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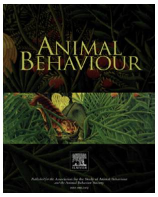

Uncovering the origins of dog–human eye contact: dingoes establish eye contact more than wolves, but less than dogs

Angie M. Johnston [a, *], Courtney Turrin [a], Lyn Watson [b], Alyssa M. Arre [a], Laurie R. Santos [a]

[a] *Department of Psychology, Yale University, New Haven, CT, U.S.A.*
[b] *Australian Dingo Foundation, P.O. Box 502, Gisborne, VIC, Australia*

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Through domestication, dogs have developed a robust ability to form interspecific bonds with humans. Recent work comparing dogs and wolves suggests that eye contact is an important behaviour underlying these social bonds; however, it remains unclear how this feature of interspecific social bonding evolved. We explored eye contact in a unique comparison species that represents an intermediate point in canid domestication: the Australian dingo (*Canis dingo*). Across two different studies with two different human handlers, we examined dingo-initiated eye contact using a method similar to one previously used with dogs and wolves. In contrast to wolves tested previously, dingoes initiated eye contact with a human, but did so for a shorter time than dogs. Given that dingoes share only an early domestication history with dogs, our results suggest that the motivation to initiate eye contact with humans may have evolved relatively early in domestication. However, the tendency to maintain prolonged eye contact with a familiar human may have evolved later. These results shed new light on the evolutionary steps by which humans and dogs developed their unique social bond.

Through domestication, domestic dogs, *Canis familiaris*, have developed a robust ability to connect with humans. One major cornerstone of this interspecies connection is shared communication. Not only are dogs highly adept at reading human social cues such as pointing and eye gaze (e.g. Hare & Tomasello, 2005; Topál, Kis, & Oláh, 2014), but they also communicate with humans using cues such as gaze alternation (e.g. Miklósi et al., 2003; Passalacqua et al., 2011; Udell, 2015). Dogs' close evolutionary relatives, wolves, *Canis lupus*, require intensive exposure to humans in order to read human cues and initiate communication with humans, suggesting that domestication has played an important role in fostering interspecies communication between dogs and humans.

Gaze appears to be a crucial cue for shared communication between dogs and humans. Not only are dogs able to use the direction of a human's eye gaze to determine the hiding location of a treat (e.g. Miklósi, Polgárdi, Topál, & Csányi, 1998; Soproni, Miklósi, Topál, & Csányi, 2001), but they can also use gaze alternation to communicate with humans. Specifically, when dogs come to a task that is difficult or impossible to solve, they gaze at humans as if to request help (e.g. Miklósi et al., 2003; Passalacqua et al., 2011; Udell, 2015).

In fact, the importance of gaze for human–dog relationships may run even deeper than previously thought. Recent work suggests that mutual gaze, or eye contact, may fundamentally support social bonds between dogs and humans. Nagasawa et al. (2015) showed that eye contact between dogs and their owners triggered the release of oxytocin, a hormone implicated in social bonding, in both species. Importantl,y, wolves and their owners did not show the same oxytocin–eye contact feedback loop, even though the wolves were hand-reared and kept as pets. Based on their findings, Nagasawa et al. (2015) suggested that this oxytocin–eye contact feedback loop may have coevolved with dog–human social bonds. However, some scholars have argued that more work is needed to fully support this hypothesis (e.g. Fiset & Plourde, 2015; Kekecs et al., 2016). For instance, the connection between oxytocin and eye contact is not as robust when the owner's sex is taken into account (i.e. the effects are seen only in female owners, not in male owners; see Kekecs et al., 2016), and increased oxytocin levels were only seen in one group of dogs (i.e. the long eye contact group; see Fiset & Plourde, 2015). Thus, more work is needed to fully establish the connection between oxytocin and dog–human eye contact.

Although the role that oxytocin plays in facilitating dog–human eye contact is still an open question, behavioural research clearly demonstrates that dogs' tendency to make eye contact with humans has drastically changed over the course of domestication. Although it

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* Correspondence: A. M. Johnston, Department of Psychology, Yale University, 2 Hillhouse Ave, New Haven, CT 06520, U.S.A.
E-mail address: angie.johnston@yale.edu (A. M. Johnston).

