

Learning interspecific communicative responses in Pampas foxes (*Lycalopex gymnocercus*)

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ABSTRACT

Domestic dogs show remarkable communicative abilities in their interaction with people. These skills maybe explained by the interaction between the domestication process and learning experiences during ontogeny. Studies carried out on other species of canids, which have not been domesticated are relevant to this topic. The purpose of this article is to study the effect of instrumental learning on captive Pampas foxes' (*Lycalopex gymnocercus*) communicative responses to humans. Seven foxes were tested in a conflict situation involving food within sight but out of their reach. In these situations dogs typically gaze at the human face to ask for food. In Study 1, there was an increase in gaze duration as a consequence of reinforcement and a decrease during extinction, when animals did not receive any more food. In Study 2, all of the four foxes tested successfully followed proximal pointing gesture to find hidden food. When a distal pointing cue was given, three out of four followed it in the first session and one in the second session. These results are consistent with those previously found in dogs, and suggest that learning experiences allow the development of communicative skills, even in not domesticated canid species.

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1. Introduction

Communication between animals occurs when an observer can detect predictable changes in the behavior of one of them (the reactor), in response to certain signals from the sender (Wilson, 1975). This definition, unlike traditional approaches that emphasized the transmission of information, highlights the influence on the receiver's behavior (Rendall et al., 2009). From an evolutionary point of view, selection favors senders whose signals affect the behavior of receivers to the sender's advantage (Carazo and Font, 2010). In this sense, the psychology of learning adds to this definition the role of reinforcement for one or both participants (Skinner, 1953). A successful communication is crucial for social species, as it allows to predict others actions and adjust their own behavior leading to a synchronization effect (Csányi, 2000). From this point of view, many interactions can be defined as communicative acts but they do not necessarily imply intention on the part of the members involved (Leavens and Hopkins, 1999).

A typical experimental situation where communicative responses are observed involves tasty food is in sight but out of the animal's reach and the only way to get it is through the interaction with a person. As Leavens et al. (2005) state, in these situations people become social tools that allow access to certain goals.

Domestic dogs proved to be successful in this kind of communicative interactions with humans. The evidence suggests that they are able to produce and comprehend signals in cooperative contexts with people (Hare and Tomasello, 2005). Among the most studied responses are the tendency to gaze at the human face in situations of uncertainty or conflict (e.g., Gaunet, 2008; Miklósi et al., 2003) and to follow human cues (e.g., pointing, body position) to find hidden food (e.g., Soproni et al., 2001). Gaze behavior is crucial to establish communication in social species. For example, it helps animals to find relevant stimulus such as food and predators (Tomasello et al., 1998; Emery, 2000). Human-directed gaze and the alternation between the receiver and the target object are considered referential responses in attention-getting behaviors (Gómez, 2007). It also provides information about the individual's emotional state (e.g., Emery, 2000). Similarly, human pointing is considered an essential element in the non-verbal referential communication (e.g., Leavens et al., 2005).

Dogs' successful performance in communicative tasks with humans is evident even at early stages of development (e.g., Riedel et al., 2008) and it is better than that of other species such as primates (e.g., Itakura et al., 1999). These capabilities were interpreted as the result of the intense process of domestication (e.g., Hare et al., 2010) undergone by dogs 14,000–16,000 years ago (Pang et al., 2009; Vila et al., 1999), and would be relatively independent from ontogenetic experiences (e.g., Bräuer et al., 2006; Miklósi, 2009). However, recent studies showed that instrumental learning is involved in the mechanisms of dog–human communication.

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Dogs increased their gaze duration towards the human face and their pointing following behavior when these responses led to a food reward. Also, a decrease in this behavior was observed during processes of extinction and omission, when they were no longer reinforced (Bentosela et al., 2008; Elgier et al., 2009).

Similarly, Marshall-Pescini et al. (2008) showed that untrained dogs gazed more often at their owners in an unsolvable task than highly trained dogs, which spent more time interacting with the baited apparatus. On the other hand, longer duration of gazing was observed in sport trained dogs in which the gaze towards humans is specially reinforced. For example, Marshall-Pescini et al. (2009) found that Agility trained dogs gazed at their owners significantly more than both pet dogs and Search & Rescue trained dogs. Moreover, Bentosela et al. (2008) found that Schutzhund trained dogs gazed more at the human face during a walk than untrained dogs. In addition, McKinley and Sambrook (2000) found that trained Gundogs were more successful than pet dogs in a human pointing following task. In summary, the evidence indicates that prior learning experiences modulate communicative responses.

