



Attachment to humans: a comparative study on hand-reared wolves and differently socialized dog puppies

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Using the Strange Situation Test originally developed for testing the mother–infant relationship in humans, we compared the attachment behaviour of extensively socialized (hand-reared) dog, *Canis familiaris*, and wolf, *Canis lupus*, puppies towards their human caregiver with that of pet dog puppies of the same age. The experiment was designed to study whether (1) dog puppies as young as 16 weeks show attachment to a human caregiver, (2) extensive socialization by human caregivers affects attachment behaviour of dog puppies and (3) evolutionary changes (in the form of species-specific differences between wolf and dog pups) affect the emergence of dog–human attachment. We found a characteristic selective responsiveness to the owner in young dogs, similar to that observed in adults. This finding supports the view that puppies show patterns of attachment towards their owners. Extensive socialization had only a minor effect on the attachment behaviour in dog puppies, as the behaviour of pet dogs and hand-reared dogs was basically similar. However, we found a significant species-specific difference between wolves and dogs: both extensively socialized and pet dog puppies were more responsive to the owner than to an unfamiliar human participant, whereas extensively socialized wolves were not. Behavioural differences could be best explained by assuming that selective processes took place in the course of domestication (genetic changes) that are related to the attachment system of the dog.

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Domestication is generally viewed as an evolutionary process controlled by human influence (Price 1984). The symbiotic relationship between humans and nonhuman animals entails adaptational demands, which create new conditions of selection for the species to be domesticated and thus might result in a wide range of genetic modifications. The dog has a long history of adaptation to the human environment (Vilá et al. 1997; Savolainen et al. 2002), and it is widely assumed that the selection process during domestication may have altered not only their morphological traits but also their behaviour and behaviour control systems (Belyaev 1979; Coppinger & Coppinger 2002).

Recent studies have suggested an unusual competence of dogs in social interactions with humans (cooperation:

Topál et al. 1997; Naderi et al. 2001, 2002; social learning: Kubinyi et al. 2003; Pongrácz et al. 2003a, b; communication: Miklósi et al. 1998, 2000; Agnetta et al. 2001; Soproni et al. 2001, 2002). However, to understand the significance of domestication-related changes in the behaviour of dogs, we need to compare dogs with wolves (Miklósi et al. 2004). In line with this, recent comparisons of the social cognitive skills in dogs and socialized wolves within the context of the interspecific relationship with humans have shed light on some genetic divergences at the behavioural level (Hare et al. 2002; Miklósi et al. 2003). Compared with wolves, the dogs' preferential looking at the human in problem-solving situations and their superior performance in using human directional gestures support the existence of genetic predispositions related to the domestication process in the emergence of social cognitive abilities in dogs.

In general, it is widely accepted that the evolutionary emergence of social cognition is closely related to the 'social field' (Kummer 1982), which often presents more complex adaptational demands for the animal than do physical characteristics of the environment (Tomasello & Call 1997).

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One of the basic behavioural phenomena of social relationships is attachment. The evolutionary approach to function and mechanism suggests that attachment is one of the main behaviour organizing systems in parent–offspring relationships, and it is also claimed to be the basic organizational factor for any species' social structure leading to group formation (Bowlby 1958). Attachment is an asymmetrical social relationship between two individuals, which can be tested experimentally in choice situations such as the Strange Situation Test (SST) originally developed to study the mother–infant relationship in humans (Ainsworth & Wittig 1969). The paradigmatic element of this procedure is that separation from the caregiver in an unfamiliar environment evokes anxiety (which is manifested behaviourally in proximity seeking), while the activated attachment system upon reunion with the caregiver manifests in different forms of contact-seeking behaviours. Importantly, attachment behaviour is oriented mainly towards the caregiver, in the sense that there is a significant difference in the level of proximity and contact seeking, and in the effort made to maintain contact, between the caregiver and an unfamiliar person in the same novel situation. Adult dogs show specific patterns of attachment behaviour towards their owner in the SST (Topál et al. 1998; Prato-Previde et al. 2003), suggesting a case of functional analogy (evolutionary convergence) to the human infant–parent attachment. Gácsi et al. (2001) reported that attachment develops rapidly: a short period of interaction with humans evoked attachment behaviour towards the handler in adult dogs that had been deprived of human contact (shelter dogs) and the dogs differentiated between their handler and a stranger in the same way as adult pet dogs did.

