture. Dog linear regression: $y = 0.12x + 3.3$, $R^2 = .075$; wolf linear regression: $y = 0.043x + 3.2$, $R^2 = .0048$. **b)** Marker gesture. Dog linear regression: $y = -0.12x + 5.9$, $R^2 = .088$; wolf linear regression: $y = -0.031x + 3.8$, $R^2 = .0021$

to the human hand or marker when choosing. L puppies only touched the human's pointing hand or the marker before making a correct choice (touching the baited bowl) on 3.6% (2 out of 55) and 4.5% (3 out of 66) of trials respectively. No subject did so on their first trial with either gesture. Again, this supports the hypothesis that dog puppies recognize the cooperative-communicative nature of basic human gestures and their responses are not only due to attraction to human bodies, hands, or things humans have touched (see also Riedel et al., 2008).

Supplementary Information The online version contains supplementary material available at https://doi.org/10.3758/s13420-023-00576-2.

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Open practices statement The data for all experiments and video examples of methods are available online (https://datadryad.org/stash/dataset/https://doi.org/10.5061/dryad.2547d7wqm).