Furthermore, shelter dogs, characterized by having low levels of social interaction with people, showed faster extinction of the gaze at the human face (Barrera et al., 2011) and a slower learning of subtle communicative responses, such as the distal pointing gesture (index finger more than 50 cm from the target) than pet dogs (Udell et al., 2008, 2010a).

These data support the “Two Stage Hypothesis” (Udell and Wynne, 2010) that states that the domestication process is not sufficient to explain these abilities, and therefore, interaction with humans during ontogeny is also necessary. These experiences must occur during the sensitive period of socialization and throughout the animal's life. Considering this debate, comparative studies with other species of canids, genetically related to dogs but that did not undergo the process of domestication, are of great importance.

Fox is a common name for many species of carnivorous mammals belonging to the Canidae family. Foxes are a canid species less closely related to domestic dogs than wolves (Lindblad-Toh et al., 2005; Lucherini et al., 2004). To our knowledge the only antecedent in the literature of interspecific communication in foxes is Hare et al.'s study which evaluated silver foxes (*Vulpes vulpes*). Hare et al. (2005) showed that silver foxes of 2–3 months of age were able to follow the proximal pointing gesture accompanied by gazing towards the target, but were less successful than a group of similar age foxes selected for their docility over 45 generations. However, this species has not been tested for their comprehension of other cues such as proximal pointing without gaze or distal pointing or for responses involving gaze in a communicative context with humans.

In the present studies we evaluate another fox species, the Pampas fox (*Lycalopex gymnocercus*), which is one of the six species in the genus *Lycalopex*. It occurs in Bolivia, Paraguay, Uruguay, Argentina and Brazil. It prefers open habitats but also occurs in areas of Pampas grassland. Pampas foxes are generalist, adaptable and opportunistic predators. They may form monogamous pairs. These pairs are frequently observed from mating until pups leave the natal den. However, they hunt and spend most of their time alone (Lucherini and Luengos Vidal, 2008; Lucherini et al., 2004).

Our first objective was to assess the effect of learning in the development of a communicative response in adult Pampas foxes with low human socialization. To achieve this aim we evaluated the effect of reinforcement and extinction on the communicative behavior of gazing to the human face when there is food in sight but out of reach, using a procedure similar to dogs' studies (Bentosela et al., 2008; Jakovcevic et al., 2010). Foxes had to learn that if they gazed to the human face, the person changed her behavior offering the reward to them.

Gaze response was scarcely assessed in the comparative studies with other canid species. The most important study is Miklósi

et al. (2003). After training the dogs to pull a rope to open a box and obtain food, the animals were exposed to an unsolvable trial in which the box was blocked. In this situation dogs looked more quickly and for longer to the owner's face than socialized wolves. However in this study there was no attempt to train the gaze response. Also in this study it was not possible to rule out certain alternative explanations of the between-species difference. For example, wolves may be more impulsive than domestic dogs, and therefore take longer to inhibit the actions directed to the device or maybe are more resistant to extinction of learned responses. The behaviors directed to the device would be incompatible with the possibility to respond to other environmental stimuli including people. Because of that, it would have been interesting to test both groups in the same unsolvable task but when they are alone, without any human presence and evaluate if species differences are observed.

Our second objective was to evaluate the comprehension of human communicative cues. With this purpose we evaluated foxes' following of proximal and distal pointing in an object choice task.

These studies highlight the role of learning experiences upon the development of interspecific communicative skills in a new canid species that have not been assessed yet. Also they contribute to the debate about the origin of these abilities in dogs.

2. Study 1

The purpose of this study is to evaluate the acquisition, extinction and re-acquisition of the gaze towards the human face to ask for food in Pampas foxes. To achieve this aim, animals were exposed to a conflict situation involving food in sight but out of their reach. During acquisition, an experimenter placed herself beside the food source and reinforced with a piece of food the subject every time it gazed at her face. In the extinction phase, the experimenter did not deliver the food anymore and during re-acquisition she reinforced the fox's gaze again. In each of these three phases, the gaze response is associated with a specific result (presence-absence-presence of food). As a consequence, a change in its duration would be expected to be closely connected to these outcomes. The experimental situation is similar to that used with domestic dogs in previous studies in which they modified their gaze duration depending on the reinforcement contingencies they received (see Bentosela et al., 2008; Jakovcevic et al., 2010). If we found that the foxes' gaze response is modified by these changes in consequences (as was observed with dogs), it can be assumed that instrumental learning is involved in the mechanisms of human-canid interspecific communication.