We designed a comparative experiment to investigate the attachment behaviour of hand-reared and extensively socialized wolf and dog puppies and pet dog puppies that had received a normal socialization regimen from their owners. We investigated whether (1) pet dogs' attachment to humans is observable in the SST as early as 16 weeks of age, (2) extensive socialization by human caregivers causes any change in attachment behaviour of dog puppies and (3) there are species-specific differences between wolves and dogs in their attachment behaviour to humans.

Although one might assume that the ability to show attachment behaviour to individuals of another species (humans) in adulthood is a unique feature of the domestic dog, despite much interest (Scott 1963, 1992; Ginsburg & Hiestand 1992), there has been no clear theory explaining the emergence of the phenomenon. By comparing the emergence of attachment behaviour to humans in dogs and socialized wolves tested by the same experimental method we can examine whether inheritance (genetic background) or environmental effects (rearing history) are more important.

Two hypotheses can be formulated. The socialization hypothesis suggests that attachment could develop mainly as a result of extensive hand rearing and individual socialization to the human social environment (i.e. enculturation) during the 'critical period' of socialization (Freedman et al. 1961). The domestication hypothesis, however, claims that there could have been specific genetic changes (in the attachment behaviour organizing system) that have

emerged as the result of selective breeding for dependency and attachment to humans (see also Hare et al. 2002; Miklósi et al. 2003 for similar explanations regarding communicative abilities in dogs). The socialization hypothesis predicts that hand-reared wolf and dog puppies will show similar forms of attachment behaviour to their human caregivers, whereas pet dog puppies, being less extensively socialized, will show less attachment to their owners. In contrast, the domestication hypothesis predicts species-specific differences in attachment behaviour to humans between wolves and dogs reared in the same way (i.e. dogs should show more specific attachment behaviour than wolves towards humans). These explanations are not mutually exclusive, however, and both of the hypothesized mechanisms could affect the behaviour phenotype.

METHODS

Subjects

We tested three experimental groups: extensively socialized wolf puppies and dog puppies with two different rearing conditions.

Hand-reared wolf puppies

We studied 13 grey wolves, seven males and six females, individually hand reared by humans after being separated from their mothers and littermates 3–5 days after birth. The wolf cubs were born at an animal park (Horatius Ltd, Gödöllő, Hungary). In May–August 2001, four wolf puppies from two litters were adopted by four persons (three women and one man) and in the same period of the next year (2002) another nine puppies from three litters were weaned and fostered by nine young women (students and Ph.D. students, including the three who participated in 2001). The wolves received extremely intensive and sensitive human rearing: they spent the first 16 weeks of their lives in 20–24-h close human contact, participating in every activity of their owners. They were frequently exposed to other humans, experienced novel objects and situations on a regular basis, and became used to travelling in cars and on public transport. For the hand rearing and extensive socialization of wolf cubs our team was licensed by the Department of Nature Conservation, Ministry of Environmental Affairs and our department was also licensed by the Ethical Committee for Animal Experimentation at Eötvös University to conduct this research.

The wolf cubs were 4 months old at the time of testing (mean age \pm SD = 16.2 \pm 0.5 weeks). After the tests, the pups were placed back at the animal park where they could interact with humans and other wolves daily. The owners visited the puppies for half a day twice a week for 6–12 months, taking them for a walk and playing with them. As a result of this socialization regimen the wolves showed no sign of wariness or avoidance of humans (even strangers); in contrast, they were keen to interact with unfamiliar persons. After a gradual resocialization period, by the age of 2 years the puppies were successfully integrated into a pack of wolves.

Hand-reared dog puppies

Eleven mixed-breed dog puppies (six males, five females) were also involved in our nursing programme. Dogs were weaned and fostered individually by the same group of young women who reared the wolves (four dog puppies in August–November 2001 and nine in October 2003–March 2004). Importantly, the nursing and socialization regime for the dogs was identical to that of the wolves. Hand-reared dogs were also tested at 16 weeks of age (mean age \pm SD = 16.3 \pm 0.5 weeks).

