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SOCIABILITY AND GAZING TOWARD HUMANS IN DOGS AND WOLVES: SIMPLE BEHAVIORS WITH BROAD IMPLICATIONS

MARIANA BENTOSELA¹, C. D. L. WYNNE², M. D'ORAZIO¹, A. ELGIER¹, AND M.A.R. UDELL³

¹INSTITUTO DE INVESTIGACIONES MÉDICAS, IDIM-CONICET, BUENOS AIRES, ARGENTINA

²ARIZONA STATE UNIVERSITY, TEMPE

³OREGON STATE UNIVERSITY, CORVALLIS

Sociability, defined as the tendency to approach and interact with unfamiliar people, has been found to modulate some communicative responses in domestic dogs, including gaze behavior toward the human face. The objective of this study was to compare sociability and gaze behavior in pet domestic dogs and in human-socialized captive wolves in order to identify the relative influence of domestication and learning in the development of the dog–human bond. In Experiment 1, we assessed the approach behavior and social tendencies of dogs and wolves to a familiar and an unfamiliar person. In Experiment 2, we compared the animal's duration of gaze toward a person's face in the presence of food, which the animals could see but not access. Dogs showed higher levels of interspecific sociability than wolves in all conditions, including those where attention was unavailable. In addition, dogs gazed longer at the person's face than wolves in the presence of out-of-reach food. The potential contributions of domestication, associative learning, and experiences during ontogeny to prosocial behavior toward humans are discussed.

Key words: sociability, gaze behavior, domestic dogs, socialized wolves

One of the most important consequences of domestication is that dogs and people have become social partners (Freedman, King, & Elliot, 1961; Udell, Dorey, & Wynne, 2010a); each species accepts proximity, and even cohabitation, with the other. Moreover, it has been observed that dogs develop an attachment bond with their owners (e.g., Nagasawa, Mogi, & Kikusui, 2009; Topál, Miklósi, Csá-& Dóka, 1998; Valsecchi, Previde, Accorsi, & Fallani, 2010), which is similar to that shown by human infants with their mothers. Several studies have also demonstrated beneficial physiological and behavioral effects of these interactions for both species (McCardle, Mccune, Griffin, & Maholmes, 2010; Odendaal & Meintjes, 2003). In addition, Feuerbacher and Wynne (2014) showed that human petting can be an important reinforcer for dogs in social contexts.

Sociability, defined as the tendency to approach and interact with unfamiliar individuals, is one important aspect of the human-

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dog relationship. Dogs vary in their level of interspecific sociability and this trait can influence a variety of behavioral responses as well as individual success in different environments (Svartberg & Forkman, 2002). For example, willingness to approach unfamiliar humans can influence a dog's likelihood to be adopted from a shelter (Protopopova, Gilmour, Weiss, Shen, & Wynne, 2012; Protopopova & Wynne, 2014). Therefore, in the current study, we chose to focus specifically on canine sociability and gaze behavior toward humans, comparing the responses of both pet dogs and humansocialized wolves in contexts where social behavior was reciprocated and where it was ignored.

Studies comparing the sociability and human responsiveness of different populations of domestic dogs have demonstrated that lifetime experiences are important in the development of social bonds between dogs and humans (e.g., Scott & Fuller, 1965; Udell et al., 2010a). Barrera, Jakovcevic, Elgier, Mustaca, and Bentosela (2010) showed that, in a simple sociability test, shelter dogs remained closer to passive unknown humans than did pet dogs, but also presented more fearappeasement behaviors. Laboratory-reared dogs and dogs living in shelters have also been found to show an impaired ability to follow subtle human gestural cues to a target in

Address correspondence to Mariana Bentosela, Grupo de Investigación del Comportamiento en Cánidos (ICOC), Instituto de Investigaciones Médicas (IDIM) CONICET. Combatientes de Malvinas 3150 (1426) Buenos Aires, Argentina (email: marianabentosela@gmail.com).

object choice tasks (Lazarowski & Dorman, 2015; Udell, Dorey, & Wynne, 2008; Udell, Dorey, & Wynne, 2010b), although this effect can often be reversed with additional training (Udell et al., 2010b). Shelter dogs also exhibit a faster extinction of gaze toward a human face in the presence of out-of-reach food than do pet dogs (Barrera et al., 2010).

