Márta Gácsi
Borbála Győri
Ádám Miklósi
Zsófia Virányi
Enikő Kubinyi
Department of Ethology
Eötvös University
Budapest, Pázmány P. 1/c.
1117 Hungary
E-mail: gm.art@axelero.hu

József Topál
Vilmos Csányi
Comparative Ethology Research Group
Hungarian Academy of Sciences
Budapest, Pázmány P. 1/c.
1117 Hungary

Species-Specific Differences and Similarities in the Behavior of Hand-Raised Dog and Wolf Pups in Social Situations with Humans

ABSTRACT: *In order to reveal early species-specific differences, we observed the behavior of dog puppies (n = 11) and wolf pups (n = 13) hand raised and intensively socialized in an identical way. The pups were studied in two object-preference tests at age 3, 4, and 5 weeks. After a short isolation, we observed the subjects' behavior in the presence of a pair of objects, one was always the subject's human foster parent (caregiver) and the other was varied; nursing bottle (3 weeks), unfamiliar adult dog (3 and 5 weeks), unfamiliar experimenter (4 and 5 weeks), and familiar conspecific age mate (4 weeks). Dogs and wolves did not differ in their general activity level during the tests. Wolf pups showed preference for the proximity of the caregiver in two of the tests; Bottle-Caregiver at the age of 3 weeks and Experimenter-Caregiver at the age of 5 weeks, while dogs showed preference to the caregiver in three tests; conspecific Pup-Caregiver and Experimenter-Caregiver at the age of 4 weeks and dog-caregiver at the age of 5. Compared to wolves, dogs tended to display more communicative signals that could potentially facilitate social interactions, such as distress vocalization, tail wagging, and gazing at the humans' face. In contrast to dog puppies, wolf pups showed aggressive behavior toward a familiar experimenter and also seemed to be more prone to avoidance. Our results demonstrate that already at this early age—despite unprecedented intensity of socialization and the comparable social (human) environment during early development—there are specific behavioral differences between wolves and dogs mostly with regard to their interactions with humans.*
© 2005 Wiley Periodicals, Inc. Dev Psychobiol 47: 111–122, 2005.

Keywords: *hand-raising; domestication; inborn social preferences; communicative signals; dog; wolf*

INTRODUCTION

In recent years, the evolutionary approach to understanding dog behavior has gained wide-spread interest (Hare, Brown, Williamson, & Tomasello, 2002; Miklósi, Topál, & Csányi, 2004). This is partly due to the assumption that dogs did not evolve simply by selection for human proximity (e.g., as proposed by Coppinger & Coppinger, 2002) but more broadly to the social relationships that characterize human groups and societies. Recent studies from different research groups suggest that dogs show a specific attachment to caregivers from very early age (Topál et al., 2005), they can engage in complex communicative interaction with humans (McKinley & Sambrock, 2000; Soproni, Miklósi, Topál, & Csányi, 2001), are able to recognize minute behavioral cues characterizing human visual attention (Call, Bräuer, Kaminski, & Tomasello, 2003; Gácsi, Miklósi, Varga, Topál, & Csányi, 2004; Virányi, Topál, Gácsi, Miklósi, & Csányi, 2004), and learn readily by observing humans

Received 19 July 2004; Accepted 10 May 2005
Correspondence to: M. Gácsi
Contract grant sponsor: OTKA
Contract grant number: T029705
Contract grant sponsor: Hungarian Academy of Sciences
Contract grant number: F01/031
Published online in Wiley InterScience (www.interscience.wiley.com). DOI 10.1002/dev.20082

© 2005 Wiley Periodicals, Inc.

solving various problems (Pongrácz, Miklósi, Kubinyi, Gurobi, & Csányi, 2001; Kubinyi, Topál, Miklósi, & Csányi, 2003). These observations provided support for our earlier hypothesis that dogs have adapted to become integrated into human social groups and they evolved behavioral and cognitive skills to interact with us (Miklósi, Polgárdi, Topál, & Csányi, 2000).

Considering that the wolf is regarded to be the sole ancestor of the dog (Vilá et al., 1997; Wayne, 1993) to investigate the above hypothesis, it is critical to know the extent to which predispositions are responsible for the differences in the interspecific social behavior of dogs and wolves. In light of recent findings, we need more experimental data than former comparative studies that provide to determine how domestic dogs have acquired their unique skills. From the 1960s, a relatively large number of observational and experimental studies have investigated the similarities and species-specific differences in the social behavior of young dogs and wolves. On the basis of a series of experiments, Scott & Fuller (1965) argued that dog puppies have an ‘‘optimal'' period of socialization, but at the same time, even short periods of social stimulation seem to counteract the effects of relatively long-term isolation (Fuller, 1967). Further, Fox & Stelzner (1966) found that puppies reared in isolation from conspecifics or raised with cats (Fox, 1970) show deficits in social behavior toward conspecifics, but in both cases, normal social behavior could be reinstated after 1–2 weeks of socialization with conspecifics. Similar experiments have also been conducted with the wolf (MacDonald & Ginsburg, 1981). Although, the number of such observations is restricted, similar flexibility of early learning has been documented in relation to species-specific preferences, that is, in spite of early social deprivation, the wolf pups' behavior recovered after a period of socialization with conspecifics. In summary, these experiments suggest that both the dog and the wolf have a flexible behavioral system that is relatively buffered against environmental effects, and strong inborn preferences for interaction with conspecifics allow for the recovery of species-specific behavior even after extensive periods without appropriate social environmental stimulation.

Although the two species seem to be similar in their social developmental processes with regard to conspecifics, some marked differences in their behavior toward humans have been observed (Frank & Frank, 1982a, 1985). However, it should be pointed out that previously there have been rather few research programs using wolves and dogs with similar rearing history (Frank & Frank, 1987) but even in these studies, the sample size was small so it was difficult to clearly establish the genetically based behavioral differences. Feddersen-Petersen (1986) compared the intraspecific behavior of young wolves and dogs having limited contact with humans. Others have raised wolves and dogs in human environments (Fentress, 1967; Frank, 1980; Frank & Frank, 1982a; Frank, Frank, Hasselbach, & Littleton, 1989; Woolpy & Ginsburg, 1967) in order to investigate motivational and cognitive differences. Such comparative research usually assumes that the revealed species characteristics and/or specific differences reflect the influences of differential genetic determination. With the same general assumption, our research program is distinctive in three very important aspects from earlier ones. First, we decided that both dogs and wolves should experience the same and especially intensive socialization by humans. That is, each human caretaker spent the first 2–4 months with one individual by providing care for 24 hr a day. Observations that humans can only socialize wolf pups successfully if they are separated very early (before eye opening) from the mother (Klinghammer & Goodmann, 1987) suggest very early learning and/or strong genetic preference of conspecifics in the wolf. So we planned our socialization regime especially carefully to exclude results deriving only from the differing sensitivity for early socialization in the two species. Second, we performed numerous specific investigations to observe (and compare) the behavior of wolves and dogs toward humans with regard to attachment (Topál et al., 2005) and communication (Miklósi et al., 2003, Virányi et al., 2005). Third, we socialized a relatively great number of individuals in order to have more chance to discriminate behavioral traits that are exclusively specific to one of the species (qualitative differences) from those that are present in both species and possibly represent two extremes of the same distribution (quantitative differences).