Pet dog puppies

Eleven pet dog puppies of various breeds (seven males, four females; two mongrels, one each of border collie, Cairn terrier, cocker spaniel, Cavalier King Charles spaniel, German shepherd, golden retriever, husky, Moskow ovcarka, spitz) were also tested. All of them were reared by their mothers until 7–9 weeks of age, and at the time of the test they lived in human households and their mean age \pm SD was 16.3 \pm 2.5 weeks. They were recruited from visitors to puppy classes in TOP MANCS dog training school in Budapest.

Procedure

The SST is based on the subject's differential reaction to the owner and an unfamiliar person (stranger) in a moderately stressful environment. The test procedure was identical to that used by Topál et al. (1998) and Gácsi et al. (2001). The test took place in an enclosure measuring 5.5 \times 3.5 m with 2-m-high, opaque side walls. The owner and the stranger (both females) entered and left through a door of 90 cm \times 2 m. Two chairs placed 1.5 m from each other were in the middle of the experimental area (one for the owner and one for the stranger) and some toys were also present. The test procedure consisted of seven episodes, each lasting 2 min. Human participants had to follow a detailed protocol that determined the form and timing of their behaviour. The behaviour of the subjects was videotaped and analysed later.

Episode 1 (owner and dog/wolf): the owner entered the enclosure together with the dog/wolf, sat down and started to read. After 1 min she stimulated playing or petting the dog/wolf depending on its willingness. She stopped playing or petting after 1 min, when the stranger entered.

Episode 2 (owner, stranger and dog/wolf): the stranger entered, greeted the owner, stopped for up to 5 s to allow the animal to respond, and then sat down. After 30 s she initiated conversation with the owner. Another 30 s later the stranger started to stimulate playing or petting the dog/wolf depending on its willingness. After 1 min the owner left as unobtrusively as possible, leaving the leash on her chair.

Episode 3 (stranger and dog/wolf): in this first separation episode the stranger tried to play with the animal or offered petting. After 1 min she sat down and petted the dog/wolf for 1 min if it was close enough.

Episode 4 (owner and dog/wolf): in this first reunion episode the owner called the puppy while she

approached the closed door. After entering, she stopped for up to 5 s to allow the animal to respond and then went to the chairs. Then the stranger left. The owner stimulated playing or petting the dog/wolf, depending on its willingness, for 1 min and then sat down and petted the puppy if it was close enough. At the end of the episode she said to the puppy 'I must go, you should stay here' and left.

Episode 5 (dog/wolf alone): this was the second separation episode (total separation). Dogs/wolves were kept in the enclosure for 2 min.

Episode 6 (stranger and dog/wolf): the stranger entered and stopped for up to 5 s to allow the dog/wolf to respond, then stimulated playing or petting the animal depending on its willingness. After 1 min she sat down and petted the animal if it was close enough. She stopped playing and petting after 1 min, when the owner entered.

Episode 7 (owner and dog/wolf): in the second reunion episode the owner called the animal while she approached the closed door. After entering she stopped for up to 5 s to allow the animal to respond and then went to the chairs. Then the stranger left. The owner stimulated playing or petting the dog/wolf, depending on its willingness, for 1 min and then sat down and petted the puppy if it was close enough.

Behaviour Categories

On the basis of the detailed behaviour analysis of two samples of dogs in two previous studies ($N = 51$ in Topál et al. 1998 and $N = 60$ in Gácsi et al. 2001) we recorded seven variables. Proximity seeking upon separation was determined by the pup following the departing person (owner/stranger) and standing by the door when the owner/stranger was absent. Contact-seeking behaviours upon reunion were described by scores of contact seeking towards the entering person (owner/stranger) and from the duration of physical contact while greeting the owner/stranger. We also measured the duration of the behaviours related to other aspects of the social and physical environment: playing with the owner/stranger, exploring the environment in the presence of the owner/stranger and passivity in the presence of the owner/stranger.

We coded each behaviour category in the presence of both the owner and the stranger. The detailed definitions of the behaviour categories were as follows.

(1) Exploration (in the presence of the owner and stranger): any activity directed towards nonmovable aspects of the environment, including sniffing, distal visual inspection (staring or scanning), close visual inspection or oral examination.

(2) Passive behaviour (in the presence of the owner and stranger): time spent sitting, standing or lying down without any orientation towards the environment.

(3) Playing (in the presence of the owner and stranger): any vigorous toy- or social partner-related behaviour including running, jumping, or any physical contact with toys.