Since the animals showed fear responses to the proximity of people, including caregivers, it was necessary to modify the protocol used with dogs in order to facilitate foxes' learning performance. Modifications included a longer familiarization period, where proximity to people was reinforced, a longer duration of the acquisition phase and an instigation procedure at the beginning of this phase. These strategies were selected based on the principles of learning and behavior modification.

2.1. Method

2.1.1. Subjects

Subjects were seven adult Pampas foxes (*L. gymnocercus*; five males and two females) housed in social groups in two (8 m × 6 m) outdoor enclosures at the Experimental Zoological Station “Granja La Esmeralda” of Santa Fe, Argentina, tested with the permission of the Station's veterinarians. Enclosures were delimited by a 40 cm high brick wall and by a 2 m high wire mesh. Inside, there was a 2 m × 2 m concrete kennel. In each enclosure there were four and five foxes, respectively. Two of them could not be tested due to

intense fear of humans. All the animals were adults and had been living at the experimental station for at least five years. The foxes were found in nearby roads or in the city and taken to the station. Their origin is unknown, and there was no individual record related to their capture.

Usually, the group was fed on alternating days in the morning. The diet primarily consisted of chicken. Caregivers throw food through the fence and then withdraw. The daily routine consisted of cleaning the cages once a day. During these activities no direct contact between the caretakers and the animals was observed. Zoo visitors were not allowed to feed the animals at any time. Testing took place in the mornings before the first feeding time to ensure that the animals were highly food motivated. Water was available ad libitum.

2.1.2. Procedure

Video 1 shows the experimental setting and the procedure. Testing was conducted individually in a partition made in the outdoor area. The partition was made with a (6 m × 2 m) opaque plastic canvas resulting in a testing area that served to isolate the focus animal from its conspecifics. As this partition was opaque, focal foxes could not see their conspecifics, but could hear and smell them through the canvas, minimizing possible stressful separation effects. For testing, as animals were more prone to approach when humans were on the other side of the fence, an experimenter (E1) stood on a predetermined point outside the enclosure, sitting on the floor behind the wire mesh. The partition was placed the day before to the observations so that the animals become familiar with the new context.

Rewards were small pieces of dry liver or sausage selected by a previous preference test. Incentives were placed out of the enclosure resting on the legs of E1 in a container that was visible to the animals, but out of their reach. All trials were videotaped with a Sony DCR TRV 310 camera. The person taping the trial (E2) was located behind E1 to his side. E1 was always the same unfamiliar woman.

The procedure (see Video 1) consisted of three phases: acquisition, extinction and re-acquisition. The day prior to training, a familiarization session with E1 and E2 was performed. Since the animals showed fear responses and stayed away from people, a shaping procedure with successive approximations was employed (Skinner, 1938). Initially, E1 threw food to the foxes when they were at least 3 m away from her. Progressively, food was thrown closer until reaching a minimum distance of 0.8–1 m between E1 and the foxes. This training was performed inside the animals' enclosure while they were grouped and lasted approximately 3 h.

2.1.2.1. Acquisition. Immediately after the familiarization period, foxes participated in eight trials receiving differential reinforcement for gazing at E1.

Foxes were individualized and remained on campus for about 30 min before the test to familiarize with the situation. Then E1 sat on the floor behind the fence; in this way, her face was at the same height as the fox's. During the first two trials, to facilitate the target's response, E1 called the attention of the fox making vocal sounds while holding a piece of food between her eyes. This enabled the subject to pay attention to that specific part of her face. Each time the fox gazed at her face it received the food reward from behind the fence and directly from E1's hand. In the remaining trials (3–8) there was no more response facilitation. At the beginning of trials 3–8, E1 called the fox by a vocal sound until capturing its attention and then remained still with her arms by her side, gazing at the subject until getting back a gaze response. Usually, foxes moved their gaze from E1's face to her hand as soon as she reached for the food. A new reward was delivered when the fox turned its gaze

back to E1's face. Each trial lasted 5 min and the inter-trial intervals (ITIs) lasted at least 1 h.

