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Testing coyotes in an object choice task following a human gesture

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Interspecific communication is often studied by determining a species ability to respond to human gestures. Results emerging from pet versus free-roaming domestic dogs (C*anis familiaris*) elucidate differences in the behavioral changes that occur based on life experience and human socialization in the development of social cognition. Additional research on wild species of canids raised with minimal levels of human socialization may provide insight into the importance of human socialization in the ability of non-human animals to correctly respond to a human gesture. We used captive coyotes (*Canis latrans*) to test whether coyotes could use human pointing gestures to succeed in an object-choice task. We specifically tested two groups of coyotes; both were minimal human socialization but one group was coyote-reared while the other group had high levels of human socialization during early ontogenetic development because they were hand-reared until 12 weeks of age. We tested 12 coyotes (n = 5 hand-reared, n = 7 coyote-reared) on responses to a human distal-pointing gesture across 10 trials each. Only one coyote, a hand-reared male, performed better than expected by chance and made correct choices in eight trials (incorrect choices in trials three and four). We found no difference between coyote- or hand-reared coyotes in their abilities to respond correctly to a human distal-pointing gesture ($t = -0.043$, $P = 0.97$). Performance did not improve over time among all coyotes or within either group. The preliminary results from this study suggest that most coyotes will not respond to human gestures and early life experience does not appear to improve adult performance. These findings are in contrast to most studies of gesture studies of canids.

KEY WORDS: *Canis latrans*, domestication, social cognition, task performance.

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INTRODUCTION

Interspecific communication has been studied in a variety of taxa to assess cognitive sociability, with a surge in the literature over the last two decades. Most studies have used human gesturing towards another species as the metric for interspecific communication. While the ability to respond to human gestures has been studied in a wide array of species, from marine mammals (e.g., Pack & Herman 2007) to birds (von Bayern & Emery 2009), much of the literature has focused on domestic canids. Domestic dogs (*Canis familiaris*) have been shown to be successful at responding correctly to human gestures, including complex gestures (Miklósi & Soproni 2006; Elgier et al. 2012). These results have led to the suggestion that convergent evolution with humans (Hare & Tomasello 2005) or development of a more human-like social cognition through domestication may be at play (Hare et al. 2002; Miklósi & Topál 2013). However, these conclusions have been mostly based on tests using pet dogs, while tests using free-roaming dogs have indicated socialization and life experience may be critical to performance (Bhattacharjee et al. 2020). Further, life experience related to human interactions have been hypothesized to be important because most tests use ipsilateral pointing – a gesture animals may have learned to pay attention to prior to testing because of its common use by humans (Nawroth et al. 2020).

Studies have also extended to other canids, including gray wolf (*Canis lupus*; Udell et al. 2008; Gácsi et al. 2009), silver fox (*Vulpes vulpes;* Hare et al. 2005), and coyote (*Canis latrans*; Udell et al. 2012). Unlike domestic dogs, wild canids are not obligatorily symbiotic with humans (Coppinger & Coppinger 2001). Yet, captive populations of these species exist and some populations are domestic or semi-domesticated. Some gray wolf individuals have been hand-reared and socialized with humans to a high degree, and the genetically tame foxes of Novosibirsk, Siberia offer a unique perspective of the mechanics of domestication. Studies of these canids provide a mechanism to explore the evolutionary nature of responsiveness to human gestures and how it is influenced by domestication. Research on both captive wolves with limited human socialization and on hand-reared and highly socialized wolves give conflicting results on the ability of wolves to outperform dogs (Miklósi et al. 2003; Virányi et al. 2008; Hare et al. 2010; Udell et al. 2012). Those studies demonstrating success have been hypothesized to be linked to acceptance of humans as social companions by individual wolves (Udell et al. 2010; Heberlein et al. 2016). Human acceptance by wild individuals may allude to the mechanism that contributed to the domestication of dogs from wolves (Udell et al. 2010). Thus, studies demonstrating that wolves do not outperform dogs further the hypothesis that domestication is key in cognitive development of a species. Similar experiments comparing domesticated and non-domesticated foxes found domesticated foxes are more successful in understanding human communicative cues than their non-domesticated conspecifics (Hare et al. 2005). However, not all wild canids have domestic or even semi-domestic counterparts. In fact, some species, like the coyote, are notable for their lack of domesticated conspecifics (Sandlos 1999), and these taxa could offer a unique comparative group to understanding how canids respond to human social cues.