(4) Stand by the door (in the presence of the owner and stranger): the time spent close to the door (<1 m) with the face oriented to the exit. The behaviour of the animals was always categorized in one of the above four variables during the various episodes (nonoverlapping behaviour categories).

(5) Physical contact (with either the owner or the stranger): the time spent in any form of bodily contact.

(6) Following (the owner and stranger): to evaluate the tendency to follow the person leaving the enclosure we used exclusive conditional scores: 0: the puppy did not orient towards the leaving person at all, or only for less than 1 s; 1: it oriented towards the leaving person for more than 1 s; 2: it followed the leaving person to the door; 3: it tried to get through the door or stood by the door for more than 1 s. Following was recorded only when one person stayed with the puppy while the other left the enclosure, that is, at the beginning of episode 3 with the owner, and at the beginning of episodes 4 and 7 with the stranger. (We calculated the mean of the scores for the stranger.)

(7) Greeting (the owner and stranger): the behaviour of the puppy towards the entering owner or stranger was evaluated with the following five criteria, and the scores were summed: approach initiation (+1): the puppy moved towards the entering person; full approach (+1): the puppy approached the entering person until it was in physical contact; avoidance (-1): any sign of avoidance behaviour towards the entering person, e.g. backing, getting out of the way of the entering person; durable physical contact upon greeting (+1/2): the puppy spent more than 3 s in bodily contact with the entering person; delay of approach (-1/2): when the owner/stranger entered, the puppy hesitated to initialize any approach for more than 5 s. (The maximum score was 5 with respect to both the owner and the stranger, because both of them entered the enclosure twice.)

Data Collection and Analysis

Two trained observers analysed the videotaped sessions using the seven behaviour categories described above. We recorded behavioural data continuously during observations and we calculated the relative percentage of the time spent in Exploration, Playing, Passive, Stand by the door and Physical contact. All variables passed a normality test (Kolmogorov-Smirnov) and we therefore applied parametric statistical methods (SPSS version 9.0; SPSS Inc., Chicago, IL, U.S.A.). We analysed the behaviour of puppies in the presence of the owner and stranger (within-subject factor) and the experimental group (between-subject factor) with mixed ANOVA for repeated measures to the within-subject factor. We used Student-Newman-Keuls post hoc tests (between-groups comparisons) and paired *t* tests (within-group comparisons).

Before data analysis, we assessed interobserver agreements for all of the seven behaviours by means of parallel coding of 50% of the whole sample. We calculated Kappa coefficients (Martin & Bateson 1986) and found relatively

high values for all variables (Exploration: 0.773; Playing: 0.964; Passive: 0.810; Stand by the door: 0.909; Physical contact: 0.881; Following: 0.721). To assess the interobserver agreement for Greeting, we measured Kappa coefficients for latency to approach (0.875), avoidance (0.880) and time spent in physical contact upon greeting (0.987).

RESULTS

Regarding the behaviour observed in the presence of the owner and stranger we first give a short description of the experimental groups. 'In the presence of the stranger' always refers to those episodes in which the stranger was present (2, 3, 6), while those episodes in which the caregiver (owner) was present (1, 2, 4, 7) were labelled as 'in the presence of the owner'.

Hand-reared Wolf Puppies

In the unfamiliar situation wolves spent most of their time exploring the environment and playing (Fig. 1). In contrast, they spent hardly any time on passive behaviours or on standing by the door (Fig. 1). Wolves seemed to prefer physical contact with the stranger (21.4% of the total time) than with the owner (8.8%) and were ready to follow both of them (Fig. 2). They obtained relatively high mean scores of greeting towards the entering owner and stranger as well (Fig. 3). In total separation (episode 5) when the subject was alone in the enclosure, wolves spent most of their time exploring the environment (36% of the total duration) and standing by the door (55% of the total duration).

Hand-reared Dog Puppies

Like wolves, extensively socialized dog puppies also played a lot with the human participants and explored the environment thoroughly (Fig. 1). They spent more time being passive than wolves, and they stood by the door less when the owner was present than in the presence of the stranger (Fig. 1). They tended to follow and greet the owner more than they did with the stranger (Figs 2, 3). In episode 5 (when they were alone) hand-reared dogs spent a lot of time standing by the door (43.5%) and exploring the environment (39% of the total duration).