2.1.2.2. Extinction. After a 1 h-interval following the last acquisition trial, one 5 min-extinction trial was performed. This trial was identical to the acquisition one except that the reward that was never delivered. The trial started with E1 calling the fox using a vocal sound until the fox oriented itself towards her, but without giving it any food. If the subject gazed at E1, she maintained eye-contact.

2.1.2.3. Re-acquisition. One hour after extinction, a 5 min-re-acquisition trial of gazing was run. This trial was identical to the last acquisition one.

Long intervals were employed to avoid fatigue and loss of motivation and to facilitate a better learning using distributed trials rather than massive ones (e.g., Gomerzani and Moore, 1969).

Training was performed in three separate sessions on different days (Day 1: acquisition trials 1–3; Day 2: acquisition trials 4–6; Day 3: acquisition trials 7–8) followed by extinction and re-acquisition trials.

During acquisition, extinction and re-acquisition trials, E1 remained in the same position, gazing at the fox's face. At the end of each trial she left the area and placed herself out of the fox's view while the subject remained in the testing area.

2.1.3. Data analysis

Gaze duration (s) was measured as a dependent variable. This was defined as the orientation of the head and the gaze of the fox towards the experimenter's face. This measure correlates with gazing frequency (Bentosela et al., 2008). This behavior was scored on all trials by manually calculating (with a stop watch) the cumulative duration of gaze at the human face. Two independent observers analyzed gaze duration in all the trials from the videotaped material. To test inter-observer reliability, Pearson's coefficients of correlation were calculated for gaze duration for all the foxes. In all cases $r's > 0.99$, $N = 7$, $P < 0.0001$.

Gaze duration was found not to differ from a normal distribution (Kolmogorov–Smirnov test); therefore, parametric analyses were used. To evaluate response acquisition, a repeated measures ANOVA comparing gaze duration across acquisition trials was run. In addition, to compare different phases, related samples *t*-tests were used to compare gaze duration in (a) last acquisition (trial 8) and extinction trials and (b) extinction and re-acquisition trials.

The last acquisition trial and the extinction trial were divided into five 1 min-blocks. The fifth minute of the last acquisition trial and the five 1 min-blocks of extinction were compared by means of a repeated measures ANOVA, in order to evaluate the extinction curve across trials. The alpha value was set at 0.05. All analyses involved two-tailed tests.

2.2. Results

Fig. 1 depicts the mean and standard error of the cumulative gaze duration in each trial of acquisition, extinction and re-acquisition phases. The analysis comparing all acquisition trials revealed a significant increase in gaze duration, $F_{7,42} = 3.19$, $P = 0.008$. The difference between the last acquisition trial and the extinction one was also significant, $t_6 = 5.16$, $P = 0.002$, indicating that during extinction gaze duration significantly decreased.

Fig. 2 shows mean and standard error of the cumulative gaze duration at the fifth minute of the last acquisition trial and during the extinction trial divided in five 1 min-blocks. A repeated measures ANOVA comparing the fifth minute of the last acquisition trial and each of the five extinction minutes, showed a significant effect, $F_{5,30} = 11.90$, $p = 0.0001$. Post hoc comparisons revealed that the last

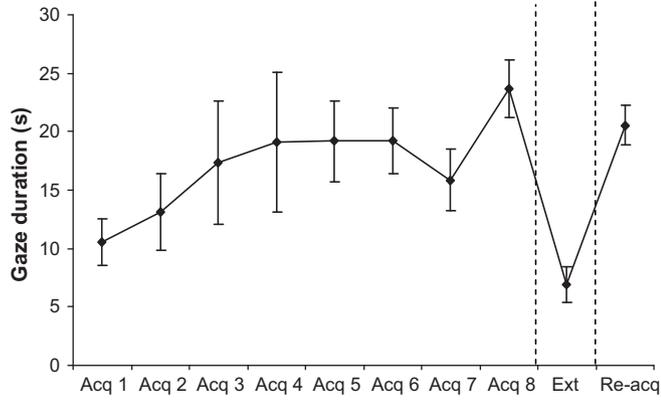


Fig. 1. Gaze duration during acquisition (Acq.), extinction (Ext.) and re-acquisition (Re-acq.) trials (means \pm 95% confidence interval). The dashed lines indicate a transition in reinforcement contingencies.

acquisition minute was significantly different from all extinction minutes (p 's < 0.005) except for the first one ($p = 0.15$). This result indicates that the animals remained gazing to the human face at the beginning of extinction but then significantly diminished the response. In this sense, the first extinction minute is significantly different from the remaining ones ($p < 0.011$), showing how the response decreases during the trial.