Several studies have suggested that canine sociability may influence communicative responses, including those between dogs and humans, and may affect behavior and performance in social problem-solving tasks. For example, dogs have been found to look at the human face when they encounter an unsolvable problem (Gácsi, Miklósi, Varga, Topál, & Csányi, 2003), and also to alternate gaze between the human face and the location of out-of-reach items (Miklósi, Polgárdi, Topál, & Csányi, 2000), which can lead to successful solicitation of human assistance in retrieving a reward

Jakovcevic, Mustaca, and Bentosela (2012) demonstrated that individual levels of sociability correlate with this communicative response in domestic dogs. An unfamiliar person remained near a source of food that was visible, but out of reach of the dog, and initially provided some of this food each time the dog gazed toward the experimenter's face. In the second phase of this study, the response was extinguished; dogs no longer received any of the food whatever their behavior. As a result, the rate of gazing behavior decreased. However, the results also demostrated that more sociable dogs exhibited longer gaze durations during the extinction phase than did dogs which had previously scored lower on a sociability test.

Domestication has altered the timing and development of social behavior in canines (Klinghammer & Goodman, 1987; Trut, 1999; Udell et al., 2010a). It is possible, therefore, that differences in sociability between domesticated and nondomesticated canines could also influence performance on tasks in which gazing at a human is measured.

Early studies comparing dog and wolf responsiveness to humans suggested that wolves were less capable of forming strong bonds to humans (Topál et al., 2005), and were less likely than dogs to look at the human face when confronted with an unsolvable task (Miklósi et al., 2003). More recently, however,

human socialized wolves have shown repeated success on human guided object choice tasks-for example, following a point made with the arm or another part of the human body to a target (e.g., Udell et al., 2008, 2012)—and have been found to have the capacity to form secure attachment bonds to humans as pups (Hall, Lord, Arnold, Wynne, & Udell, 2015). Other human-socialized wild canines, including covotes (Udell et al., 2012), dingoes (Smith & Litchfield, 2009) and foxes (Barrera, Jakovcevic, Mustaca, & Bentosela, 2012) have also been shown to perform well on human guided tasks. These findings suggest that domestication is not a prerequisite for responsiveness to human actions, and that differences in some human-directed social behaviors in wild versus domesticated canines may have more to do with developmental timing than with an inherent ability.

One outcome of genetic domestication is a shift or delay in the sensitive period for social development (Trut, 1999), thereby allowing dogs to be tamed with relative ease compared progenitors, their wild wolves (Klinghammer & Goodman, 1987). Young dogs also display differences in attachment behavior compared to wolf pups, spending more time in proximity to their owner and less time exploring their environment (Topál et al., 2005). At the other extreme, pet dogs can become so dependent on social contact with humans that even short periods of separation can cause separation anxiety; this serious condition often culminates in destructive behavior and in some cases medically significant self-injury in dogs (McCrave, 1991).

What remains unknown is the degree to which adult dogs and human-socialized wolves differ when it comes to sociability toward familiar and unfamiliar people, and their willingness to gaze at humans outside the context of an unsolvable task. The present study therefore had two goals. The first goal was to evaluate the level of sociability that humansocialized wolves and pet domestic dogs show toward people. This was accomplished through an assessment of each animal's behavioral response to the presence of an unknown person, followed by measurement of their response to their owner or caretaker when attention was either available or unavailable. The second goal was to assess the gaze duration of pet dogs and wolves toward a familiar person triggered by the presence of an out-ofreach, but visible food reward.

Experiment 1

In Experiment 1, we compared the sociability of dogs living as pets with that of human-socialized wolves, using a simple measure of voluntary approach toward, and time spent near, a human being. For a subset of wolves, it was safe to use an unfamiliar human: for all wolves and dogs, sociability toward a familiar human was measured.

Method

Subjects. Eleven human-socialized gray wolves and 11 pet domestic dogs participated in this study. All of the animals had prior experience in other communicative tests (e.g., point following, Udell et al., 2008). One additional dog was not included because the owner did not follow the experimenter's instructions during the test. See Table 1 for more details on the subjects.

Wolves resided at Wolf Park (Battle Ground, IN), and had been hand-raised by staff from 10–14 days of age under the process described by Klinghammer and Goodman (1987). The

wolves in this facility, although genetically wild, are human-socialized (tame) and interact with humans on a daily basis, regularly receiving food treats and attention from humans. Dog subjects lived in family houses as pets, and were also accustomed to receiving regular human attention and food treats. Neither group had any history of special training beyond basic obedience.