Pet Dog Puppies

Pet dogs also showed a lot of exploration and little passive behaviour (Fig. 1). They showed some preference for playing with the owner and stood by the door less when the owner was present (Fig. 1). However, pet dogs spent similar times in physical contact with the owner (11% of the total duration) and stranger (14.1%). As with hand-reared dogs, we observed a significant asymmetry regarding greeting and following behaviours (higher greeting and following scores with the owner; Figs 2, 3). In the total separation episode pet dogs either explored

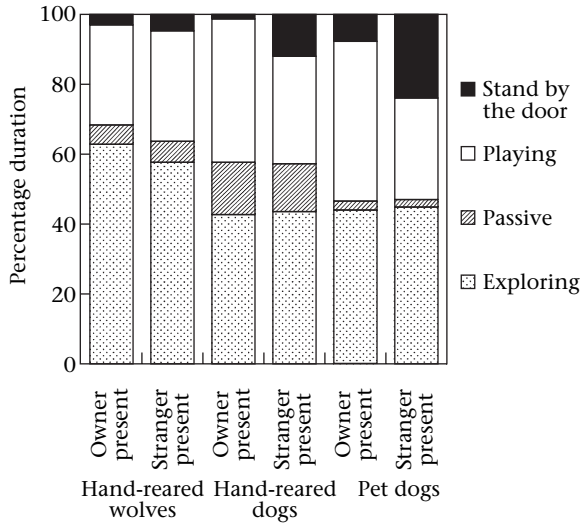


Figure 1. Percentage of time spent on various behaviours (nonoverlapping) by wolf and dog puppies in the presence of the owner or the stranger.

the environment (59%) or stood by the door (41% of the total duration).

Exploring the Environment

The groups showed significant differences (wolf puppies explored more than dogs; $F_{2,33} = 3.41$, $P = 0.045$), but neither the within-subject factor (i.e. exploration in the presence of the owner versus the stranger) nor the interaction proved to be significant ($F_{1,32} = 0.21$, $P = 0.65$ and $F_{2,33} = 0.71$, $P = 0.50$, respectively). Paired comparisons of exploration in the presence of the owner versus the stranger failed to show significant differences in any of the groups (wolves: $t_{12} = 1.51$, $P = 0.15$; hand-reared dogs: $t_{10} = 0.49$, $P = 0.63$; pet dogs: $t_{10} = 0.12$, $P = 0.91$).

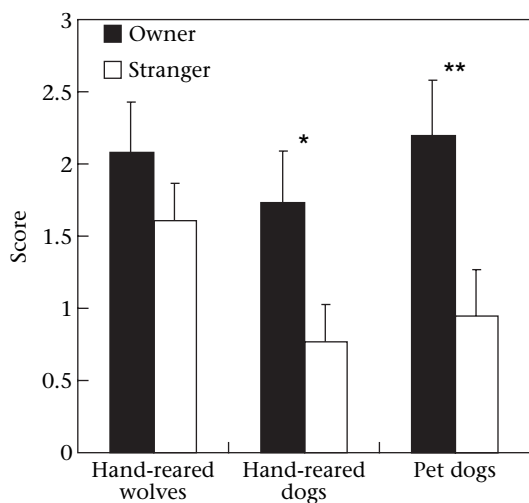


Figure 2. Mean scores + SE (range 0–3) for following the owner and stranger when she left the test room (averaged over episodes 2, 4 and 3, 6, respectively, see Methods). Paired t test: * $P < 0.05$; ** $P < 0.01$.

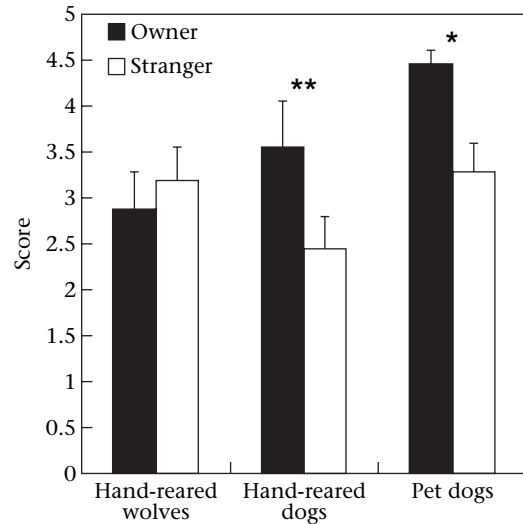


Figure 3. Mean scores + SE (maximum 5) of greeting behaviour towards the owner and stranger when she entered the test room (averaged over episodes 4, 7 and 2, 6, respectively, see Methods). Paired t test: * $P < 0.02$; ** $P < 0.002$.