For the present study, three possible hypotheses can be formulated: First, given the same environmental conditions, no differences emerge between the species at this early developmental stage. Second, dog-wolf differences in behavior can be explained by wolves' different (faster) developmental speed that has been documented earlier (Frank & Frank, 1982a; Zimen, 1987). Third, the behavioral differences can have a more specific genetic basis selected for during domestication. A good example for this was the selection for ‘‘tame'' behavior toward humans (approaching human hand) in ‘‘domesticated'' foxes, which resulted in a prolonged capacity of socialization (Belyaev, Plyusnina, & Trut, 1985). These differences could be based on various aspects of the developmental process, for example, on a decreased specificity of the learning constraints or on a change in the duration of the sensitive period.

In the first set of experiments, we wanted to see whether members of both species developed similar preference for their primary (human) caregiver. For the testing, we have applied an object-preference test, a method often used to look for early effects of social experience. The subject usually has the opportunity to choose between two (social or nonsocial) simultaneously presented objects by spending more time with one or the other stimulus object (e.g., Sackett, Porter, & Holmes, 1964). This method allowed us to use a natural set-up that interfered relatively little with the behavior of the subjects.

Because of earlier indication for differences in temperament traits already at this age (e.g., Frank & Frank, 1982b, 1987), we have also measured signs of aggressive and avoidance behavior.

In previous studies, we have provided evidence that dogs have an advantage to use face and eye-related gestural cues (e.g., Soproni et al., 2001). Further, there appears to be a species-specific difference in the use of face/eye contact in social interactions with humans when comparing 4-month-old wolves and dogs (Miklósi et al., 2003). To address this question, we investigated whether the species-specific differences can be traced back to an earlier stage of development, and in a separate test we tried to study whether these differences can be masked by a learning procedure.

METHODS

Subjects

In year 2000–2003, our group raised 13 gray wolf pups (*Canis lupus)* born at Horatius Ltd. Animal Park (6 males and 7 females, from five different litters) and 11 dog puppies *(Canis familiaris)* from three shelters (6 males and 5 females from five different litters, all mongrels). All the animals were socialized and tested the same way.

Not all of the subjects could participate in every test (caregiver was ill or subject had injury) and in some cases (9 subjects' 16 tests from the total 144 tests), the data were lost due to technical problems (recording failure and a lost video cassette). This means that the actual number of individuals varies in the tests, so in each case we give the exact number of the animals whose data were analyzed (see Tab. 1).

Socialization Procedure

Subjects (dogs and wolves) were individually hand raised by humans after being separated from their mothers and littermates on Day 4–6 after birth (before their eyes opened). The hand raising and the socialization procedure were based on a detailed protocol (Ujfalussy, 2003). Fentress (1967) reared one wolf most similarly to our procedure, but the pup was already 4 weeks old when he obtained it. In our case, each subject spent the first months of their lives in 24-hr close contact with their human foster parents, they lived in the homes of the caregivers and slept together with them at night. They were bottle-fed and from the age of 4–5 weeks hand fed also with solid food. The caregivers carried them in a pouch, so the pups could participate in their everyday activities (traveling by public transport, attending classes at the university, visiting friends, etc.). The pups frequently met unfamiliar humans, and at least twice a week they also met conspecifics of about the same age and adult dogs. This way, they were regularly exposed to novel stimuli and situations as well as to familiar individuals. The basic principle of socialization was avoiding competitive situations and aggressive interactions with the animals, that is, to behave rather like a mother than a dominant conspecific.

Our team was licensed by the Department of Nature Conservation, Ministry of Environmental Affairs (No.3293/2001) to hand rear and expose the wolf pups to extensive socialization, and our department has also been licensed by the Ethical Committee for Animal Experimentation at the Eötvös University to conduct such research. At the age of 4 months, wolves were placed back at the animal park where they could interact daily with humans and other wolves. The caretakers carried on visiting them once or twice a week, so the wolves were regularly taken out of the pack for further testing,

Table 1. The Sequence of Testing at the Age of 3, 4, and 5 Weeks

3 Weeks (20–22 Days)	4 Weeks (27–29 Days)	5 Weeks (34–36 Days)
	5-min isolation in box	
Bottle-caregiver object-preference test ($N_{(W)} = 12$, $N_{(D)} = 9$)	Conspecific pup-caregiver object-preference test ($N_{(W)} = 9$, $N_{(D)} = 8$)	Dog-caregiver object-preference test ($N_{(W)} = 12$, $N_{(D)} = 11$)
	10–15-min in pen	
	5-min isolation in box	
Dog-caregiver object-preference test ($N_{(W)} = 12$, $N_{(D)} = 11$)	Experimenter-caregiver object-preference test ($N_{(W)} = 12$, $N_{(D)} = 11$)	Experimenter-caregiver object-preference test ($N_{(W)} = 12$, $N_{(D)} = 11$)

Note. On each occasion, the procedure started with a 5-min-long isolation. Immediately after the isolation, subjects participated in the first object-preference test. It was followed by a 10–15-min period when the animals rested in the pen. Then the pups were isolated again and the second object-preference test came next. The number of participating subjects is indicated in case of each test (some of the tests could not be analyzed due to technical problems; these are omitted from the table).

some regular training and other free social interactions. After a gradual resocialization period by the age of 1 year, they were successfully integrated into a pack (living in captivity). Seven of the dog puppies were adopted by their caregivers, and we could find loving home for the other four as well.

EXPERIMENTAL PROCEDURES

Object-Preference Test

The subjects were presented with all together six object-preference tests; two tests were conducted on every subject at the age of 3, 4, and 5 weeks. On each occasion, all subjects were observed first in the first test one-by-one and then in the same order in the second test. The tests were performed in the morning and the caregivers fed the animals with milk at least 2 hr earlier. Before the tests, each subject was isolated for 5 min in a. 9 m × .9 m × .9 m cardboard box situated in an unfamiliar empty room.

(This was done in order to elicit similar motivational levels in all pups to initiate social interactions during the test.) The subjects was put into the box and taken out of it by a familiar female experimenter.

Following the isolation period, the subject was carried into another room (2.6 m × 3.6 m) that was unfamiliar to them at the first occasion (at the age of 3 weeks). All object-preference tests were carried out in the same room. In each case, two objects were placed in the room that otherwise was empty, except the cameraman who stood behind a 1.2 m high plastic screen and recorded the behavior of the subjects. The position of the two objects and the starting location of the subject formed an equilateral triangle. The objects' location (right or left side) was counterbalanced on the same day. The familiar experimenter (the same person who took the subject out of the isolation box) placed the subject to the starting point, held it for a second making it orient toward the objects, and then let it go while stepping back two steps and remained still from then on (see Fig. 1 for the testing design). After placing the subject to the starting location, she interfered only if the animal fell asleep during the first 90 s. In this case, at the 90th s she woke it up by gently rubbing it for a few seconds and then placed it to the starting point again. The subjects' behavior was observed for 5 min. At the end of the test, the familiar experimenter slowly approached the subject from the front, caught, and lifted it without talking to it.