On the other hand, during extinction the average gaze duration was significantly lower than during re-acquisition, $t_6 = 4.58$, $P = 0.004$ (see Fig. 1), indicating that foxes increased their response when they were reinforced again.

Together, these results show that the animals quickly adjust their gaze response to the reinforcement contingencies of each phase.

2.3. Discussion

Foxes' gaze at the human face in a conflict situation with food in sight but out of their reach was modified by associative learning processes. This communicative behavior was scarcely assessed in comparative studies with other no domesticated canids. Gaze response increased when it was associated with food (acquisition and re-acquisition) and decreased when the reward was no longer delivered (extinction). Foxes learnt to direct a communicative response towards a human to solve a problem that they could

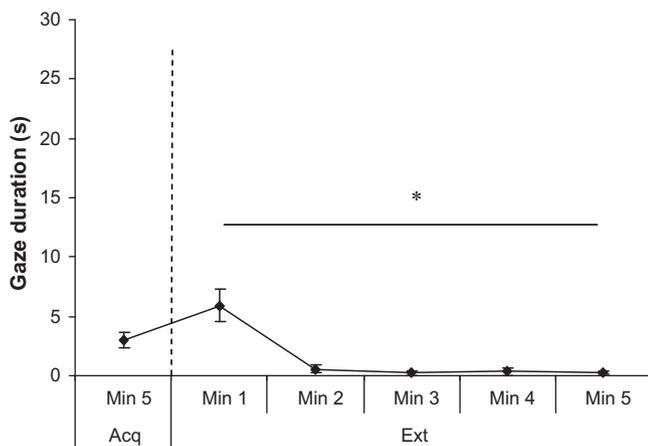


Fig. 2. Gaze duration during the fifth acquisition minute and the five 1 min-blocks of extinction (means \pm 95% confidence interval). The dashed line indicates a transition in reinforcement contingencies between the phases of acquisition (Acq.) and extinction (Ext.) * $P < 0.01$.



Fig. 3. Experimental set up for Study 2.

not resolve by themselves. In this context, humans may be regarded as “social tools” (Leavens et al., 2005) as they provide significant resources (e.g., food) to domestic dogs and other species living in captivity.

The present results suggest that through brief systematic learning experiences communicative responses can be easily developed, even in an undomesticated species with low level of socialization with people.

From a comparative point of view, these results are consistent with those previously found in dogs with a similar procedure (Bentosela et al., 2008). Meanwhile, socialized wolves exposed to this type of conflict, instead of gazing at the human face, persisted in their attempts to access the food by themselves (Miklósi et al., 2003). However, as we mentioned above, further studies would be required to evaluate if that behavior in wolves could be easily modified by instrumental learning procedures. In addition, the experimental situation was different from Miklósi et al.'s. In their study, animals first had to solve a problem (e.g., to pull a rope to get food) and then the problem became unsolvable. Also, the characteristics of the task could produce different behavioral outcomes.

3. Study 2

The aim of the second study was to test foxes' performance in an object choice task using two different human cues to find hidden food: proximal pointing and distal pointing gestures. The cues were evaluated in a fixed order according to their complexity.

3.1. Method

3.1.1. Subjects

Four adult foxes, three males and one female were evaluated. All of them had previously participated in Study 1. Two of the subjects who participated in the previous study died, and another one could not be evaluated since it showed an intense fear response towards humans. The interval between the two studies was nine months.

3.1.2. Procedure

Each subject was tested for its ability to find hidden food after receiving different human communicative cues. Fig. 3 shows the experimental set up. Testing was conducted individually in the experimental area, with subjects separated from the rest of the group. For each trial E1 stood on a predetermined location in the middle of two identical opaque containers (diameter 22 cm, 1.20 m apart). She was 60 cm from the two containers, which were placed

on two 5 cm high platforms, which were on the floor. To control for odor cues, both containers had a piece of liver under a false bottom, and were previously smeared with the reward. As foxes showed less avoidance responses when people stayed behind a wire fence, E1 and the containers were located behind a 3 m wide \times 0.9 m high wire mesh partition that separated them from the subject. In order to mark off the choice area, a 1 m vertical line was drawn on the floor in the foxes' area, from the position of E1. This line divided the area in two parts (see Fig. 3).