Passive Behaviours

A two-way ANOVA showed significant differences between groups (hand-reared dog puppies spent more time on passive behaviours than wolves and pet dogs: $F_{2,33} = 4.84$, $P = 0.015$). In contrast, the within-subject factor (i.e. passive behaviours in the presence of the owner versus the stranger) and the interaction were not significant ($F_{1,32} = 0.13$, $P = 0.72$ and $F_{2,33} = 0.17$, $P = 0.84$, respectively). In agreement with this, within-group comparisons did not show differences in passive behaviours with the owner versus the stranger (wolves: $t_{12} = 0.42$, $P = 0.67$; hand-reared dogs: $t_{10} = 0.46$, $P = 0.65$; pet dogs: $t_{10} = 0.17$, $P = 0.87$).

Physical Contact with Owner/Stranger

Wolf puppies spent more time in close bodily contact with their human partner than hand-reared dog puppies did, while the behaviour of the pet dog group was intermediate (between-group effect: $F_{2,33} = 3.99$, $P = 0.028$). The within-subject factor was also significant (physical contact with the owner versus the stranger: $F_{1,32} = 8.67$, $P = 0.006$), but the interaction was not ($F_{2,33} = 1.56$, $P = 0.23$). Both hand-reared dogs and wolves had more bodily contact with the stranger than with the owner (hand-reared dogs: $t_{10} = 2.85$, $P = 0.017$; wolves: $t_{12} = 2.52$, $P = 0.027$), but similar differences were not found in pet dogs ($t_{10} = 0.72$, $P = 0.49$).

Playing

The groups did not show significant differences in play ($F_{2,33} = 0.39$, $P = 0.68$); however, both the person present (i.e. owner or stranger) and the interaction were highly significant ($F_{1,32} = 18.83$, $P < 0.0001$ and $F_{2,33} = 10.02$,

$P < 0.0001$, respectively). Both hand-reared and pet dogs but not wolf puppies tended to play more with their owner than with the stranger (hand-reared dogs: $t_{10} = 3.75$, $P = 0.004$; pet dogs: $t_{10} = 5.13$, $P < 0.0001$; wolves: $t_{12} = 0.81$, $P = 0.43$).

Following the Owner/Stranger

The analysis of the subjects' reaction to the person going away failed to show differences between groups ($F_{2,33} = 1.30$, $P = 0.29$), whereas the within-subject factor was highly significant ($F_{1,32} = 16.73$, $P < 0.0001$). We did not find a significant interaction in this case ($F_{2,33} = 1.16$, $P = 0.34$). Within-group comparisons showed that while wolves did not discriminate between humans in this case (owner versus stranger: $t_{12} = 1.2$, $P = 0.26$), both pet and hand-reared dog puppies were more ready to follow the owner than the stranger (pet dogs: $t_{10} = 4.03$, $P = 0.002$; hand-reared dogs: $t_{10} = 2.35$, $P = 0.041$).

Standing by the Door

A two-way ANOVA showed significant effects for both the comparisons between groups ($F_{2,33} = 3.86$, $P = 0.031$; pet dogs stood at the door more than hand-reared dogs or wolves) and within subjects ($F_{1,32} = 21.96$, $P < 0.0001$). The interaction was also significant ($F_{2,33} = 4.54$, $P = 0.018$). Hand-reared and pet dogs spent more time standing by the door when the owner was absent versus present (hand-reared dogs: $t_{10} = 2.77$, $P = 0.020$; pet dogs: $t_{10} = 3.25$, $P = 0.009$), in contrast to wolves ($t_{12} = 1.38$, $P = 0.19$).