As the human population continues to expand, wild canids are more frequently encountering and interacting with humans. These frequent encounters shape behavioral responses of canids to humans (e.g., Barocas et al. 2018; Young et al. 2019a); however wild canids have varying and extremely different encounters with humans. Humans can be a source of food and shelter or persecute canids (Srivathsa et al. 2019).

Free-ranging dogs have been shown to respond differently to different human cues (Bhattacharjee et al. 2018) and coyotes (Breck et al. 2019) have been shown to respond differently to humans in different social contexts. Parental fear in coyotes has been shown to reduce with accumulating experiences with humans across time, with resulting phenotypic shifts in offspring behavior (Schell et al. 2018). Thus, we would predict that wild canids with different previous parental and human experiences may respond differently to human gesture cues.

Coyotes, a close evolutionary relative to wolves and dogs, are known for their ability to live and thrive in human environments (Bateman & Fleming 2012); however, they are not domesticated, and very few captive populations exist. To date, only two coyotes in captivity, both hand-reared and extremely socialized with humans, have been tested on human gesture performance tasks. While both showed trends in their ability to follow a human pointing gesture, only one was statistically significant (Udell et al. 2012). Since it remains unclear if coyotes can successfully follow human gestures in an object choice task, we tested coyotes with limited human interactions in an object choice task following a human-distal pointing gesture. We evaluated overall success and success across trials to determine if performance improved over time. Because parental effects allow parents to shape offspring phenotypic development (Benard & McCauley 2008; Champagne 2008; Uller 2008; Duckworth et al. 2015), we also compared the results from coyotes tested that were hand-reared by humans and therefore had high levels of human socialization during early life development to the tested coyotes that were raised by coyote parents and without human socialization during this stage. This study provides preliminary results that contribute to the greater understanding of how animals respond to human social cues.

MATERIALS AND METHODS

Study site

The study was conducted at the U.S. Department of Agriculture, National Wildlife Research Center's Predator Research Facility in Millville, Utah, USA. The facility houses about 100 coyotes, primarily kept as male-female pairs in outdoor enclosures and serves as a platform from which researchers can observe coyotes that have a behavioral repertoire similar to that documented for coyotes in the wild (Shivik et al. 2009). All coyotes used in the experiment ($n = 12$) were housed singly in 1000-m^2, tear-drop shaped, outdoor pens (Fig. 1). The pens were situated in groups of three, with the narrow end of each pen converging at a common observation building. Adjacent pens shared a common 2-m high cement sidewall. Pen floors consisted of natural substrate of soil, low vegetation, and some grasses. Animals had constant access to a PVC den box (0.5 m high × 0.5 m diameter). In addition, each pen contained two 0.7 m high plywood shade tables (1.2 m × 0.9 m × 0.6 cm) that coyotes could use as a shelter or platform. Water was provided ad libitum.

All coyotes at the facility experienced similar levels of human interaction other than during their first ~ 12 weeks of life. Coyote-reared coyotes were born to a breeding pair at the facility and received minimal human interaction as pups, while hand-reared coyotes were brought to the facility from the wild at 2–5 weeks of age (typically around 2–3 weeks old), bottle fed until they are 8–10 weeks old, and received other additional human care until they are 12–15 weeks. Beyond 12–15 weeks of age, staff interact with the pups the same as for coyote-reared pups: they are each fed 650 g of commercial mink food (Fur Breeders Agricultural Cooperative, Logan, Utah) by animal care staff, who enter the pen and scatter feed the ration 6–7 days each week. Human interactions are otherwise limited to capturing and handling coyotes for their annual vaccines or