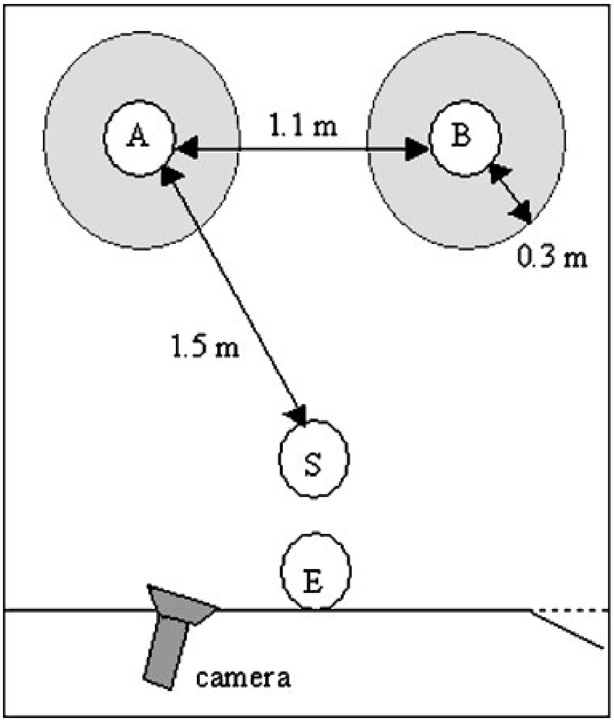

FIGURE 1 Schematic illustration of the test room. (A) and (B) indicate the position of the two different types of objects that were presented simultaneously during the 5-min tests (*caregiver, experimenter, adult dog, conspecific pup, milk bottle* according to the type of the test). The gray-shaded areas represent the *proximity* of the objects. At the beginning of the object-preference test, the familiar female experimenter (E) put the subject (S) on the starting point, which had been marked on the floor. The two objects were 1.1 m from each other and 1.5 m from the subject's starting position. A cameraman, standing behind a 1.2 m high plastic screen, recorded the tests with a camera positioned on a tripod.

Object Pairings

In all tests, the caregiver of the subject was one of the objects (''reference'') who were paired with different kinds of other ''social objects'' with the only exception of the nursing bottle in the very first test (see Tab. 1). The human participants always sat cross-legged and motionless on the floor quietly facing the subject. Their hands were placed on the floor in front of them with upturned palms.

Bottle-Caregiver. There was some lukewarm milk (used for feeding) in the nursing bottle that was placed on a small cloth soaked with milk. The caregiver was looking at the subject during the test.

Experimenter-Caregiver. Both humans were looking at the subject during the test. In both tests, the same female experimenter took part. At the first time, she was unfamiliar to the subjects, and did not have any contact with them between the similar tests at the age of 4 and 5 weeks.

Dog-Caregiver. The adult dog was positioned facing the starting point of the subject. He was a well-trained, adult Belgian shepherd male that at the time of the first test was unfamiliar to the subjects and had no contact with them apart from the tests. The dog laid calmly at his place for 5 min. This time the caregiver adjusted her behavior to that of the adult dog, that is, she oriented to the subject only when the dog did so.

Conspecific Pup-Caregiver. We always selected a same age sleeping conspecific from the subject pool in order to avoid interactions. Conspecific subjects knew each other equally well, as they had the possibility to meet regularly from the age of 2 weeks. The sleeping pup was gently placed to the floor and watched for a few seconds whether it was lying calmly. The caregiver sat motionless looking at the subject.

Behavior Categories

As the duration of the test sessions varied slightly, we calculated the relative percentage of the time spent with each behavior.

Activity (%). In this early age, social behavior obviously cannot be analyzed without considering the animals' general mobility or activity level. Taking into account the immature motor behavior of the subjects, we assessed activity observing the time (s) spent standing or moving on four legs. (We only considered the time when the subjects were not in physical contact with the objects.) For statistical analysis, we used the mean activity value measured in the two tests on the same day (i.e., activity level at the age of 3 weeks; $(A_1/t_1 + A_2/t_2)/2$, where $A_1 =$ time standing or moving on four legs during the first test at the age of 3 weeks, $t_1 =$ total time of the first test at the age of 3 weeks, $A_2 =$ time standing or moving on four legs during the second test at the age of 3 weeks, $t_2 =$ total time of the second test at the age of 3 weeks.)

Proximity (%). We measured the relative duration of the total time spent in proximity with each object closer than the length of the subject's own body (i.e., the subject is closer than approximately 25–35 cm to any part of the stimulus). For statistical analysis, a preference index was calculated (see below).

Vocalization (%). We measured the relative duration of the total time spent with any form of vocalization. For statistical analysis, we used the mean vocalization value measured in the two tests on the same day (same calculation as in case of activity).

The occurrence of vocalization (score, 0–1) was also recorded by the familiar experimenter just before she entered the room where the subject was isolated.

Gazing at Face (Relative Frequency). Gazing was defined as orienting the nose toward the human's face, which was characterized by lifting of the head. This variable was recorded only while the animal was in proximity with a human (caregiver and unfamiliar experimenter). The frequency of gazing at human face was calculated by dividing the number of gazings by the time spent in proximity with the humans. For statistical analysis, we used the mean of gazing frequencies measured in the two tests on the same day. (The adult dog's eyes were not high enough to identify the subjects' head movements as gazing.)

Tail Wagging (Score, 0–1). The subject was given a score 1 if it wagged its tail when approaching either of the objects for the first time (getting closer than 30 cm) or while first getting into physical contact with either of them. A score 0 was given if this behavior was not observed on these occasions or the animal did not get into proximity with a stimulus during the test.

We have recorded signs of avoidance and aggressiveness of the subjects toward the approaching familiar experimenter both before and after each test when the animal was handled: first, at the end of the isolation periods when the familiar experimenter took the subject out of the box and for the second time, when she slowly approached, caught, and lifted the subject at the end of the object-preference test.

Avoidance (Score). The subject scored 1, if it showed avoidance toward the familiar experimenter, or a score 0, if it did not show avoidance (i.e., behaved passively or approached her).

Aggressiveness (Score). We categorized the reaction of the animal as aggressive if it growled or tried to bite the familiar experimenter. The subject was given a score 0 if it showed no aggression toward the familiar experimenter and a score 1, if it growled or tried to bite.

All object-preference tests were videotaped and analyzed later by one of the authors (B.G.). Interobserver agreement between her and a naïve observer on the behavior categories was assessed by comparing their parallel coding of the same video records and evaluation of the 22% of the data (eight wolves, eight dogs). The following Cohen Kappa results were obtained (Martin & Bateson, 1986): activity = .85; proximity = .96; vocalization = .76; tail wagging = 1; gazing at face = .93; avoidance = 1; aggressiveness = 1.