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is clear that training and past experience with humans can strongly influence gazing behaviour in dogs (e.g. Barrera, Mustaca, & Bentosela, 2011; D'Aniello & Scandurra, 2016; Marshall-Pescini, Frazzi, & Valsecchi, 2016), there is also evidence that this behaviour is at least partially influenced by factors other than ontogenetic experience. Crucially, wolves do not use gaze alternation to communicate with humans even when they are hand-reared by humans and heavily socialized (e.g. Miklósi et al., 2003; Udell, 2015). In fact, even when dogs and wolves have a similar rearing history, dogs more readily establish eye contact with humans as early as 5 weeks of age (Gácsi et al., 2005). Likewise, even when humans actively attempt to initiate eye contact with dogs and wolves, dogs establish eye contact more quickly than wolves (Gácsi et al., 2009; Virányi et al., 2008; for review see Prato-Previde & Marshall-Pescini, 2014). Thus, it seems that gaze is an important aspect of human–dog communication that has evolved through domestication.

However, the evolutionary timeline of interspecific eye contact within canids remains unclear. To understand the steps by which interspecific eye contact evolved to the level that we see in modern-day domesticated dogs, we must look beyond the extreme points of canid domestication (dogs and wolves) to additional species that represent intermediate points in this unique process. To this end, we tested a previously unstudied comparison species that is thought to represent an intermediate point in the canid domestication process: the Australian dingo, *Canis dingo*. Dingoes offer a rare snapshot of early canid domestication. The most recent common ancestor of dogs and dingoes is estimated to have lived at least 5000 years ago. Additionally, unlike dogs, dingoes have not undergone evolutionarily recent artificial selection (Cairns & Wilton, 2016; Oskarsson et al., 2011; Savolainen, Leitner, Wilton, Matisoo-Smith, & Lundeberg, 2004; for review see Fillios & Taçon, 2016; Smith, 2015). As such, dingoes provide the unique opportunity for a more fine-grained analysis of how and when different evolutionary changes, such as the tendency to make eye contact, occurred during canid domestication.

Indeed, recent work suggests that dingoes' behaviour falls between that of dogs and wolves on a number of sociocognitive tasks. For instance, dingoes follow human social cues (e.g. pointing and direction of gaze) more readily than wolves but less robustly than dogs (Smith & Litchfield, 2010; see Wobber, Hare, Koler-Matznick, Wrangham, & Tomasello, 2009 for converging evidence with New Guinea singing dogs, *Canis hallstromi*). Likewise, when encountering an unsolvable task, dingoes look back at humans for help more quickly than wolves, but for a shorter duration than dogs (Smith & Litchfield, 2013). Given that dingoes represent a rare intermediate case between wolves, which were never domesticated, and dogs, which have been extensively domesticated over the past 10 000+ years (e.g. Larson et al., 2012), this species offers an ideal comparison for understanding how interspecific eye contact evolved.

To better understand how interspecific eye contact evolved across domestication, we examined interspecific eye contact between dingoes and humans using a task adapted from prior research testing wolves and dogs. Specifically, we investigated whether spontaneous dingo-initiated eye contact more closely resembled the patterns we see in dogs or wolves (Nagasawa et al., 2015). Given that dingoes represent an intermediate point in canid domestication, we hypothesized that dingoes might fall somewhere between wolves and dogs and thus show some elements of wolf-like eye contact (e.g. short durations of eye contact) and some elements of dog-like eye contact (e.g. at least some eye contact for all individuals). We first report an initial experiment testing this question (experiment 1a) and then a replication of the initial experiment (experiment 1b) in which we generalize our results to a new human handler.

EXPERIMENT 1A

We examined dingo-initiated eye contact using the same method previously used with dogs and wolves (Nagasawa et al., 2015). In prior work, wolves were much less likely to initiate eye contact with their owners than dogs were (55% of wolves versus 100% of dogs), and even when wolves did initiate eye contact, their eye contact was only fleeting compared to dogs (<1 s versus >30 s). We investigated where dingoes fall along this spectrum by comparing new data with dingoes to previously published data on domesticated dogs and nondomesticated wolves (Nagasawa et al., 2015).

Methods

Subjects

We tested 23 genetically pure dingoes (12 females; see Supplementary Table S1) at the Dingo Discovery Centre in Victoria, Australia. We attempted to test two additional dingoes, but these individuals were excluded due to camera malfunction (1) or repeated attempts to leave the testing area (1).