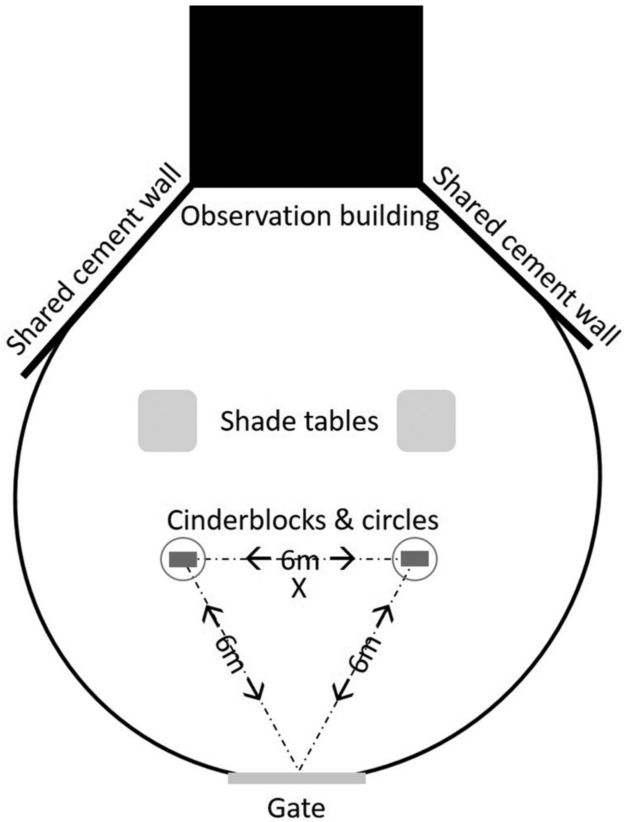

Fig. 1. — Depiction of the set up to test human-given pointing gestures in an object choice task for captive coyotes. The cinderblocks (dark gray rectangles) were placed 6 m from the pen entrance and from each other, forming an equilateral triangle. Circles were spray-painted in a 60-cm circle from the center of the cinderblock. The researchers met and one remained standing between the two cinderblocks during trials; the spot is marked by an X. Figure is not to scale.

to move among enclosures for colony management and research. All applicable institutional guidelines for the care and use of animals were followed, in accordance with the ethical standards of the NWRC and approved by its Institute for Animal Care and Use Committee (QA-2739).

Study design

We aimed to follow trials and statistical procedures described in Udell et al. (2012) to allow for direct comparisons with the coyotes tested in that study, but made modifications to accommodate the temperament of the captive coyotes as described here. Two hollow cinderblocks 15-cm^3 were buried level to the ground prior to the coyote being housed in the enclosure to avoid neophobic responses (Mettler & Shivik 2007) and remained as permanent fixtures throughout the study. They served as the receptacle for food during training and as the response choice objects during testing (Fig. 1). The cinderblocks were placed below ground so as not to allow the coyote to see if a reward was contained inside without coming close enough to investigate.

Two researchers participated in each trial, but the same person always conducted the gestures during all trials. Both researchers wore dark sunglasses to avoid eye gaze cues. The main researcher wore a small camera on a chest harness to record each trial. Each researcher also carried a small 2.5-gall bucket in a neutral position in which to keep the food reward. The buckets were of the same type that the coyotes are fed from each day, and both buckets contained food to neutralize scent cues. All food used in the experiment came from a portion of the coyotes' normal daily food rations. The coyotes received the remaining portion of their normal daily ration in a different area of their pen after the training, testing, or control trials were completed each day.

We first trained study animals to eat food off of the cinderblocks in the presence of observers because this was atypical to their regular feeding regime, where a human typically enters the pen, scatter feeds, and then exits the pen. During training, both researchers would enter the pen and proceed to a pre-determined cinderblock, randomly chosen with a coin flip. They would simultaneously make the motions of placing a food item inside one of the cinderblocks, with only one researcher placing the food item. The cinderblock that first received the food was randomly chosen with a coin flip and was then alternated for each trial and each day. After the food was placed, the researchers would meet at a point between the cinderblocks and the assistant would leave the pen. The main researcher would then stand in a neutral position facing forward for 5 sec before backing to the gate of the enclosure and waiting an additional 60 sec. If a coyote was particularly reluctant to approach the researcher, a small amount of food would also be placed near the cinderblock until the coyote was comfortable enough to eat from the cinderblock. The main researcher would then leave, noting whether the coyote had approached and eaten the food while the researcher was present. The procedure was repeated 2 times per day. Coyotes were considered suitable for testing when they had eaten from the cinderblocks for 3 consecutive days (six trials). This indicated that the coyotes knew food was present after the researchers retreated, and that they were sufficiently comfortable in the researcher's presence. The training phase continued for up to 2 weeks but ended earlier if the coyote met the standards for testing.