Reinforced Eye Contact

In case of three dog and four wolf pups, we tried to increase the frequency of eye contact with a familiar experimenter by reinforcing them with food for the required behavior. The 4-min test sessions were conducted at a familiar place; first, when the subjects were 5 weeks old (after the object-preference tests) and later when they were 9 weeks old. Prior to the test, the incentive value of the food reward was tested by placing small pieces on the floor 1 m from the subject. When we released the subjects, each of them ran to the food and ate it up immediately. Then a familiar experimenter (the same person in all tests) sat on the floor facing the subject continuously. A plate of food (small pieces of cold cut) was placed on a table beside the experimenter out of subjects' reach. The animal could move freely around and when it made eye contact with the experimenter, she signed it with a clicker (a small device that gives a sudden snapping sound when pushed) and immediately threw a piece of food to the animal. If the animal went farther than 1.5 m from the experimenter, she made noise with the plate to redirect its attention. The caregiver sat still 2 m away from the experimenter. The whole session was videotaped. Reviewing the tapes, we counted the number of "clicks," which equaled the number of eye contacts between the experimenter and the animal.

Data Analysis

If variables were distributed normally, analysis of variance or *t*-tests were used. In the case of proximity, we have calculated a preference index as follows: (relative duration of time spent with caregiver−relative duration of time spent with other object)/(relative duration of time spent with caregiver + relative duration of time spent with other object). In case of the preference index, first we tested for divergence from zero (i.e. no preference) by one-sample *t*-tests. Then we compared the preference index of dogs and wolves by one- and two-way ANOVA. We scored it as missing value, if the denominator was zero (no time spent in proximity of any of the two objects).

'Gazing at face' did not show normal distribution, therefore nonparametric Mann–Whitney *U*-test was used for analysis. 'Tail-wagging' 'avoidance,' and 'aggressiveness' were analyzed with Fisher exact test.

RESULTS

Object-Preference Test

Activity. First of all, we wanted to determine whether there was any difference in the motor ability or general activity level of the species during the object preference tests. This was measured by calculating the mean activity level for the two tests at all three ages. The two-way ANOVA (species × age, with repeated measures for age) revealed no difference between the activity level of the wolf and dog pups at any age ($F_{1,20} = 1.878$, $p = .186$). However, the subjects spent more time with active behavior as they got older ($F_{2,40} = 7.995$; $p = .001$) (Fig. 2). The species-age interaction was not significant ($F_{2,40} = 1.649$; $p = .205$).

Proximity (Preference Index). To assess the social behavior after a short isolation, we compared the time spent in close proximity to the objects presented. Comparing the preference index to zero (assuming no preference for either object presented), we found that both dogs and wolves tended to show either no preference at all or preference for the caregiver. Wolves preferred to be in the proximity of the caregiver in two tests: at the age of 3 weeks (Bottle-Caregiver) and at the age of 5 (Experimenter-Caregiver). Dogs tended to spend more time with the caregiver in three tests: at the age of 4 weeks in both tests (Pup-Caregiver and Experimenter-Caregiver) and at the age of 5 (dog-caregiver) (see Tab. 2).

The preference index of dogs and wolves was compared by one-way ANOVA in case of the two pairings that were carried out only once (Bottle-Caregiver and conspecific Pup-Caregiver). Two-way ANOVA (with repeated measures for age) was used to compare the species in those two pairings (Experimenter-Caregiver and Dog-Caregiver), which were tested two times (at different ages).

We found no difference in the preference index of dogs and wolves at the age of 3 weeks in the Bottle-Caregiver

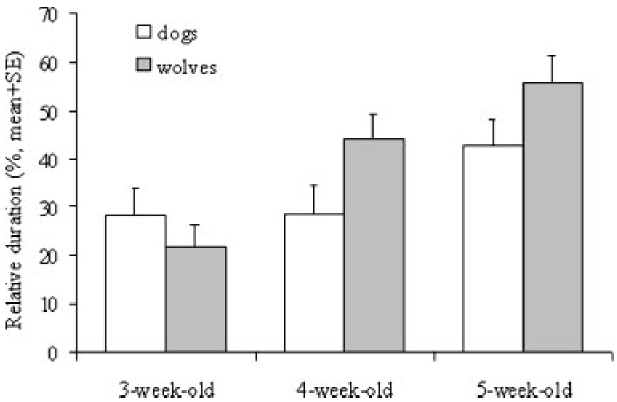

FIGURE 2 Mean value (+SE) of relative durations of the time spent in activity at the age of 3, 4, and 5 weeks averaged the results of the two object-preference tests. The comparison of the activity values at different age categories by repeated-measures ANOVA revealed no significant difference between wolves and dogs. The activity increased with age, the species-age interaction was not significant.

Table 2. Results of the Comparison of Preference Indexes in all Tests

	3 Weeks	4 Weeks	5 Weeks
	Bottle-caregiver	Conspecific pup-caregiver	Dog-caregiver
Wolves	$\mathbf{t_9 = 5.489, p < .05}$	$t_8 = 1.043, p = .327$	$t_{11} = -.524, p = .611$
Dogs	$t_4 = .662, p = .544$	$\mathbf{t_5 = 3.83, p\ .05}$	$\mathbf{t_9 = 12.131, p\ .01}$
	Dog-caregiver	Experimenter-caregiver	Experimenter-caregiver
Wolves	$t_{10} = 1.664, p = .127$	$t_9 = 1.648, p = .128$	$\mathbf{t_{11} = 3.768, p = .01}$
Dogs	$t_7 = .777, p = .462$	$\mathbf{t_9 = 2.72, p\ .05}$	$t_9 = 1.532, p = .159$

Note. The differences of the preference index from zero were analyzed with one-sample *t*-tests, and the *p*-values were corrected with False Discovery Rate adjustment (Benjamini, Drai, Elmer, Kafkafi, & Golani, 2001). In all cases, significant differences (highlighted with bold face) refer to preference to be in the proximity of the caregiver.

test ($F_{1,14} = 2.54$, $p = .135$) and also at 4 weeks of age in the Conspecific Pup-Caregiver test ($F_{1,14} = .77, p = .395$). Similarly, no effect of the species has been found in the Experimenter-Caregiver tests ($F_{1,17} = .05$; $p = .824$), lacking also the effect of age ($F_{1,17} = .113$; $p = .74$) and interaction ($F_{1,17} = 1.45$; $p = .24$). The Dog-Caregiver tests also showed no overall difference in the social preferences of the two species ($F_{1,16} = 2.16$; $p = .16$) and no effect of age was found either ($F_{1,16} = .04$; $p = .84$). However, the significant interaction ($F_{1,16} = 7.08$; $p = .02$) indicates that compared to wolves dogs showed more pronounced preference for the caregiver when they were 5 weeks old.

It also seemed informative to analyze which unfamiliar social partner (experimenter or dog) took greater effect on the animals in the presence of the caregiver, that is, in case of which object showed they less preference toward the caregiver. Comparing the preference index values in the two tests at the age of 5 weeks, we found that dog puppies tended to prefer the caregiver less if the other object was the unfamiliar human ($t_8 = 2.77$, $p = .024$) while wolf pups showed less (actually no) preference toward the caregiver when the other choice was the unfamiliar adult dog ($t_{11} = -3.84$, $p = .003$) (Fig. 3).

Vocalization. During the isolation period, distress vocalization was characteristic mainly for dogs. While seven of eight dogs vocalized (high pitched sounds or howl) at least on one occasion just before the experimenter entered the room, only three of nine wolves showed similar behavior. (Unfortunately, data of some subjects could not be analyzed due to the lost video cassette.)