Since past work has highlighted the role that socialization can play in modulating affiliative behaviours between canids and humans (e.g. Barrera et al., 2011; D'Aniello & Scandurra, 2016; Marshall-Pescini et al., 2016), it is crucial to keep these socialization differences in mind between subject populations. Our dingo population was chosen in part because they were familiar and comfortable around humans. The dingoes in our sample lived at a sanctuary and were housed in mated pairs. Although they lived independently from humans and were not kept as pets, they were highly familiar with the staff members who fed them once daily in the morning, and they spent considerable time each day in their enclosures with human caretakers (for further description of this population; see Smith & Litchfield, 2013). For comparison, in Nagasawa et al.'s (2015) study, the dogs tested were kept as pets and the wolves were kept in pet-like conditions. Specifically, the wolves spent a large amount of time with their handler, and slept in their handler's sleeping quarters at night. Thus, the dingoes in our sample were less heavily socialized than either the wolves or the dogs in Nagasawa et al. (2015). In this way, it important to consider what these socialization results predict to determine whether they may explain any present species differences. Specifically, if socialization is the sole factor influencing eye contact, then dingoes should make less eye contact than either wolves or dogs. Any other pattern of results would suggest that domestication is playing at least some role in modulating eye contact.

Ethical note

All experiments reported in this paper were performed in accordance with the ASAB/ABS guidelines and were approved by the Institutional Animal Care and Use Committee of Yale University (IACUC protocol number 2014-11616).

Procedure

At the start of testing, a familiar handler brought the dingo into the testing area and allowed them to explore the enclosure until they were comfortable (see Fig. 1 for an overhead shot of the testing area). Once the dingo was comfortable, the handler sat down on a bench and announced the start of the trial. Each dingo participated in one 5 min trial in which they were allowed to wander freely around the enclosure and interact with the handler if desired. The handler was blind to the hypothesis of the study and was provided with the same instructions described in Nagasawa et al. (2015). Specifically, as in Nagasawa et al. (2015), the handler was told that she could interact

Figure 1. Overview photo of testing area for experiments 1a and 1b. The handler was asked to remain seated on the bench, but she was told she could interact with the dingo in any way she liked.

with the dingoes however she desired as long as she remained seated and refrained from giving the dingo food or toys.

Only two aspects of our design differed from Nagasawa et al. (2015). First, given that the dingoes did not have owners, the human handler was a highly familiar sanctuary staff member who cared for the dingoes multiple times per week. Second, as per our IACUC requirements, dingoes were always on leash when interacting with the handler. To avoid any unnecessary restrictions the leash might pose, we only tested dingoes who were comfortable and habituated to the leash and we used a retractable leash (secured to the bench on which the handler was sitting) that allowed dingoes free access to all areas of the enclosure. Crucially, we did not code any looking times that were affected by the leash. Fortunately, these instances were rare. In all of our footage, there were only three brief instances where the leash influenced the dingoes' looking time (either by causing them to look or preventing them from looking). To ensure we did not overestimate instances of eye contact, we did not code any of these leash-influenced instances as eye contact. Only eight dingoes at the sanctuary were unable to be tested due to their hesitation about the leash. The remainder of the dingoes participated in the study. In our replication, we were able to gain approval to test dingoes off leash, and we report these data in experiment 1b.

Coding and analyses

All statistical analyses were conducted using R statistical software (version 3.4.0). As in prior work (Nagasawa et al., 2015), we captured our videos using a camera mounted to the top of the enclosure. We attempted to code three variables (as in Nagasawa et al., 2015): duration of dingo-to-human eye contact, duration of handler touching the dingo (dingo-touching) and duration of handler talking to the dingo (dingo-talking). However, the microphone on our overhead camera was unable to capture dingo-talking in experiment 1a, so we only report results for dingo-to-human eye contact and dingo-touching. We report results for dingo-talking in our replication in experiment 1b. For each variable, we used the same coding criteria as Nagasawa et al. (2015). Specifically, dingo-to-human eye contact was defined as whether the dingo's nose was angled up towards the handler's face, and dingo-touching was defined as the amount of time the handler voluntarily touched the dingo, excluding any incidental physical contact. Two coders (the first author and an additional coder blind to the hypothesis) reliably coded 100% of the videos ($r = 0.80$ for dingo-to-human eye contact and $r = 0.97$ for dingo-touching). Our results remained the same regardless of which coder's data were used.

To contrast dingo-to-human eye contact with dog-to-human and wolf-to-human eye contact, we compared our results with those previously published by Nagasawa et al. (2015; data obtained from their supplementary material). Based on a cluster analysis, Nagasawa et al. (2015) divided dogs into two groups based on the duration of time they made eye contact with their owners: the short eye contact group and the long eye contact group. To provide the most conservative estimate of dog–human eye contact when comparing to dingo–human eye contact, we used the data for dogs in the short eye contact group.