As foxes could not be manipulated by a handler, they were called by an E2 located outside the enclosure opposite to E1. Distance between experimenters was approximately 3.5 m. To move the subject away from the choice area, E2 called its attention using vocal sounds and by showing it food. When the subject approached E2, she gave it small pieces of food intermittently to keep it close to her and distracted from E1's actions. In this way, when the subject approached E2, it could not see E1, and vice versa. During the baiting process while E2 distracted the subject, E1 picked up the containers and hid a piece of sausage into one of them. She then placed the containers on the platforms and started to call the subject's attention. E1 only emitted the pointing cue when the subject was attentive. Across trials, food location was counterbalanced and randomly varied, with the stipulation that it was never placed in the same container for more than two consecutive trials. Pieces of sausage were used as rewards.

There were two successive phases in which two different cues were tested in order of increased difficulty: proximal and distal pointing. Considering that animals tended to react fearfully to human movements, we use a dynamic point in which the E's arm and hand are extended in the direction of the target container while the subject watches. The E's arm remains in place and motionless until the trial ends (Udell et al., 2010b). Moreover, to ensure that subjects were not able to discern the location of the food from any scent or unintended experimenter cue, a total of eight control trials were run. The procedure was as follows.

Warm up. In order to introduce each subject to the test situation, E1 showed the subject a piece of food with her hand. Once E1 caught the subject's attention (sometimes this required calling it several times with various vocal sounds), she would then place the food into one of the two containers while the subject watched. When the subject approached the baited container, it was reinforced by placing the reward on the floor, next to him. In this way, foxes could learn that the containers had food inside. Six warm up trials were performed. Food location was counterbalanced, running three trials in each side. ITIs were of 30 s or to recover subject's attention.

Proximal point. E1 knelt on the floor in the middle of the two containers and called the subject's attention by using vocal sounds. When the fox responded, she pointed at the baited container with the equilateral hand and remained in this position until the subject made a choice. The distance between the pointing finger and the container was less than 10 cm. Each subject received 10 proximal pointing trials and 30 s-ITIs were employed. If the choice was correct, the fox received the food. If the choice was incorrect it did not receive the reward and proceeded to the next trial. Food location was semi randomized and balanced across the right and left sides. The same place for the reward was not used more than twice in succession. We used a correction procedure in which when the animal made an incorrect choice, the same side was repeated until the fox made the correct choice, to facilitate discrimination learning (e.g., Hull and Spence, 1938). All the trials were included in the analysis. This phase was repeated until the animals' performance exceeded chance level (8 out of 10 correct responses, binomial $p = 0.05$).

At the end of this phase, two control trials were run. In these trials E1 performed the same baiting procedure as for the test conditions, then returned to her original position in the middle of the containers and stared straight ahead. She called the subject's

attention by using a vocal sound but did not produce any cue. Only two control trials were run at this phase, to prevent loss of motivation among the animals and lack of participation in the second phase.

Distal point. After an interval of at least 20 min, 10 trials of distal pointing (index finger more than 50 cm from the container) were run. In this case, E2 stood in the middle of the two containers. The remaining conditions were the same as in proximal pointing trials. At the end of this phase six more control trials (except for one subject, Gris, who received four) similar to the previous control ones were run. Only one subject did not reach the criterion of 8 over 10 correct trials, so one more session of 10 distal pointing trials was run for this subject.

3.1.3. Data analysis

A choice was considered correct when the subject was closer than 30 cm from the container. In order to do that, its forelegs had to cross the vertical midline orienting its head and body to one of the containers. Responses were coded in the moment by E1 and E2 and they had a 100% of agreement. The maximum latency to make a choice was of 30 s. If the subject did not choose, the trial was scored as no-choice. Such trials were considered as incorrect responses.

We calculated the percentage of correct choices in each session for each individual. As sample size was small we analyzed individual performance by means of binomial tests. The alpha value was set at 0.05. All analyses involved two-tailed tests.

3.2. Results

Table 1 shows the percentage of correct, incorrect and no choice responses with the different cues and during control trials for each individual. During the first session with proximal pointing gesture all four foxes performed above chance, $P \leq 0.043$.