We have never observed growling and barking during the object-preference tests with regard of the objects. All vocalizations were high-pitched sounds (e.g., whining or yelping: see Cohen & Fox, 1976; Ohl, 1996) thus reflecting most probably signs of distress because the animals vocalized mainly when they were not in the proximity of the objects. Using two-way ANOVA (with repeated measures for age), we have found that dog puppies spent more time with vocalization during the tests than wolf pups did ($F_{1,20} = 11.24$; $p = .003$) without an effect of age ($F_{2,40} = 1.954$; $p = .115$). However, significant interaction ($F_{2,40} = 3.912$; $p = .028$) indicated that the tendency for vocalization decreased with age in dog puppies, while in case of wolf pups, no such change was evident (Fig. 4).

Tail Wagging. Wolf pups never wagged their tails while approaching the objects for the first time or while first getting into physical contact with them. (Even if we consider the entire period of tests, there was only one pup

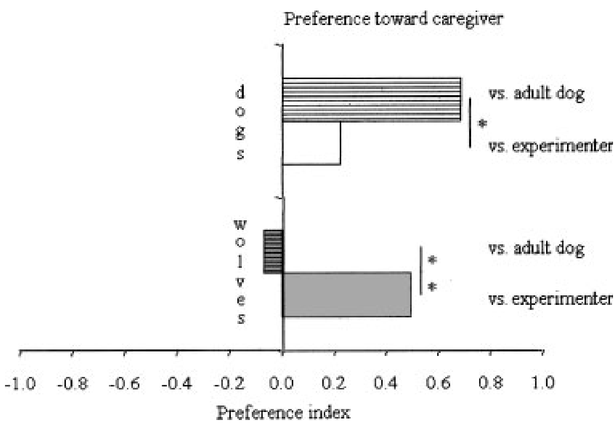

FIGURE 3 Preference index values of 5-week-old dogs (two upper bars) and wolves (two lower bars) in the "Caregiver-Dog" (■, filled bars) and the "Caregiver-Experimenter" (, dotted bars) object-preference tests. Index values different from zero refer to preference to be in the proximity of the indicated objects. The index values were calculated as: (relative duration of time spent with caregiver−relative duration of time spent with other stimulus)/(relative duration of time spent with caregiver + relative duration of time spent with other stimulus). A comparison of the index values from the two types of tests at the same age reveals in which test subjects showed greater preference toward their caregiver. Dogs preferred their caregiver less when the other object was the experimenter, while wolves showed actually no preference toward their caregiver in the presence of an adult dog (paired *t*-tests). Significant differences are indicated with asterisks ($^*p < .05$, $^{**}p < .01$).

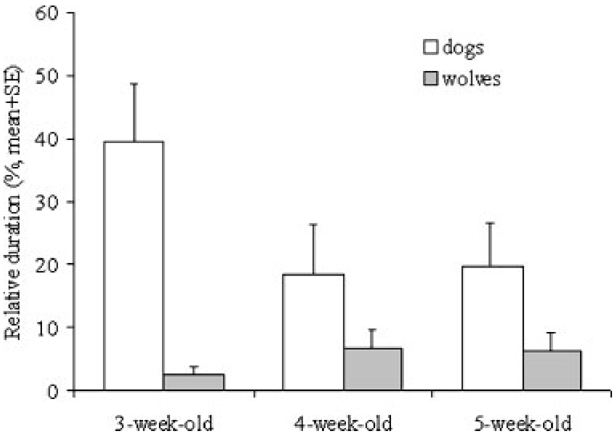

FIGURE 4 Mean value (+SE) of relative durations of time spent with vocalization at the age of 3, 4, and 5 weeks averaged the results of the two object-preference tests. The values of the two species at different age categories were compared by repeated-measures ANOVA. Dogs spent more time vocalizing than wolves, with no effect of age. Significant interaction indicated that vocalization tended to decrease with age in the case of dogs, while wolves' vocalization did not change with age.

that showed this behavior orienting toward the adult dog and also toward the caregiver in one test at the age of 5 weeks. This happened, however, not at the first approach or in physical contact with the objects.) Despite the lack of tail wagging in wolves during the observed periods, the two groups did not differ statistically in the tendency for showing tail wagging in respect of any object at the age of 3 weeks. In the proximity of the nursing bottle and the adult dog, none of the animals showed tail wagging and only few dog puppies (two subjects in the Bottle-Caregiver and three in the Dog-Caregiver test) wagged their tail when approached or contacted the caregiver.

However, 4- and 5-week-old dog puppies significantly differed from wolf pups in case of all objects. Compared to wolves, more 4-week-old dog puppies showed some tail wagging toward the caregiver both in the Experimenter-Caregiver (Fisher exact test; $p < .001$) and in the Pup-Caregiver test ($p = .029$). We found the same species difference in tail wagging in Experimenter-Caregiver test toward the experimenter ($p = .037$) and in the Conspecific Pup-Caregiver test toward the pup ($p = .029$). This difference was also characteristic in case of 5-week-old subjects as dogs wagged their tail more often toward all objects (Dog-Caregiver test: caregiver: $p < .001$; adult dog: $p = .005$, Experimenter-Caregiver test: experimenter: $p = .001$; caregiver: $p < .001$). In all but one occasions, dogs wagged their tails horizontally or in a high position rather than holding it low or between the legs.

Gazing at Face. As we found no difference between the caregiver and the unfamiliar human in respect of gazing at their face (dogs: $z = -1.69$, $p = .09$; wolves: $z = -.45$, $p = .66$ by Wilcoxon test), and considering the relative rare occurrence of this behavior, we added up the number of gazings at any human face during the tests at a certain age.

Three- and 4-week-old animals gazed rarely at the human face, and no difference was found between the species ($N_{d,w} = 8;11$, $U = 38.50$, $p = .241$; $N_{d,w} = 11;11$, $U = 40.00$, $p = .104$, respectively). At the age of 5 weeks, however, dog puppies gazed at the humans' face more often than wolf pups did ($N_{d,w} = 11;12$, $U = 31.00$; $p = .02$) (Fig. 5).

Avoidance. Considering all three age categories together only one dog showed avoidance on 1 occasion (1%) of 98 interactions (taking up the puppy by the experimenter) in contrast to eight wolves displaying such behavior on 19 occasions (17%) of 106 interactions. Due to the small sample size and the relatively rare occurrence of this behavior, however, this did not mean significant difference between the species in avoidance shown toward a familiar experimenter at the age of 3 and 4 weeks (Fisher exact test; $p = .214$ and .242, respectively) and only a tendency could be demonstrated in case of the 5-week-old pups ($p = .057$).