As our data were not normally distributed, we used nonparametric tests. First, to examine whether the proportion of dingoes that made eye contact differed from dogs or wolves, we conducted an initial Fisher's exact test comparing all three populations together. Following up on this initial analysis, we conducted Bonferroni-corrected post hoc tests comparing the proportion of dingoes that made eye contact to the proportion of dogs and wolves that made eye contact. Next, to examine whether the duration of dingo-to-human eye contact differed from that of wolves or dogs, we conducted an initial Kruskal–Wallis test comparing all three populations, including only those animals that made eye contact. Following up on this initial analysis, we used Mann–Whitney *U* post hoc tests with Bonferroni corrections to compare the duration of dingo-to-human eye contact with dog-to-human and wolf-to-human eye contact. Finally, we examined whether dingo-touching influenced dingo-to-human eye contact by conducting a Spearman correlation between the amount of time the handler touched the dingo and the duration of dingo-to-human eye contact. Additionally, we compared dingo-touching to that of dogs and wolves using the same analyses described above for dingo-to-human eye contact. Our results remained the same regardless of whether we used nonparametric tests on non-normally distributed data or whether we transformed our data using a logarithmic function and used parametric tests.

Results

As shown in Fig. 2, dingo-initiated eye contact represented a clear intermediate case between the levels of eye contact shown in wolves and dogs. When examining the proportion of dingoes that initiated eye contact with the human, there were clear differences among the

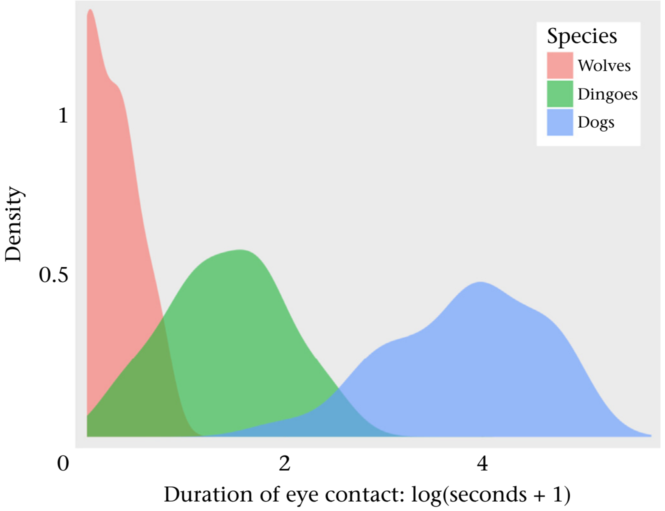

Figure 2. Kernel density plot depicting the probability density function of duration of eye contact for wolves, dingoes and dogs, including dogs in both the short eye contact and long eye contact groups. Duration of eye contact data was log transformed. Given the large number of subjects who made eye contact for 0 s, we added 1 s to each subject's duration of eye contact before taking the log. Wolf and dog data are taken from Nagasawa et al. (2015).

three species (Fisher's exact test: $P < 0.001$), however, Fisher's exact post hoc tests revealed that dingoes were more similar to dogs than to wolves. Dingoes were nearly twice as likely to initiate eye contact (22 out of 23 dingoes) than were wolves (6 out of 11 wolves; Fisher's exact test: $P = 0.008$, Bonferroni-corrected cutoff $P < 0.025$), but were no different than dogs (20 out of 20 dogs, $P = 1.00$). However, when examining the duration of eye contact (for those animals that initiated eye contact), dingoes scored between wolves and dogs (Kruskal–Wallis test: $\chi^2_2 = 35.16$, $P < 0.001$). Mann–Whitney U post hoc tests revealed that dingoes made eye contact with the human handler for more time (median for dingoes: 2.7 s) than wolves (median for wolves: 0.45 s; $U = 123.5$, $N_{\text{Dingo}} = 22$, $N_{\text{Wolf}} = 6$, $P = 0.001$, two-tailed Bonferroni-corrected cutoff $P < 0.025$), but for less time than dogs (median for dogs: 40 s; $U = 8$, $N_{\text{Dingo}} = 22$, $N_{\text{Dog}} = 20$, two-tailed $P < 0.001$; see Fig. 2). These results remained the same even when we compared our minimum estimate of dingo eye contact (median for dingoes: 2.49 s, calculated by taking the lowest score for each dingo across the two coders) to that of wolves (median for wolves: 0.45 s; $U = 123.5$, $N_{\text{Dingo}} = 22$, $N_{\text{Wolf}} = 6$, $P = 0.001$) and our maximum estimate of dingo eye contact (median for dingoes: 3.65 s, calculated by taking the highest score for each dingo across the two coders) to that of dogs (median for dogs: 40 s; $U = 9$, $N_{\text{Dingo}} = 22$, $N_{\text{Dog}} = 20$, $P < 0.001$).