Regarding distal pointing, during the first session three of the foxes behaved over chance level, $P = 0.009$, while the other one was at chance level ($P = 0.24$). Only this latter fox had an extra 10-trial session of distal pointing and its performance was significantly above chance level ($P = 0.0001$).

During control trials, where no social cues were provided, binomial tests indicated that only one fox was significantly below chance level, $P = 0.015$, the other behaved at chance level, $P \geq 0.10$. This is due to the fact that during control trials animals showed a higher percentage of no-choice responses than in proximal and distal pointing trials, $F_{2,6} = 12.89$, $P = 0.007$. No-choice responses were equally observed in the two initial control trials ($83.33 \pm 28.87\%$, $N = 2$) as in the last six ($41.66 \pm 39.67\%$, $N = 6$). This would rule out the possibility that animals do not make choices due to lack of motivation during training. The absence of choice behavior could be due to a minor disposition to approach the person when it does not produce any relevant signal associated with food. The unsuccessful performance during control trials without a cue indicates that foxes were not using other inadvertent cues to find food during proximal and distal pointing trials.

3.3. Discussion

Results indicate that foxes, an undomesticated species with low socialization to humans, were able to follow human gestures to find hidden food. Specifically, they followed a relatively simple cue like proximal pointing and a more complex one such as distal pointing. This was observed despite the foxes had to be tested from outside the enclosure, something that had been shown to cause, in some circumstances, a decrement in performance for domestic dogs (Udell et al., 2008).

These data extend Hare et al.'s (2005) findings to a population of adult foxes and to the use of other more complex cues (proximal

Table 1

Percentage of correct, incorrect and no choice responses of each subject during training sessions of Study 2.

Subject	Proximal pointing			Distal pointing 1			Distal pointing 2			Control		
	C	I	NCH	C	I	NCH	C	I	NCH	C	I	NCH
Koko	100*	0	0	90*	0	10	–	–	–	37.5	25	37.5
Zorri	100*	0	0	50	30	20	100*	0	0	25	12.5	62.5
Orejas	100*	0	0	100*	0	0	–	–	–	25	50	25
Gris	80*	10	10	90*	10	0	–	–	–	0	16.6	83.3*

Note: C, correct; I, incorrect; NCH, no choice responses.

* Performance above chance level, $P < 0.05$ (binomial tests).

pointing without gaze and distal pointing). Furthermore, these results agree with those found in a breed of dogs closely related to the dingoes, the New Guinea Singing Dogs (Wobber et al., 2009) and other species of canids such as adult wolves (Gácsi et al., 2009; Udell et al., 2008; Virányi et al., 2008), and dingoes (Smith and Litchfield, 2010). These evidences show that several species of undomesticated canids are capable of using human communicative gestures that, unlike the foxes tested here, had a high level of socialization with humans.

Although this sample of foxes had few opportunities to interact with people, it is likely that the previous experience in Study 1 and at the warm up sessions of the present study allowed them to acquire the hand-food association as an essential component for pointing following behavior. In addition, the development of this communicative behavior would be relatively easy and would not require a systematic intervention. The fact that many domesticated species such as domestic goats, cats, horses, and undomesticated animals, such as capuchin monkeys, orangutans, gorillas, chimpanzees, dolphins, a grey seal and fur seals have been able to successfully follow the human pointing gesture supports this idea (see Elgier and Bentosela, 2009).

Finally, these results would provide evidence in favor of associative learning as one of the mechanisms involved in canid–human communication.

4. General discussion

The purpose of this paper was to study the effect of learning in the communicative responses of Pampas foxes living in captivity with a low level of human socialization. With that aim, two similar experimental procedures that have previously been studied in dogs were used (e.g., Bentosela et al., 2008; Elgier et al., 2009).

First, we tested the acquisition, extinction and re-acquisition of the gaze response towards the human face in a conflict situation where there was food in sight but out of their reach. There are few studies with other canids that evaluate this communicative behavior. Foxes showed a significant increase in gaze duration at the acquisition phase when they received a reward for producing such a response. In the extinction phase, there was a sharp decrease in the communicative behavior. Gaze duration increased again during re-acquisition phase. These results indicate that the gaze response changes according to the reinforcement contingencies. These modifications occur even with few training trials, evidencing that it is a highly flexible behavior that quickly adjusts to environmental changes. Systematic and brief learning experiences during ontogeny, such as those used in this study, would facilitate the emergence of communicative responses in canids, even when they have not been domesticated and have a low level of socialization with people.