Aggressiveness. None of the dog puppies behaved aggressively in the 99 interactions with the familiar experimenter during the tests. Among the 13 wolf pups,

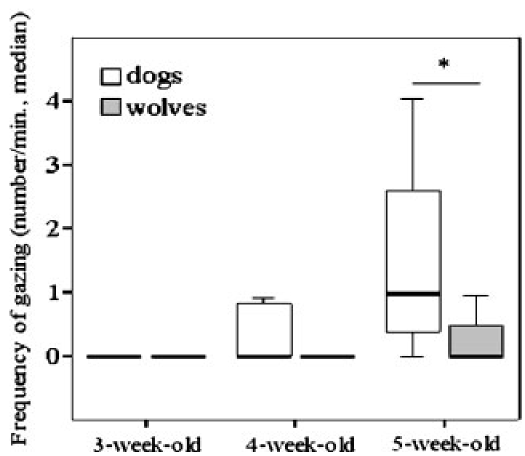

FIGURE 5 Frequency (number/min) of gazings at the humans' face in the three age categories during the two tests. The medians of nonparametric data are represented by bold lines, and boxes indicate the 50% of the data (lower and upper interquartile range). Whiskers extend to the smallest and largest values excluding outliers and extremities. Mann–Whitney *U*-tests showed that 5-week-old dogs gazed at the humans' face significantly more frequently than wolves did. Significant differences are indicated with asterisks (*$p < .05$).

however, there were nine individuals that one or more times growled at the familiar experimenter and/or tried to bite her (in 29 cases of 112 interactions, 26%). Comparing the species by age-categories, we have found that aggressive behavior was more pronounced in wolves than in dogs at each age (Fisher exact test: 3-week-olds, $p = .04$; 4-week-olds, $p = .013$; 5-week-olds, $p = .001$).

Eye Contact. This experiment was carried out only with three dog puppies and four wolf pups, so the results should be regarded as preliminary. Subjects were tested both at the age of 5 and 9 weeks, but most 5-week-old wolf pups fell asleep during the session so only the result of the dogs could be analyzed for this age.

Comparing the number of eye contacts at the age of 9 weeks, no difference was found between the performance of the species in the first minute ($t_5 = .985$, $p = .370$). At the beginning, all animals made intensive attempts to take the food directly from the plate, which was unreachable for them. As the session went on, however, dogs tended to gaze more at the experimenter's face. Wolves, on the contrary, kept mainly orienting toward the plate, even though they always got a food pellet from the experimenter if they happened to gaze at her.

Compared to wolves, dogs achieved significantly more eye contact with the experimenter during the fourth minute ($t_5 = 4.811$, $p = .005$).

To look for any learning effect across the two ages in dogs, we compared their performance (difference between number of eye-contact in min 4 and min 1) at the age of 5 and 9 weeks, and found very similar pattern of performance ($t_2 = -.615$, $p = .601$) (Fig. 6).

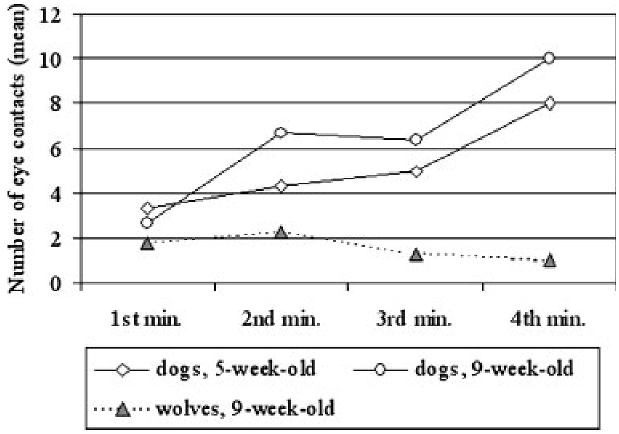

FIGURE 6 Mean number of eye contacts with a familiar experimenter during the 4-min long operant conditioning test sessions of dogs at the age of 5 and 9 weeks versus that of 9-week-old wolves. (The results of 5-week-old wolves could not be evaluated.) Comparing the number of eye contacts in the presence of a plate with food, 9-week-old dogs' and wolves' behavior did not differ during the first minute. During the last minute, however, dogs initiated more eye contacts than wolves. No significant difference was found in the performance of dogs at the age of 5 and 9 weeks.

DISCUSSION

This study presents a part of a longitudinal study observing the social behavior of 13 wolves and 11 dogs reared in identical human social environment and aiming to reveal the species-specific differences during the course of development. Though some of our questions were already addressed in past studies (e.g., Zimen, 1987), the analysis of experimental data on the social relationship and interaction between the socialized animal and its human caregiver received less attention. Such observations are of great importance to understand specific behavioral characteristics in dogs, which are assumed to be the result of the domestication process.

The effects observed in this study can be grouped into three main categories. First, the behavior differences could be affected by maturation. According to our data, the activity level of dog and wolf pups did not differ significantly. Therefore, it is unlikely that species differences are related to differing motor abilities; however, we cannot exclude that wolf pups may develop faster in other respects.

Second, preference to stay in the proximity of the caregiver could be the result of the interaction of various and not necessarily exclusive processes. The behavior of the subjects could be controlled by their familiarity to the objects, revealing itself in a tendency to approach the familiar, or alternatively, to explore the (relatively) novel, less familiar stimulus. In case of attachment, it is generally assumed that for young animals, it is more advantageous to "choose" the familiar stimulus ("parent") in a novel and hazardous environment (Rajecki, Lamb, & Obmascher, 1978), and this preference is often interpreted as a result of a recognition process, that is, the subject identified one of them as being the same or (more) similar to its "parent." One way to show the effect of learning is to manipulate the "parent" and look for preference changes in choice tests. In our case, both dogs and wolves had human "parent," so the question was whether similar experience affected their choice behavior differently, or in other words even similarly intensive socialization could not compensate for different learning constraints.

Wolves preferred the caregiver to the bottle at the age of 3 weeks, which affirms the findings that in some contexts, social stimuli have higher incentive value than food reinforcement for wolf pups (Frank & Frank, 1988). Dogs displayed preference for the caregiver starting from the 4th week, and this preference disappeared only in the last test when they were tested with two humans. This could suggest that dogs develop a preference toward humans as they get older, and additionally this preference is not restricted to the caregiver but becomes more generalized by the age of 5 weeks. It is also possible that dog puppies are more sensitive to being "ignored" by their motionless caregiver than are wolf pups, thus are more prone to seek contact (try to initiate social interaction) also with the experimenter. Wolf pups show a clear preference for the human individual recognized as the "parent" (at the age of 5 weeks) but this can be masked when the other human is either a novel stimulus or is a canid (adult dog or wolf pup). It could be assumed that "noncaregiver" social stimuli evoked exploratory behavior on the part of the wolf. This is supported by the observation that wolves showed no preference for the caregiver at the age of 4 weeks but it emerged 1 week later when the test was repeated and the other human had lost its "novelty value." An alternative explanation might be that for this time the (relatively) novel stimulus may evoke some fearfulness besides the exploratory behavior in wolf pups.

Taken together, this suggests that both species are able to learn about its heterospecific (human) foster parent but there might be differences in the ability to generalize its characteristics to other similar "objects." If we assume that such recognition (or preference) is based on learning a set of features of the parent then the difference may be that wolves are more restrictive in their choice when the caregiver is highly different from the natural parent. While the recognition of a "wolf-like" parent seems to be the "default" state of wolves' learning system, domestication might have changed this in dogs by making the recognition process less precise, that is, recognition can occur in greater ranges of these characteristic features. This relaxed (or generalized) recognition in case of nonconspecifics might have been advantageous for young dogs living in human setting, which have been raised (fed, etc) not exclusively by a single human (caregiver) but a group of humans ("family").