Similar to wolves in prior work (Nagasawa et al., 2015), there was no significant correlation between the amount of time the handler touched the dingoes and the amount of time the dingoes maintained eye contact with the handler ($r_S = -0.177$, $P = 0.418$). When looking at the proportion of individuals that were touched by the handler, there were marginal differences among the three species (Fisher's exact test: $P = 0.051$). However, Fisher's exact post hoc tests revealed no significant differences between the proportion of dingoes that were touched by the handler ($N = 23$ out of 23), compared to either wolves ($N = 9$ out of 11; Fisher's exact test: $P = 0.098$, Bonferroni-corrected cutoff $P < 0.025$) or dogs ($N = 19$ out of 20; Fisher's exact test: $P = 0.465$). When examining the duration of dingo-touching (for those animals that the handler touched), there were clear differences among the three species (Kruskal–Wallis test: $\chi^2_2 = 27.86$, $P < 0.001$). Mann–Whitney U post hoc tests revealed that the handler touched the dingoes for more time (median for dingoes: 137.4 s) than either the wolves (median for wolves: 67.7 s; $U = 178$, $N_{\text{Dingo}} = 23$, $N_{\text{Wolf}} = 9$, $P = 0.001$, two-tailed Bonferroni-corrected cutoff $P < 0.025$) or the dogs (median for dogs: 18 s; $U = 413$, $N_{\text{Dingo}} = 23$, $N_{\text{Dog}} = 19$, two-tailed $P < 0.001$). Thus, although the handler in the present study touched the dingoes for more time than either the wolves or the dogs in previous work, there was no significant relationship between the amount of time the handler touched the dingoes and the amount of eye contact dingoes made with the handler. In this way, dingoes were more similar to wolves in prior work than to dogs, given that the amount of eye contact dogs made with their owners was correlated to the amount of time their owners touched them, but this correlation was absent for wolves (Nagasawa et al., 2015).

EXPERIMENT 1B

Experiment 1a provided initial evidence that dingoes are distinct from both wolves and dogs in their spontaneous human-directed eye contact. Nevertheless, there were several important limitations of our experimental set-up in experiment 1a that could have led to these differences between dingoes, dogs and wolves. First, dingoes in experiment 1a were tested on leash, while wolves and dogs in prior work were not (Nagasawa et al., 2015). Second, dingoes in experiment 1a were only tested with one handler, leaving open the possibility that our results were driven by the unique behaviour of a single human handler. To address these limitations, we conducted a replication in experiment 1b where we tested dingoes off leash and generalized our results to a different, yet equally familiar, human handler.

Methods

Subjects

We tested the same 23 dingoes tested in experiment 1a (see Supplementary Table S1). Only one individual was excluded based on unwillingness to enter the testing area, leading to a final sample that included 22 of the original 23 dingoes tested in experiment 1a.

Procedure

The procedure was identical to experiment 1a with three crucial changes. First, dingoes were no longer tested on leash. Second, dingoes were tested with a different, yet equally familiar, handler to allow us to generalize our results across handlers. Third, we included an additional camera outside the testing area that not only allowed us to record an additional video angle, but also allowed us to code the amount of time the handler talked to the dingoes (dingo-talking).

Coding and analyses

All coding and statistical analyses were identical to those used in experiment 1a. However, our new camera angle allowed us to also code the duration of dingo-talking, which was defined as the amount of time the handler talked to the dingo (as in Nagasawa et al., 2015). Only one dingo needed to be excluded from dingo-talking analyses due to secondary camera failure. As in experiment 1a, two coders (the first author and an additional coder blind to the hypothesis) reliably coded 100% of the videos ($r = 0.77$ for dingo-to-human eye contact; $r = 0.98$ for dingo-touching; $r = 0.94$ for dingo-talking). Crucially, the results remained the same regardless of which coder's data were used and with both parametric and nonparametric analyses.

However, given the somewhat low reliability for dingo-to-human eye contact in both experiment 1a ($r = 0.80$) and 1b ($r = 0.77$), we further specified the existing coding criteria and had a third coder code this variable in experiment 1b. Specifically, we developed an additional guideline to clarify that the dingo's eyes should be at least somewhat visible to the overhead camera when the dingo's nose was angled up towards the handler's face. Based on this additional criterion, the third coder for experiment 1b achieved higher reliability with the first author ($r = 0.88$). The results remained the same when this third coder's data were used.