During testing, the researchers would proceed as they had during training, but neither researcher would place food in their respective cinderblock. Instead, once the second researcher left the pen, the main researcher would stand facing forward in a neutral position for 5 sec. After the 5 sec had passed, the researcher would perform a distal-pointing gesture towards one of the two cinderblocks. The distal-pointing gesture was performed by the researcher bringing his ipsilateral arm out from the side of the body to point towards one of the cinderblocks for 4 sec. The position was held with the body oriented forwards, looking directly ahead. The cinderblock was randomly chosen with a coin flip prior to entering the pen. Immediately after, the main researcher would back up in a straight line to the gate of the pen and resume facing forward in a neutral position. The main researcher would then remain in place for an additional 60 sec or until the coyote indicated a choice. A choice was indicated by the coyote crossing the 30-cm buffer around a cinderblock (Fig. 1).

When a correct choice was made, the coyote would receive an immediate food reward held by the main researcher and tossed to the correct cinderblock. If an incorrect choice was made or if 60 sec passed without a choice, the researcher immediately left the pen with no reward given. Only a correct choice resulted in a reward and was counted as a success for analysis. A failure to choose was considered an incorrect choice. Each coyote was tested 2 times a day at 08:00 and 12:00 for 5 days for a total of 10 trials. This schedule was used in an attempt to follow procedures used during training and ensure there was sufficient time to test all coyotes each day.

We also ran a control phase that was identical to the testing phase, but no gesture was given. The correct cinderblock was randomly chosen with a coin flip prior to entering the pen. A correct choice was rewarded with food. After an incorrect choice or after 60 sec with no choice the researcher would leave the pen and proceed to the next trial. During the control phase, each coyote was tested 6 times. All control trials were performed in a single day. Unfortunately, we were unable to follow the two-tests per day schedule due to logistical restraints with colony management but the overall amount of time the human interacted with the coyotes during testing was only slightly longer than on trial days since the control tests took less time to conduct.

Data analyses

Two-tailed binomial tests were conducted for each individual to determine if it performed better than chance. Chance was considered a 50% success rate over the 10 trials. A two-sample t-test was used to determine whether there were differences in the correct responses between coyote-reared or hand-reared coyote groups. A one-sample t-test was also used to determine whether coyotes performed better than chance within groups. We also performed a two-sample t-test of the first trial data to compare total correct of coyote- and hand-reared coyotes. Using "geepack" package (Højsgaard et al. 2006) in program R (R Core Team 2017), a generalized estimating equation (GEE; Liang & Zeger 1986; Zeger & Liang 1986) using an autoregressive correlation structure and binomial distribution was performed to compare hand-reared and coyote-reared coyote performance over time.

RESULTS

Twenty-five coyotes (15 male, 10 female) were selected for use on this study, 16 that were hand-reared (7 males, 9 females). Only 12 were tested based on successful completion of training trials. The 12 coyotes tested included five hand-reared coyotes (3 male, 2 female) and seven coyote-reared coyotes that were all male. Tested coyotes ranged from 2–7 years old. One male coyote would only participate if, after giving the signal, the researcher retreated an additional meter and closed the gate to the pen. Apart from this, he was tested the same as the other subjects and his inclusion or omission in statistical analyses does not change the results.

Binomial tests showed that only one coyote performed significantly better than chance ($P = 0.05$; Table 1). This coyote, a hand-reared male, chose 8 of 10 trials correctly. GEE results showed there was a difference across time ($\beta = -0.11$, $P = 0.03$), with coyote success declining across trials. We found no difference between coyote-or hand-reared coyotes in their abilities to respond correctly to the indicated signal ($t = -0.043$, $P = 0.97$), even if only assessing the first trial ($t = -1.3065$, $P = 0.22$). There was also no difference between groups in performance relative to chance in the control phase (coyote-reared: $t = -0.28546$, $P = 0.78$; hand-reared: $t = 0.07943$, $P = 0.94$), or across trials ($\beta = 0.04$, $P = 0.93$).