Procedure. Wolves were tested individually in familiar outdoor enclosures. Dogs were tested in the part of their home where they spent most of their time (indoor-living dogs were tested indoors, whereas outdoor-living dogs were tested outdoors). During testing, the experimenter sat on a familiar bucket (wolves) or a chair (dogs). A circle 1 m in circumference was marked around the chair in order to simplify assessment of the animal's proximity to the person.

Following the procedure of Jakovcevic et al. (2012), the sociability test consisted of a passive and an active phase, each of 2 min duration. In the passive phase, the experimenter entered, sat on a chair or bucket, remained quiet and ignored the subject by looking down toward the floor. If the animal sought physical contact, then the experimenter touched the subject twice. She never

Table 1 Subject Details

Name	Breed	Age (years)	Sex	Testing Location	Familiar Condition Only
Ayla	Grey Wolf	8	F	Outdoors	
Ćhetan	Grey Wolf	17	M	Outdoors	
Dharma	Grey Wolf	2	F	Outdoors	
Kalani	Grey Wolf	8	F	Outdoors	X
Marion	Grey Wolf	14	F	Outdoors	X
Miska	Grey Wolf	16	F	Outdoors	X
Renki	Grey Wolf	8	M	Outdoors	X
Ruedi	Grey Wolf	8	M	Outdoors	
Tristan	Grey Wolf	14	M	Outdoors	
Wolfgang	Grey Wolf	7	M	Outdoors	X
Wotan	Grey Wolf	7	M	Outdoors	
Canela	Poodle	6	F	Indoors	X
Elvis	Mongrel	2	M	Indoors	X
Fido	Mongrel	4	M	Outdoors	
Goofy	Poodle	6	M	Indoors	
Juanita	Mongrel	10	F	Indoors	
Julieta	Beagle	9	F	Indoors	X
Mia	Poodle	5	F	Indoors	
Mirko	Border collie	3	M	Indoors	X
Rimini	Mongrel	2	M	Indoors	
Sasha	Labrador	5	F	Indoors	
Tato	German shep	2	M	Outdoors	X

spoke to or looked at the animal and remained looking at the floor throughout. The active phase followed immediately and was identical to the passive phase except the experimenter stood and called the animal by name, and tried to make contact with it. She spoke to and touched the subject if it came close enough to reach while remaining near the bucket or chair. If the animal moved away, then the experimenter called again to recover its attention.

Six naive individuals from each subspecies were tested on this procedure, first by an unfamiliar and then by a familiar experimenter. Five additional individuals from each subspecies were tested by a familiar experimenter only. Safety concerns prevented five wolves from participating in the unfamiliar condition at the time of testing; thus, five dogs were also tested with this modification.

An assistant filmed each session from 4 m away. The following were later coded from video by two independent raters (interrater reliability, IRR, for approach latency and proximity: correlation coefficient, R = .99).

Approach latency (s). Measured from the time the experimenter sat down until the animal approached (forelegs within 1 m of the experimenter) during the passive phase.

Proximity. Duration (s) the subject remained close to the experimenter—defined as any part of the body less than 1 m from the experimenter, summed over the active and passive phases.

Results and Discussion

Subjects experiencing both the familiar and unfamiliar conditions. The data were not normally distributed; therefore, raw values were transformed to ranks prior to carrying out ANOVA (this method only permits analysis of main effects: Iman, Hora, & Conover, 1984). For each variable, a mixed-model ANOVA was carried out with the within-subjects factor Experimenter familiarity (Familiar vs. Unfamiliar), and the between-subjects factor Subspecies (Wolf and Dog). An alpha level of .05 was adopted.

Ranked approach latency. The ANOVA revealed a significant main effect of subspecies (F(1,10) = 10.10, p < .01). The effect of familiarity of the experimenter was not significant. Dogs approached the experimenters with a

shorter latency than did wolves (dog mean rank 8.5, latency 44.6 s, wolf mean rank 8.6, latency 100.6 s).

Ranked time in proximity of humans. The ANOVA revealed a main effect of subspecies (F(1,10) = 20.50, p < .01). Dogs spent longer in proximity to experimenters than did wolves (dog mean rank 8.13, duration 168 s, wolf mean rank 16.88, duration 60 s). There was also a significant main effect of familiarity (F(1,10) = 10.10, p < .01). Subjects spent longer in the proximity of a familiar experimenter than an unfamiliar individual (familiar mean rank 9.42, mean duration 153 s; unfamiliar mean rank 15.58, mean duration 75 s).