Results

Our results in experiment 1b fully replicated our results from experiment 1a. As in experiment 1a, dingo-initiated eye contact represented a clear intermediate case between the levels of eye contact shown in wolves and dogs. When examining the proportion of dingoes that initiated eye contact with the human, there were clear differences between the three species (Fisher's exact test: $P = 0.002$), however, Fisher's exact post hoc tests revealed that dingoes were more similar to dogs than to wolves. Dingoes were nearly twice as likely to initiate eye contact (20 out of 22 dingoes) than were wolves (6 out of 11 wolves; Fisher's exact test: $P = 0.027$, Bonferroni-corrected cutoff $P < 0.025$), but were no different than dogs (20 out of 20 dogs; $P = 0.489$). However, when examining the duration of eye contact (for those animals that initiated eye contact), dingoes scored between wolves and dogs (Kruskal–Wallis test: $\chi^2_2 = 34.94$, $P < 0.001$). Mann–Whitney U post hoc tests revealed that dingoes made eye contact with the human handler for more time (median for dingoes: 2.67 s) than wolves (median for wolves: 0.45 s; $U = 114$, $N_{\text{Dingo}} = 20$, $N_{\text{Wolf}} = 6$, $P = 0.001$, two-tailed Bonferroni-corrected cutoff $P < 0.025$), but for less time than dogs (median for dogs: 40 s; $U = 8$, $N_{\text{Dingo}} = 20$, $N_{\text{Dog}} = 20$, two-tailed $P < 0.001$). These results remained the same even when we compared our minimum estimate of dingo eye contact (median for dingoes: 2.67 s, calculated by taking the lowest score for each dingo across the three coders) to that of wolves (median for wolves: 0.45 s; $U = 112$, $N_{\text{Dingo}} = 20$, $N_{\text{Wolf}} = 6$, $P = 0.002$) and our maximum estimate of dingo eye contact (median for dingoes: 6.10 s, calculated by taking the highest score for each dingo across the three coders) to that of dogs (median for dogs: 40 s; $U = 15$, $N_{\text{Dingo}} = 20$, $N_{\text{Dog}} = 20$, $P < 0.001$).

As in experiment 1a, there was no significant correlation between the amount of time the handler touched the dingoes and the amount of time the dingoes maintained eye contact with the handler ($r_S = -0.071$, $P = 0.755$). When looking at the proportion of individuals that were touched by the handler, there were marginal differences between the three species (Fisher's exact test: $P = 0.054$). However, Fisher's exact post hoc tests revealed no significant differences between the proportion of dingoes that were touched by the handler ($N = 22$ out of 22) compared to either wolves ($N = 9$ out of 11; Fisher's exact test: $P = 0.104$, Bonferroni-corrected cutoff $P < 0.025$) or dogs ($N = 19$ out of 20; Fisher's exact test: $P = 0.476$). When examining the duration of dingo-touching (for those animals that the handler touched), there were clear differences between the three species (Kruskal–Wallis test: $\chi^2_2 = 18.73$, $P < 0.001$). Mann–Whitney U post hoc tests revealed that the handler touched the dingoes for marginally more time (median for dingoes: 118.82 s) than the wolves (median for wolves: 67.70 s; $U = 145$, $N_{\text{Dingo}} = 22$, $N_{\text{Wolf}} = 9$, $P = 0.048$, two-tailed Bonferroni-corrected cutoff $P < 0.025$) and for significantly more time than the dogs (median for dogs: 18 s; $U = 368$, $N_{\text{Dingo}} = 22$, $N_{\text{Dog}} = 19$, two-tailed $P < 0.001$).

As for dingo-touching, there was no significant correlation between the amount of time the handler talked to the dingo and the amount of time the dingoes maintained eye contact with the handler ($r_S = -0.164$, $P = 0.478$). When looking at the proportion of individuals that were talked to by the handler, there were significant differences between the three species (Fisher's exact test: $P = 0.042$). However, Fisher's exact post hoc tests revealed no significant differences between the proportion of dingoes that were talked to by the handler ($N = 21$ out of 21), compared to either wolves ($N = 9$ out of 11; Fisher's exact test: $P = 0.111$, Bonferroni-corrected cutoff $P < 0.025$) or dogs ($N = 20$ out of 20; Fisher's exact test: $P = 1.00$). When examining the duration of dingo-talking (for those animals that the handler talked to), there were clear differences between the three species (Kruskal–Wallis test: $\chi^2_2 = 16.82$, $P < 0.001$). Mann–Whitney U post hoc tests revealed that the handler talked to the dingoes for marginally more time (median for dingoes: 56.73 s) than the wolves (median for wolves: 34.30 s; $U = 142$, $N_{\text{Dingo}} = 21$, $N_{\text{Wolf}} = 9$, $P = 0.032$, two-tailed Bonferroni-corrected cutoff $P < 0.025$) and significantly more time than the dogs (median for dogs: 20.65 s; $U = 360$, $N_{\text{Dingo}} = 21$, $N_{\text{Dog}} = 20$, two-tailed $P < 0.001$).