DISCUSSION

Our preliminary results indicate that most coyotes are unable to intuit the meaning of a human pointing gestures. Only one coyote of the 12 tested performed better than would be expected by chance. This is unlike in dogs, where most can follow a human gesture (Soproni et al. 2002), even when the human is merely a projected figure (Pongrácz et al. 2003), and wolves that have been raised using dog-like conditions related to human socialization (Miklósi et al. 2003). However, the success of wolves was poor relative to dogs. This was attributed to lower willingness to look at humans (Miklósi et al. 2003). In our study, we noted that the coyotes did not look at the humans consistently during tests.

Table 1.

The proportion of testing (out of 10) and control (out of 6) trials that a hand-reared or coyote-reared coyote succeeding at during gesture following tasks. Results are listed by coyote ID and whether it was hand-reared or coyote-reared as a puppy at the USDA-National Wildlife Research Center's Predator Research Facility. Only one coyote performed better than expected by chance during the tests (*) but none performed better than chance during control trials.

Coyote ID	Type	Tests	Controls
1151	Coyote-reared	0.30	0.00
1521	Coyote-reared	0.50	0.67
1331	Coyote-reared	0.30	0.33
1143	Coyote-reared	0.30	0.00
1347	Coyote-reared	0.50	0.67
1071	Coyote-reared	0.40	0.50
1162	Coyote-reared	0.60	0.50
1033	Hand-reared	0.30	0.50
1408	Hand-reared	0.10	0.67
1031	Hand-reared	0.30	0.00
1405*	Hand-reared	0.80	0.50
1413	Hand-reared	0.60	0.50

Over half of the coyotes randomly selected to participate in this study failed to perform during training, suggesting phobia to human or object presence may have influenced behavior. Neophobia, fear of novel objects, has previously been shown in coyotes (Mettler & Shivik 2007). Captive and wild coyotes have also been shown to more likely avoid novel stimuli in familiar settings (Harris & Knowlton 2001). In this study, we attempted to reduce object neophobia by placing coyotes in pens where the cinder blocks were already in place. The coyotes only experienced a novel feeding stimulus (i.e., human presence during feeding). This technique has been effective for other studies reliant upon object-based testing with captive coyotes (e.g., Young et al. 2019b). However, even if the coyotes habituated to the object, the presence of the human for a longer than normal period of time may have altered the behavioral state of the coyotes and their ability to perform the task. An anxious behavioral state related to the longer presence of humans was suspected to alter free-roaming dog gesture performance (Bhattacharjee et al. 2020).

We expected to observe a difference between hand-reared and coyote-reared coyotes. Some of the hand-reared coyotes appear to have a greater tolerance to human presence and maternal effects have the potential to drive both the direction and strength of evolutionary change in a population (Wolf et al. 1998; Marshall & Uller 2007; Bonduriansky & Day 2009). The lack of a difference within our preliminary results is likely caused by one of three mechanisms: object/human-phobia affecting the behavioral state of the test subjects as described above, the minimal length of time hand-reared coyotes were hand reared, or the differences between our test and that performed by others. We do not think the modifications made for coyotes would cause the high rate of failure we observed, especially because the modifications were made to accommodate coyote behavior that may otherwise have inhibited performance. Previous tests have been altered to accommodate the behavior of coyotes when using coyotes at the facility (e.g., Young et al. 2019a, 2019b) and different conditions have also been used to test gesture ability by other canids that also could not be tested in ways that pet dogs are typically tested (e.g., Bhattacharjee et al. 2020). Instead, we suspect the lack of a difference between groups was related to the early cessation (i.e., at 12–15 weeks of age) of extreme human interactions.