Familiar experimenter condition (all subjects). We carried out additional analyses of the familiar experimenter condition including the data from all 22 subjects, comparing wolves and dogs with a Mann-Whitney U-test to account for the non-normality of the data. A Bonferroni correction was used because a portion of the data had already been analyzed, making the corrected alpha level .025. Dogs approached the experimenter with a shorter latency than did approach $\hat{U}(11,11) = 15$, p < .005; median: dogs 3 s, wolves 43 s. Dogs also spent longer in proximity to the experimenter: U (11,11) = 0, p < .001; median: dogs 185 s, wolves 100 s.

Figure 1 shows median approach latency and proximity times for wolves and dogs in Experiment 1 tested with an unfamiliar experimenter and with a familiar experimenter, both for all subjects and separately for those subjects not tested with an unfamiliar experimenter.

These results indicate that dogs displayed higher levels of sociability than wolves as evidenced by shorter latencies to approach a human, and more time spent in proximity with the human. This difference was observed both when considering those subjects that experienced both familiar and unfamiliar experimenters, and the larger group of subjects that were only exposed to a familiar experimenter.

Experiment 2

Jakovcevic et al. (2012) found a relationship between higher sociability scores in individual domestic dogs and prolonged gaze toward a human in the presence of out-of-reach

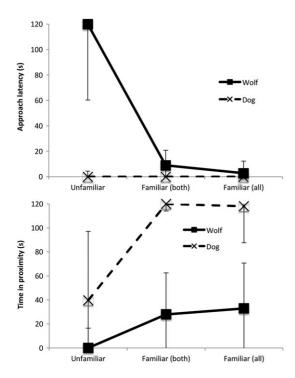


Fig. 1. Median approach latencies and time in proximity of a familiar human experimenter for each subspecies in Experiment 1. Data are shown separately for the test with an unfamiliar experimenter, and with a familiar experimenter, both for all subjects and separately for those subjects not tested with an unfamiliar experimenter. Error bars show interquartile ranges.

food—even during extinction where food was no longer provided by the human. In Experiment 2, we asked whether pet domestic dogs were also more likely to show prolonged gazing toward humans during extinction compared to human-socialized wolves, given their higher sociability scores in Experiment 1.

Method

Subjects and Procedure. Five minutes after Experiment 1, we tested the same 11 wolves and 11 dogs in a simple gaze task divided into two phases:

Pre-training. A container holding small pieces (approximately 1 cm³) of sausage was placed next to a familiar standing experimenter, in sight of the subject but out of the animal's reach. The experimenter called the subject, drawing attention to the location of the food while extracting one piece and giving it to the subject to consume. During Phase 1, a

total of five pieces of food was delivered to the subject at variable times, independent of where the subject was gazing. After 2 min, the test began.

Test Phase. The experimenter stood beside the treat container, called the animal once by name, and gave it one last piece of food. At this time, the experimenter made eye contact with the subject and attempted to maintain it during the whole trial. No further food was provided for the remaining 2 min. Gaze duration (s) toward the human face was later coded from video (IRR was high, correlation, R = 0.99).

Data analysis. Gaze duration was normally distributed (Kolmogorov-Smirnov test, p > .05); so, subspecies were compared using a t-test for independent samples. An alpha level of .05 was adopted.

Results. Dogs gazed at the human face significantly longer than did wolves during the Test Phase, t (20) = 3.82, p < .001, means: dogs = 34 s, wolves = 5 s).

General Discussion

Compared to human-socialized wolves, pet domestic dogs had higher sociability scores, maintaining longer durations of proximity to both familiar and unfamiliar humans during both the passive and active phases of Experiment 1. In Experiment 2, dogs gazed longer than wolves at a human face, even when the experimenter no longer provided assistance in obtaining the out-of-reach food item.

Although both the human-socialized wolves and the pet dogs approached and sought the proximity of humans during the sociability test, and would look to the face of a human when she assisted in providing out-of-reach food, pet dogs generally prolonged this response for extended periods—even when the human was unresponsive or no longer provided food. In contrast, wolves were more likely to return to independent behavior after initial greetings in the sociability test, and were more sensitive to extinction in the gaze test.