Third, in the case of some communicative signals, further species differences were observed. Dogs vocalized more during the tests that could be the result of a decreased threshold for the elicitation of distress calls in dogs, which is supported generally by the observation that dogs are more vocal in comparison to wolves (Fox, 1971a). Young wolves could be more prone to situations of being left alone in comparison to dogs, or vocalization while alone would make a wolf pup more vulnerable to predators, but selection against this trait has been relaxed in dogs living in the human social environment lacking predators (Fox, 1971a, see also Frank & Frank, 1982a).

Wolf pups showed more avoidance and aggression toward a familiar human, though the observed difference in such responses might be not unique to interactions with humans. The greater number of growls and attacks (e.g., attempted biting) in wolves and the absence of these behaviors in the case of dogs could be best explained by supposing that wolves either did not like to be touched or constrained in their movements, or they had a lower threshold for the elicitation of aggressive behavior. Humans must have successfully selected against such behaviors in the case of dogs. A recent comparative study observing young wolves' and dogs' attachment behavior toward their caregiver in the Strange Situation procedure has also shown differences in temperament traits such as approach-avoidance behaviors (Topál et al., 2005). These findings might also help in finding new methods for wolf–dog hybrid identification (e.g., comparing the aggressive–avoidance behavior of animals of unknown origin with that of dogs) even at very early age.

Although tail wagging is listed as a behavior unit in the ethogram of the wolf (McLeod, 1996; McLeod & Fentress, 1997; Schenkel, 1967; Zimen, 1987), it has been observed usually in the context of active submission. Although this behavior has been observed in wolf pups as early as 3 weeks of age (Fox, 1971a; McLeod & Fentress, 1997; Zimen, 1987), and was present also in our pups' behavior during interactive social contexts, we did not found tail wagging in the wolves during the observed periods. It is also interesting to note that tail wagging became also more frequent in the foxes selected for tameness (Belyaev, 1978). Considering the context of our test arrangement, dog puppies are either more prone to show submission toward passive social stimuli at the age of 4–5 weeks, or may use tail wagging for a somewhat broader communicative intention to facilitate interaction. The high position of their tail during tail wagging seems to give some support to the latter explanation.

Further differences were found in relation to gazing behavior toward humans. Despite extensive socialization with humans, wolves seem to avoid looking at the face of the experimenter, which was revealed in the low frequency of gazing in the object-preference tests. Their behavior in the eye contact test 4 weeks later supports the idea that this difference cannot be explained simply by a delay in the development of their social communication system.

As wolves proved to be motivated by the food when they could get it for "free" prior to the eye contact test at both ages, we suggest that their reaction could be explained by the strategy observed in wolves in other situations as well when responding to "unsolvable" problems they first tried on their own and then gave up and had a rest (Miklósi et al., 2003).

In the conditioning test, the required behavior was a very simple one and food reinforcement always followed the eye-contact right away. There are two possible explanations for increased tendency to gaze at the human's face in dogs; either they learned the association between eye-contact and food reward very quickly, or they might have not learned much, but in this moderately stressful situation, they looked more into the human's eyes only because ''solicitation'' came more natural to them.

In the first case, the difference in the performance could stem again from two factors; looking into the eyes of a human can be less ''convenient'' behavior for wolves, or there might be some other type of learning difference between the two species in this situation (i.e., dogs were simply more quick in this conditioning task).

However, comparative studies on the problem solving abilities and species-specific constraints on learning in the two species have revealed no inferior performance of wolves (Frank & Frank, 1985, 1988; Frank et al., 1989). Moreover, in other tests, we found some plasticity in young wolves' willingness to look into the eyes of a familiar experimenter, which supports that after extensive training, learning can overcome initial differences (Virányi et al., 2005).

When comparing the gazing behavior of the two species, it is important to note that in the wolf, gazing plays a crucial role in agonistic communication, that is, dominants express threat by gazing at the subordinates, and both the dominant and the subordinate can avoid conflict by trying to avoid gaze contact (Fox, 1971a, Schenkel, 1967). Although no direct quantitative behavioral comparisons are known, it is generally assumed that the use of gazing in intraspecies aggressive interactions in dogs is basically similar to that of described for the wolf (Fox, 1971b), and in dogs, direct staring can release very easily aggressive behavior or attack. Additionally, in recent experiments, we have shown that dogs also perceive human gazing accompanied with other behavioral cues as indication of threat (Vas, Topál, Gácsi, Miklósi, & Csányi, 2005). However, with respect to nonaggressive communicative interactions, we have described that wolves and dogs differ in their willingness to look at the humans face (Miklósi et al., 2003). At present, two different, not exclusive processes can account for the difference between the wolf and the dog. Dogs could have been selected for being more resistant to gazing, that is, only more extended gazing would induce subordinate or agonistic behavior, or dogs could be selected for gazing preferentially at humans. Interestingly, on the basis of comparative investigations, Frank and Frank (1985) seem to support the latter view when noting that dogs might have been selected for soliciting human intervention. Elsewhere we have also proposed that increased gazing at humans could pave the way for the emergence of complex social skills in dogs that are able to utilize this visual communicative channel used predominantly by our species (Miklósi et al., 2003, Miklósi et al., 2004).

In summary, it seems that while both species are able to learn about the human caregiver, their social preferences differentiate during early development mainly because human and conspecific social stimuli affect their preferences differently.

In addition, the behavior of the dog puppies is characterized by less aggression and avoidance toward humans in parallel with the increase in communicative signals such as vocalization, tail wagging, and gazing, which can provide a basis for positive feedback on interspecific dog–human interaction.

NOTES

The authors thank the hand raising caregivers for their devotion and assistance during the project. We are grateful for the cooperation of Zoltán Horkai in helping the hand raising of the wolf pups and providing home for them at his wolf-park after the observations.

REFERENCES

Belyaev, D. K. (1978). Destabilizing selection as a factor in domestication. Journal of Heredity, 70, 301–308.

Belyaev, D. K., Plyusnina, I. Z., & Trut, L. N. (1985). Domestication in the silver fox (Vulpes fulvus): Changes in physiological boundaries of the sensitive period of primary socialization. Applied Animal Behavior Science, 13, 359–370.

Benjamini, Y., Drai, D., Elmer, G., Kafkafi, N., & Golani, I. (2001). Controlling the false discovery rate in behavior genetics research. Behavioural Brain Research. 125, 279–284.

Call, J., Bräuer, J., Kaminski, J., & Tomasello, M. (2003). Domestic dogs are sensitive to the attentional state of humans. Journal Of Comparative Psychology, 117, 257–263.

Cohen, J.A., & Fox, M. W. (1976). Vocalization in wild canids and possible effects of domestication. Behavioral Processes, 1, 77–92.

Coppinger, R. P., & Coppinger, M. (2002). Dogs. A new understanding of canine origin, behavior and evolution. Chicago: University of Chicago Press.

Feddersen-Petersen, D. (1986). Observations on social play in some species of Canidae. Zoologischer Anzeiger, 217, 130–144.

Fentress, J. C. (1967) Observations on the behavioral development of a hand-reared male timber wolf. American Zoologist, 7, 339–351.

Fox, M. W. (1970). Behavioral effects of rearing dogs with cats during the 'critical period of socialisation. Behavior, 35, 273–280.

Fox, M. W. (1971a). Behavior of wolves, dogs and related canids. London: The Trinity Press.