GENERAL DISCUSSION

Together, these results shed light on the way in which spontaneous canid-initiated eye contact may have evolved across domestication. Specifically, our results suggest that the initial motivation for canids to initiate interspecific eye contact with humans evolved early in domestication, but the motivation to maintain prolonged eye contact with a familiar human may have evolved later. Although nondomesticated wolves tested in prior work (Nagasawa et al., 2015) rarely initiated any eye contact with a human handler, nearly all dingoes initiated at least some eye contact with the human handler in both experiments 1a and 1b. Given that dingoes share only a very early domestication history with dogs, these findings suggest that the general motivation to initiate eye contact with humans appeared early in the domestication process. However, the tendency to maintain prolonged eye contact with a familiar human may have evolved significantly later in the domestication process, as dingoes in both experiments 1a and 1b initiated eye contact with the familiar human for less time than dogs in prior work (Nagasawa et al., 2015). As such, these results provide important hints about the individual evolutionary steps that may have led modern-day domesticated dogs to develop the unique and rich social bonds that they maintain with humans.

However, it is important to consider a few alternative interpretations and limitations. First, although we used the same coding criteria used in Nagasawa et al. (2015) and initially established by Gácsi et al. (2005), it is possible that some of the patterns we observed were influenced by different coding practices across these laboratories. However, it is unlikely that the full magnitude of the difference among dingoes, dogs and wolves can be explained by different coding practices across laboratories. Specifically, even when we conducted the most conservative analyses and compared our minimum estimate of dingo eye contact to wolves and our maximum estimate of dingo eye contact to dogs, we still found that dingoes made significantly more eye contact with humans than wolves and significantly less than dogs.

One additional potential limitation of our study involves the difference in the amount of physical contact handlers made with dingoes in our study compared to dogs and wolves in previous work. In keeping with Nagasawa et al. (2015), our handlers were allowed to freely interact with the subject. Although the amount of eye contact dingoes made with the handler was not correlated with the amount of time the handler touched the dingoes, the dingo handlers spent significantly more time touching the dingoes overall than the wolf and dog handlers spent touching the wolves or dogs. Given that the dingo handlers spent more time touching the dingoes than both the wolf and the dog handlers, the difference in eye contact across species cannot be fully explained by differences in the amount of time handlers touched the animals. However, it is still possible that some portion of the difference in dingo-to-human eye contact and wolf-to-human eye contact was influenced by the fact that handlers spent more time touching the dingoes than the wolves. To address this issue, future work could compare dingo-to-human eye contact and wolf-to-human contact in a more artificial setting in which handlers are asked to refrain from touching the animals during the interaction period.

Finally, the rearing and socialization histories of the species we compared in the current studies were not identical, and both of these factors have been shown to influence gazing behaviour in prior work (e.g. Barrera et al., 2011; D'Aniello & Scandurra, 2016; Marshall-Pescini et al., 2016). In particular, although the dingoes in our study were highly familiar with the handler, they spent the majority of their time independently from their handler. This contrasted with both the wolves and dogs tested in Nagasawa et al. (2015). The dogs in Nagasawa et al. (2015) lived with their owners as pets, and although the wolves were not kept as pets, they spent a large amount of time with their handler, including in their sleeping quarters at night. For this reason, it would be incredibly valuable for future work to compare dogs, dingoes and wolves with identical rearing and socialization histories. However, given that the challenges of accessing such a population are prohibitive, it is worth considering the ways in which our current results overcome these limitations of discrepant rearing histories. Specifically, if anything, the dingoes were less familiar with the human handler than the wolves were in Nagasawa et al. (2015), yet the dingoes were more likely to make eye contact with the human handler than wolves were. Given that dingoes made more eye contact with the human handler even though they were less familiar with their handler, our results strongly support the idea that the motivation to make eye contact is the result of early domestication and not simply experience with humans.

Although our results with dingoes suggest that the motivation to maintain prolonged eye contact with a familiar human evolved later in domestication, future work could probe this question further. In particular, the dingoes in our study were not kept as pets, and thus they were not as familiar with the handler as pet dogs in prior work (Nagasawa et al., 2015). Future work could compare dingoes to populations of domesticated dogs that are not kept as pets, such as feral dogs, to investigate the role that experience with humans plays in facilitating eye contact between dogs and humans. Alternatively, future work comparing pet dingoes to pet dogs could more directly examine the role that familiarity plays on eye contact when dingoes are even more familiar (and perhaps bonded) to a particular human.