Thus, instead of supporting the idea that gaze toward humans is a communicative response unique to domesticated canids (Miklósi et al., 2003), the current findings suggest that—although both subspecies have the capacity for prosocial responses, including

gaze and attentiveness toward companions there may be differences in the duration and degree of social responses of dogs and wolves in some contexts. This finding is also consistent with Range and Virányi's (2014) recent finding that wolves learned faster than dogs on an observational learning task with conspecific demonstrators. The authors of that study concluded that the cooperative breeding system of wolves produces more intense attention toward and monitoring of the actions of a social partner. Such findings provide additional support for the idea that dogs and wolves may use gaze behavior in a similar way, but its expression and duration depend on the context and social relationships involved.

It is possible that the prolonged social responses of dogs in this study—especially with respect to sociability—are related to changes associated with canine domestication. One important outcome of genetic domestication is an elongation of the sensitive period for socialization in dogs and other domesticated canines (Scott and Fuller, 1965; Trut, 1999). This makes dogs easier to socialize or tame than their genetically wild counterparts. It is possible that these biological changes may also lead to prolonged social responses more generally—possibly resulting in hypersocial behavior in adult dogs compared to their wild counterparts in some cases. Coupled with the close proximity most pet dogs share with humans, this may predict the high levels of prosocial behavior and social sensitivity many pet domestic dogs display in the presence of humans (Udell et al., 2010a & b). Longer initial durations of approach by dogs may also provide more opportunities for humans to reinforce these social behaviors in informal contexts. Furthermore, the fact that gaze behavior is flexible to the consequences in the environment (i.e., decreases during an extinction procedure; Bentosela, Barrera, Jakovcevic, Élgier, & Mustaca, 2008) suggests that learning plays an important role in the development of these prosocial behaviors. Thus, evolutionary and lifetime processes likely build on one another to produce the high levels of social responsiveness seen in many pet domestic dogs.

It is not possible to rule out differences in lifetime experiences between pet dogs and captive wolves that could further contribute to the differences in sociability seen in this and previous studies. Although the wolves in this study were human-socialized and interact with unfamiliar humans on a regular basis, they may still do so less frequently than many pet dogs. Humans, especially unfamiliar humans, interacting with dogs and wolves outside of experimental sessions, may also behave differently toward these populations based on different levels of comfort with or understanding of each subspecies. For example, wolves are often not encouraged to make prolonged close contact with unfamiliar people in the way that many dogs are, and behaviors such as jumping up or excessive face licking may be less tolerated. Differences in the quality of experience with humans may well translate into differences in sociability. The same considerations likely apply to small versus large dogs or breeds with different societal reputations.

It is well established that different lifetime experiences with humans influence the adult social behavior of domestic dogs. For example, Frank and Frank (1982) showed that a dog's level of socialization to humans during ontogeny, especially during the sensitive period, can influence the quality of relationship dogs and humans share. Unsocialized domestic dogs characteristically show fear, hostility, or avoidance behaviors when approached by humans (Scott & Fuller, 1965). Dogs living in different environments, such as shelter dogs compared to pets, have also been shown to have differing levels of sociability (Barrera et al., 2010); these sociability scores in turn have predicted performance on gaze tasks even between groups of dogs (Jakovcevic et al., 2012). Thus, it is unlikely that different social predispositions of dogs and wolves, if present, work in isolation. Further investigation of the biological underpinnings of sociality will contribute to our understanding of the relevant lifetime and evolutionary factors that lead to differences in canine social behavior.

In conclusion, our results show that sociability—defined as the duration of time adult individuals spend in proximity to familiar and unfamiliar humans—differs significantly between pet dogs and human-socialized wolves. This is true even for populations of wolves that have previously performed well on socio-cognitive tasks, such as human point following (Udell et al., 2008).

In human environments, most valuable resources for both captive wolves and pet dogs

come from people. In this sense, humans may become "social tools" (Leavens, Russell, & Hopkins, 2005) or a means to achieve different goals; it is therefore not surprising that both dogs and wolves approach humans and gaze at them when attention or food reward is initially available. Both domestication and lifetime experiences could produce changes in social behaviors in dogs in the same direction; this synergistic effect may be reflected in the prolonged contact and gaze with humans compared to their wild counterparts, even when this behavior is no longer reciprocated or rewarded by humans.

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