Greeting the Owner/Stranger

The subjects' greeting behaviour towards the entering owner and stranger did not differ significantly between groups ($F_{2,33} = 2.07$, $P = 0.14$). However, the identity of the entering person (within-subject factor: $F_{1,32} = 8.13$, $P = 0.008$) and interaction ($F_{2,33} = 4.62$, $P = 0.020$) proved to be significant. Paired comparisons of the greeting behaviour showed that while dogs of both groups greeted the owner more intensely than the stranger (pet dogs: $t_{10} = 2.85$, $P = 0.017$; hand-reared dogs: $t_{10} = 4.35$, $P = 0.001$), wolves did not make such a discrimination ($t_{12} = 0.61$, $P = 0.55$).

Total Separation Stage

Subjects in all groups spent episode 5 (subject alone) mainly exploring the enclosure (on average 44.7% of the total duration) or standing by the door (on average 46.5% of the total duration). Between-group comparisons showed no significant differences for exploration ($F_{2,32} = 1.11$, $P = 0.34$) and standing by the door ($F_{2,32} = 2.66$, $P = 0.085$). The increased durations (41–55%) of standing by the door when subjects were alone in the enclosure (in other episodes dogs and wolves stood by the door for 1.4–24%, respectively) clearly show that

puppies in all groups found this episode distressing. This conclusion is also supported by the fact that almost all puppies (all hand-reared dogs and all but one wolf and pet dog) followed the leaving person when they were left alone (which meant they got the maximum score for following at the end of episode 4).

DISCUSSION

The SST seems to be a useful method not only for human developmental psychologists (Ainsworth & Wittig 1969) but also for those who want to analyse human–animal relationships (e.g. human–chimpanzee: Miller et al. 1990). Attachment behaviour can be observed in a stressful unfamiliar situation as a response to separation from and reunion with the caregiver (attachment figure) that is distinct from responses to other human participants.

In agreement with earlier studies, which suggested that adult pet dogs (Topál et al. 1998) and adult shelter dogs after a short handling procedure (Gácsi et al. 2001) show patterns of attachment behaviour towards the owner/handler, our results suggest that this behaviour can be evoked in dog puppies as early as 16 weeks after birth. Table 1 summarizes the paired comparisons of the behavioural variables in the presence of the owner and the stranger and gives further support for this conclusion. Traditionally fostered 4-month-old dog puppies showed in most respects the same discrimination between human participants (owner versus stranger) as adult pet dogs did in our earlier study (Topál et al. 1998). This suggests that the attachment behaviour system is activated upon separation from the owner but not the stranger (standing by the door upon separation and following the owner leaving the enclosure), and upon reunion with the owner (increased proximity and contact seeking). This characteristic selective responsiveness to the owner supports the view that both adult dogs and puppies show the same patterns of attachment towards their owners.

One may assume that as a result of extensive socialization, during which pups were frequently exposed to other humans and experienced novel objects and situations on a regular basis, distress evoked by the unfamiliar environment should be lower in hand-reared puppies than pet dogs and this difference should be manifested in the attachment behaviour pattern of the two experimental groups. However, our results show only a minor effect of the socialization history on the attachment behaviour of dog puppies. Pet dog puppies spent less time on passive behaviours than hand-reared ones, whereas hand-reared puppies spent more time close to the door than pet dogs when their owner was absent. Furthermore, hand-reared dogs showed a preference for physical contact with the stranger whereas pet dogs did not discriminate between human participants in this respect. We should note that greater interest in an unfamiliar human could be an artefact of hand rearing as this was the only apparent feature that was typical for both hand-reared groups (dog and wolf puppies). Furthermore, hand-reared animals might have spent more time in physical contact with the stranger (mainly during separations from the owner)

Table 1. Summary of the paired comparisons of the behavioural variables in the presence of the owner (O) versus the stranger (S)

Group	Contact-seeking score	Physical contact	Stand by the door	Following	Playing	Passive	Exploring
Pet dog puppies <i>P</i> (N=11)	O > S 0.017	0.487	O < S 0.009	O > S 0.002	O > S 0.0001	0.870	0.904
Hand-reared dog puppies <i>P</i> (N=11)	O > S 0.001	O < S 0.017	O < S 0.019	O > S 0.041	O > S 0.004	0.655	0.631
Hand-reared wolf puppies <i>P</i> (N=13)	0.551	O < S 0.027	0.192	0.255	0.432	0.677	0.156
Adult pet dogs* <i>P</i> (N=51)	O > S 0.0001	0.131	O < S 0.0001	Data not available	O > S 0.0001	0.145	O > S 0.013

P values are from paired *t* tests.