Fox, M. W. (1971b). Integrative development of brain and behavior in the dog. Chicago: University of Chicago Press.

Fox, M. W., & Stelzner, D. (1966). Approach/withdrawal variables in the development of social behavior in the dog. Animal Behavior, 14, 362–366.

Frank, H. (1980). Evolution of canine information processing under conditions of natural and artificial selection. Zeitschrift für Tierpsychologie, 59, 389–399.

Frank, H., & Frank, M. G. (1982a). On the effects of domestication on canine social development and behavior. Applied Animal Ethology, 8, 507–525.

Frank, H., & Frank, M. G. (1982b). Comparison of problem-solving performance in six-week-old wolves and dogs. Animal Behavior, 30(1), 95–98.

Frank, H., & Frank, M. G. (1985). Comparative manipulation-test performance in ten-week-old wolves (*Canis lupus*) and Alaskan malamutes (*C. familiaris*): A Piagetian interpretation. Journal of Comparative Psychology, 99, 266–274.

Frank, H., & Frank, M. (1987). The University of Michigan Canine Information Processing project (1979–1981). In H. Frank (Ed.), Man and wolf (pp. 275–292). Dordrecht, The Netherlands: W. J. Publishers.

Frank, M. G., & Frank, H. (1988): Food reinforcement versus social reinforcement in timber wolf pups. Bulletin of the Psychonomic Society, 26, 467–468.

Frank, H., Frank, M.G., Hasselbach, L.M., & Littleton, D. M. (1989). Motivation and insight in wolf (*Canis lupus*) and Alaskan malamute (*Canis familiaris*): Visual discrimination learning. Bulletin of Psychonomic Society, 27(5), 455–458.

Fuller, J. L. (1967). Experiential deprivation and later behavior. Science, 158, 1645–1652.

Gácsi, M., Miklósi, Á., Varga, O., Topál, J., & Csányi, V. (2004). Are readers of our face readers of our minds? Dogs (*Canis familiaris*) show situation-dependent recognition of human's attention. Animal Cognition, 7(3), 144–153.

Hare, B., Brown, M., Williamson, C., & Tomasello, M. (2002). The domestication of cognition in dogs. Science, 298, 1634–1636.

Klinghammer, E., & Goodmann, P. A. (1987). Socialization and management of wolves in captivity. In H. Frank (Ed.), Man and wolf (pp. 31–59). Dordrecht: W. J. Publishers.

Kubinyi, E., Topál, J., Miklósi, Á., & Csányi, V. (2003) Dogs learn from their owner via observation in a manipulation task. Journal of Comparative Psychology, 117, 156–165.

MacDonald, K., & Ginsburg, B. E. (1981). Induction of normal prepubertal behavior in wolves with restricted rearing. Behavioral and Neural Biology, 33, 133–162.

McKinley, J., & Sambrock, T. D. (2000). Use of human-given cues by domestic dogs (*Canis familiaris*) and horses (*Equus caballus*). Animal Cognition, 3, 13–22.

McLeod, P. J. (1996). Developmental changes in associations among timber wolf (*Canis lupus*) postures. Behavioral Processes, 38, 105–118.

McLeod, P. J., & Fentress, J. C. (1997). Developmental changes in the sequential behavior of interacting timber wolf pups. Behavioral Processes, 39, 117–136.

Martin, P., & Bateson, P. (1986). Measuring behavior. Cambridge: Cambridge University Press.

Miklósi, Á., Polgárdi, R., Topál, J., & Csányi, V. (2000). Intentional behaviour in dog-human communication: An experimental analysis of "showing" behaviour in the dog. Animal Cognition, 3, 159–166.

Miklósi, Á., Kubinyi, E., Topál, J., Gácsi, M., Virányi, Zs., & Csányi, V. (2003). A simple reason for a big difference: Wolves do not look back at humans but dogs do. Current Biology, 13, 763–766.

Miklósi, Á., Topál, J., & Csányi, V. (2004.) Comparative social cognition: What can dogs teach us? Animal Behavior, 67, 995–1004.

Ohl, F. (1996). Ontogeny of vocalisation in domestic dogs, breed standard-poodle. Bonner Zoologische Beitrage, 37, 199–215.

Pongrácz, P., Miklósi, Á., Kubinyi, E., Gurobi, K., & Csányi, V. (2001). Social learning in dogs I: The effect of a human demonstrator on the performance of dogs (*Canis familiaris*) in a detour task. Animal Behavior, 62, 1109–1117.

Rajecki, D. W., Lamb, M. E., & Obmascher, P. (1978). Toward a general theory of infantile attachment: A Comparative review of aspects of the social bond. Behavioral and Brain Sciences, 3, 417–464.

Sackett, G. P., Porter, M., & Holmes, H. (1964). Choice behavior in rhesus monkeys: Effect of stimulation during the first month of life. Science, 147, 304–306.

Schenkel, R. (1967). Submission: Its features and function in wolf and dog. American Zoologist, 7, 319–329.

Scott, J. P., & Fuller, J. L. (1965) Genetics and the social behavior of the dog. Chicago: University of Chicago Press.

Soproni, K., Miklósi, Á., Topál, J., & Csányi, V. (2001). Comprehension of human communicative signs in pet dogs. Journal of Comparative Psychology, 115, 122–126.

Topál, J., Gácsi, M., Miklósi, Á., Virányi, Zs., Kubinyi, E., & Csányi, V. (2005) Attachment to humans: A comparative study on hand-reared wolves and differently socialized dog puppies. Animal Behavior (in press).

Ujfalussy, D., Virányi, Zs., & Kubinyi, E. (2003) Individual and intensive hand-rearing of wolves: The method and its results in handling the wolves. ASAB 2003 Summer Meeting, Grünau, Austria.

Vas, J., Topál, J., Gácsi, M., Miklósi, Á., & Csányi, V. (2005) A friend or an enemy? Dogs' reaction to an unfamiliar person showing behavioral cues of threat and friendliness alternately. Applied Animal Behavior (in press).

VilÃ, C., Savolainen, P., Maldonado, J. E., Amorim, I. E., Rice, J. E., Honeycutt, R. L., Crandall, K. A., Lundeberg, J., & Wayne, R. K. (1997). Multiple and ancient origins of the domestic dog. Science, 276, 1687–1689.

Virányi, Zs., Topál, J., Gácsi, M., Miklósi, Á., & Csányi, V. (2004). Dogs respond appropriately to cues of humans' attentional focus. Behavioral Processes, 66, 161–172.

Virányi, Zs., Miklósi, Á., Gácsi, M., Kubinyi, E., Topál, J., Belényi, B., Ujfalussy, D., & Csányi, V. (2005). Comprehension of human pointing gestures in young socialized wolves and dogs (submitted).

Wayne, R. K. (1993). Molecular evolution of the dog family. Trends in Genetics, 9, 218–224.

Woolpy, J. H., & Ginsburg, B. E. (1967). Wolf socialization: A study of temperament in a wild social species. American Zoologist, 7, 357–363.

Zimen, E. (1987). Ontogeny of approach and flight behavior towards humans in wolves, poodles and wolf–poodle hybrids. In H. Frank (Ed.), Man and wolf (pp. 275–292). Dordrecht, The Netherlands: W. J. Publishers.