Although early life-stage interactions can have life-long impacts on behavioral phenotoypes of coyotes (Schell et al. 2018), it is likely that the hand-reared care ended at an early enough stage in coyote development to not have long-term impacts on their responsiveness to human gestures, even despite subsequent daily interactions with humans during feeding and welfare checks. The tests performed in human socialized wolves indicated the wolves received a great deal more socialization than the hand-reared coyotes we tested. This includes more physical contact, daily interaction with humans, and participation in educational presentations with the public (Miklósi et al. 2003; Hare et al. 2005; Udell et al. 2010). These wolves performed better than their less tame conspecifics (Hare et al. 2005). Similarly, dogs with more human socialization perform better than less socialized dogs (Udell et al. 2010; Bhattacharjee et al. 2020). Even so, all the coyotes that were tested had demonstrated that they knew food was present and were willing to approach and eat while the experimenter was present. Indeed, most coyotes continued to approach the researcher and search for food throughout the trials. These conditions should allow for an animal with the ability to intuit human social gestures to successfully complete the object choice tasks. If socialization is an important component to understanding human social gestures, then further tests could be made using coyotes that have been raised with human socialization beyond ~ 12–15 weeks. However, few coyotes fitting this description exist, and the one study to use such coyotes was limited to a sample of two and with ambiguous results (Udell et al. 2012). Further, the inability of all but one coyote in this study to succeed at following human gestures suggest it is rare for coyotes to understand the meaning of human gestures.

Our preliminary results also suggest coyotes did not improve their response to human gestures over time (i.e., learn a correct response across trials). We had anticipated that successful coyotes would be more likely to continue to be successful in subsequent trials via a learned response. Instead, we found a slight decrease in the proportion of successful trials across time. This may have been a result of coyotes not tolerating the continued presence of a human in their pen over a short period of time, since trials were conducted 2 times a day over 5 consecutive days. Or it may suggest coyotes were unable to learn the task. Working but not domestic pet dogs showed improved performance across trials in a similar gazing study, suggesting an ability to "learn to learn" must first be present (McKinley & Sambrook 2000). In that study, McKinley and Sambrook (2000) also suggest the better performance of domestic dogs relative to horses (*Equus caballus*) may relate to selective pressures imposed by humans in recent history resulting in dogs having more cognitive traits responsive to human cues. Thus, although captive and wild coyotes interact with coyotes and can live in human-dominated landscapes (Bateman & Fleming 2012), human-related trait selection is unlikely related to human cues such as gesturing.

CONCLUSIONS

Our preliminary results contribute to the growing body of literature on interspecific communication and may help explain why no populations of domestic coyotes exist, though anecdotes and speculations of domesticated coyotes and coyote-like dogs among Native Americans can be found in the historical record (Coues 1873; Young & Jackson 1951). Unlike the experiments with the silver fox (*Vulpes vulpes*) in Siberia (Trut 1999), no concerted effort has been made to domesticate the coyote through controlled breeding in modern times. The domestication of the dog took place over thousands of years, and it is debated whether dogs inherited their unique cognitive abilities from their ancestors or if these traits evolved as a consequence of domestication (Miklósi et al. 2003; Hare & Tomasello 2005; Udell et al. 2008; Miklósi & Topál 2013). Further studies on coyote's cognitive ability will allow for more detailed comparison among canids. Coyotes that are hand reared for a longer period of time than our hand-reared coyotes could show greater ability to understand human behavior than those that were tested here. Some researchers suggest raising cohorts specifically for studies of this nature (Hare et al. 2010). This would be difficult in the case of coyotes but would control for previous experience with humans.

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DISCLOSURE STATEMENT

The authors declare that they have no conflict of interest.

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ETHICAL STANDARD

All applicable institutional guidelines for the care and use of animals were followed, in accordance with the ethical standards of the NWRC and approved by its Institute for Animal Care and Use Committee (QA-2739).

AUTHOR CONTRIBUTION

N. Floyd conceived of the study, collected and coded data, wrote the first draft of the manuscript, and analyzed data. J.K. Young helped design the study, assisted with data analyses, and contributed to writing the manuscript. Both authors commented on previous versions and read and approved the final manuscript.

SUPPLEMENTAL DATA

Supplemental data for this article can be accessed at https://doi.org/10.1080/03949370.2020.1837966.

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DATA ACCESSIBILITY

All data generated or analyzed during this study are included as a supplementary information file.

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