More broadly, it is possible that the motivation to maintain prolonged eye contact with familiar humans evolved early in domestication but was subsequently lost in the dingo lineage. On this account, both the initial motivation to initiate interspecific eye contact and the motivation to maintain prolonged eye contact with a familiar human evolved in the early stages of canid domestication. However, the tendency to maintain prolonged eye contact with a familiar human may have been lost as dingoes underwent at least 5000 years of subsequent natural selection. Without the selection pressures imposed by domestication, the motivation to maintain eye contact with familiar humans may have been lost. If this account were true, one would expect that early generations of domesticated animals, such as domesticated foxes (e.g. Trut, Oskina, & Kharlamova, 2009), would begin to show a tendency to maintain eye contact with a familiar human at around the same time they begin to initiate eye contact with humans at all.

Considered more broadly, our demonstration that dingoes show an intermediate pattern of eye contact within canids not only sheds light on the way in which interspecific eye contact developed across domestication, but also has important implications for understanding how social bonds developed between dogs and humans. Recent work suggests that eye contact is a particularly important behaviour underlying the social bonds between dogs and humans, as eye contact triggers the release of oxytocin, a hormone implicated in social bonding, in both species (Nagasawa et al., 2015; but see Fiset & Plourde, 2015; Kekecs et al., 2016, for critiques). Specifically, dog-initiated eye contact is thought to lead to an increase in human oxytocin, which prompts humans to affiliate more with the dog (e.g. more petting, touching). Such human-initiated affiliation, in turn, is thought to lead to an increase in oxytocin levels in the dog, which then prompts the dog to make more eye contact with humans (Nagasawa et al., 2015). Put simply, it seems that dog–human eye contact works as a sort of positive feedback loop that facilitates social bonding between the two species.

However, we did not see evidence of this sort of positive feedback loop in dingo–human interactions. Specifically, there was no correlation between the amount of time dingoes made eye contact with the human handler and the amount of time the handler touched or talked to the dingoes, although there was a correlation between eye contact and both of these affiliative behaviours for dogs in previous work (Nagasawa et al., 2015). Thus, although dingoes' tendency to initiate eye contact with humans may have been the first evolutionary step in the development of this powerful feedback loop, this tendency may not have been fully integrated into a more general system of interspecies social bonding until later in domestication. However, as mentioned earlier, it will be crucial for future work to compare pet dogs and pet dingoes to more directly test this hypothesis.

Based on our results, then, it seems that the human–dog bond may have developed in two stages. The earliest selection pressures of domestication may have favoured those canids that showed any tendency to make eye contact with humans. This initial tendency would have been adaptive because it co-opted a preexisting system of parent–child bonding in humans (one that takes eye contact as an input; e.g. Dickstein, Thompson, Estes, Malkin, & Lamb, 1984). Thus, the first stage of domestication encouraged humans to treat ancestral dogs as social partners. Once humans treated dogs as social partners, they would have begun to exhibit many of the same affiliative behaviours they would when interacting with a human infant (e.g. touching, talking in a high-pitched voice). These affiliative behaviours then in turn may have co-opted the canine system of conspecific bonding (Romero, Nagasawa, Mogi, Hasegawa, & Kikusui, 2014, 2015), which in turn encouraged early canids to treat humans as social partners.

In line with this possibility, recent work comparing different dog breeds suggests that dogs' responsiveness to human social cues may have undergone a second phase of selection with the selection of breeds. For instance, although dogs of all breeds show a proclivity to follow human pointing and gaze direction, working breeds (e.g. shepherds and huskies) are more likely to follow human social cues like pointing and gaze direction than nonworking breeds (e.g. basenji and toy poodles; Wobber et al., 2009). These differences between breeds suggest that dogs' tendency to follow human social cues underwent further selection later in domestication. In fact, even within working breeds, there are surprising differences in dogs' interspecific social behaviour. In one recent study, researchers administered oxytocin to dogs from cooperative working breeds (e.g. border collies) and independent working breeds (e.g. Siberian huskies) in order to compare how oxytocin impacted their interspecific social behaviour (Kovács, Kis, Pogány, Koller, & Topál, 2016). Dogs from cooperative working breeds were more likely than dogs from independent working breeds to gaze to an experimenter in an unsolvable task, to socially reference their owner in a potentially dangerous situation and to tolerate sustained eye contact from an experimenter. These findings line up with our own, suggesting that domestication selection on interspecific social behaviour between dogs and humans may have been applied in multiple phases.

Our findings not only shed light on the way interspecific eye contact and interspecific bonding may have evolved across canid domestication, but they also highlight the importance of considering more than just the extremes of domestication. By including species like dingoes that represent intermediate points across domestication, we can gain unique insight into the precise way in which particular behaviours, such as interspecific eye contact, evolved.

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Supplementary material

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