The development of this behavior is especially important in human communication. In general, when someone looks at us, we tend to interpret that the other expects something from us and therefore, we act accordingly (Kendon, 1967). Thus, if another species gaze at us, we understand this behavior as help request and

therefore modify our behavior to solve the problem. This does not mean that for the other species (dog or fox) this behavior has the same meaning that it has for us. The mechanisms of gazing behavior may be related to simpler associative learning processes that link the response with desired food as an outcome.

In the second study, we tested Pampas foxes' performance in an object choice task using human cues to find hidden food. Even though the number of tested subjects was small, results showed that foxes followed the proximal pointing gesture since the first trials and without requiring explicit training during the task. In turn, three out of four foxes successfully followed the distal pointing gesture from the first trials and the remaining fox was above chance level in the second session. During control trials, animal's performance was at chance level, ruling out the possibility that foxes were guided by other inadvertent cues. These results show that Pampas foxes seem to be able to use human gestures of different complexity to find hidden food.

This successful performance was observed from the first training trials even when the animals had a low socialization with people. However, it is necessary to consider that they were exposed to a highly relevant experience with humans in Study 1, before being evaluated in the object choice task. In that first study, the experimenter gave out the food directly with her hand, facilitating the learning of hand-food association. However, the effect of the experience of the first study was minimized by the wide time interval (9 months) between both studies.

Moreover, as both gestures were sustained (i.e., the experimenter kept the pointing signal until the fox had made its choice) may have facilitated the response.

Finally, the cues were administered in a fixed order of increasing complexity. For this reason, it is possible that the experience that foxes achieved during proximal pointing in the first phase had favored the successful performance during distal pointing. However, this would indicate that a brief human interaction experience is enough to develop this ability.

From a comparative perspective, these studies extend our knowledge about these interspecific communicative abilities and introduce another non-domesticated canid into the debate about the origins of the dog's responsiveness to human action. It should be noted however that comparative studies have a number of limitations related, for example, to species-specific preferences or phobias that can counteract the performance in experimental tasks (Udell et al., 2010b; Virányi et al., 2008). In order to exclude these influences it is therefore appropriate to make the necessary modifications in the procedures so that the target behavior can manifest itself even in the presence of fear. In the case of foxes, compared with domestic dogs, it was necessary to perform prior training to reduce avoidance behavior towards humans, and to facilitate the emergence of the gaze response through instigation processes. Possibly, these differences might be associated with domestication, which in the case of dogs, would facilitate the willingness to interact with people (Gácsi et al., 2009) and would decrease fear responses (Virányi et al., 2008). The fact that silver foxes selected for their docility over 45 generations are more prone to approach people

than non-selected foxes (Trut, 1999) support this hypothesis. On the other hand, it is also possible that a lower level of socialization with humans during ontogeny increases fear responses in foxes (e.g., Pedersen et al., 2002).

In conclusion, the fact that an undomesticated canid species can develop communicative responses towards humans with relative ease contributes to the debate about the origins of communicative abilities in domestic dogs. Some authors assume that these skills are the result of the domestication process and independent from ontogenetic experiences (e.g., Hare et al., 2010), while others underline the role of ontogeny (Udell et al., 2010a) as well as the role of associative learning (e.g., Bentosela et al., 2008) in the expression of these behaviors. The data gathered would reinforce the importance of associative learning and support the “Two Stage Hypotheses” (Udell and Wynne, 2010) according to which the communicative abilities of domestic dogs cannot be solely explained by domestication. Experiences during ontogeny are also necessary, both early interaction with humans and the subsequent conditions to which animals are exposed throughout their lives. These learning processes can occur spontaneously during interactions between animals and people, especially when the latter controls the majority of the valuable resources animals need to survive, as in the case of dogs (Reid, 2009; Udell et al., 2010a) and of other captive species. Systematic experiences such as those used in these studies, can maximize the effect of learning in a limited period of time, thus facilitating the acquisition of communicative responses. Individuals may not require intense socialization with humans to succeed on human guided tasks (although socialization could still reduce fear and thus improve performance). Instead some species may be able to succeed given additional associations between humans and food. Human oriented behavior can be modified quite rapidly (over the course of 5 min) if it is made contingent upon food rewards.

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at doi:10.1016/j.beproc.2011.10.013.

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