*The data for adult dogs are taken from Topál et al. (1998).

because they had more extensive experience with different unfamiliar humans ('strangers') during their first months than pets did. The preferential seeking of physical contact with the owner may be relevant to attachment behaviour only in the reunion parts of the test (i.e. greeting when the owner comes back).

Importantly, regarding the other behaviour variables observed in the SST there is an apparent similarity between the two groups of dog puppies in the sense that both showed the same type of discrimination between owner and unfamiliar human (Table 1). Dog puppies of different socialization history selectively responded to the separation from the owner (stood by the door significantly more upon separation, tended to follow the owner leaving the enclosure, played significantly more with the owner and obtained significantly higher scores upon greeting the owner). All of these strongly argue for a small influence of intensive socialization in dogs on attachment to the human caregiver.

Regarding the evolutionary emergence of dog-human attachment our results suggest a significant effect of domestication in the form of species-specific differences between wolves and dogs. The comparative analysis of the subjects' behaviour towards human participants in the experimental situation shows that, even after extensive socialization, wolves do not show patterns of attachment to humans comparable to those observed in pet dogs of different rearing conditions. This conclusion is supported by the fact that wolf puppies failed to show different responsiveness towards the owner and unfamiliar human participant in the SST (Table 1).

Our results also provide little support for the hypotheses that the attachment to humans is the outcome of extensive human socialization or of processes related to heterochronic changes in rates of behaviour development alone (Goodwin et al. 1997; Coppinger & Coppinger 2002). This is in contrast to currently widely held views that both processes are implicated in explaining the development of dog-human attachment. Such theories have assumed that the behaviour of dogs towards the owner is derived directly from the puppy-mother relationship in wolves, supposing a behavioural homology between dog and wolf behaviour. Regarding the wolf cub's attachment behaviour to its mother, many researchers have observed that proximity and contact-seeking behaviour towards the mother gradually decreases after weaning (6–8 weeks of age,

Mech 1970) and social attachment could be observed mainly towards the pack and not a specific individual (King 1954; Rabb et al. 1967; Beck 1973). Sixteen-week-old wolf cubs are often left alone at a 'meeting point' where they wait for the hunting group (Mech 1991). For 2-month-old dog puppies, mothers have only a minor role in reducing the effect of separation stress (Frederickson 1952; Ross et al. 1960; Elliot & Scott 1961) and in choice situations puppies do not prefer their mothers to unfamiliar bitches (Pettijohn et al. 1977). On the basis of these results many researchers have questioned whether puppies are able to show attachment behaviour to their mothers at all, despite their ability to discriminate and choose the mother in certain situations (Rajcecki et al. 1978).

Importantly, however, our study highlights a species-specific difference in attachment behaviour towards humans between hand-reared dog and wolf puppies. While socialized wolf pups did not show the specific patterns of attachment (person-specific proximity seeking upon separation and contact seeking upon reunion), this behaviour mechanism was unequivocally activated in 16-week-old dog puppies. In addition, even socially deprived adult dogs show such attachment behaviour after a short social handling by an unfamiliar person (Gácsi et al. 2001).

In line with these results, we suggest that there is no direct functional relationship between puppy-mother attachment in wolves and the life-long behaviour phenomenon that can be called attachment between a dog and its owner. Based on our results, the most plausible hypothesis is that, besides a destabilizing selection (Belyaev 1979) that resulted in the fragmentation of the well-organized behaviour repertoire of the wolf, dogs have evolved a capacity for attachment to humans that is functionally analogous to that present in human infants. In parallel to other dog-wolf comparisons arguing that evolutionary changes contributed to the emergence of communicative ability in dogs (Miklósi et al. 2003), this is the first experimental evidence that specific selection processes (genetic changes) might be associated with the emergence of attachment behaviour in dogs. This behaviour system not only allows for developing a close relationship to a different species but it also operates for an extended period into adult life. The attachment system in dogs could serve as the scaffolding on which many forms of complex social behaviour between dogs and humans can develop. This observation also points to a clear and testable behavioural difference

between the results of a socialization process (often referred to as 'taming') and the effects of domestication that are reflected in adaptive genetic changes. In the case of the dog such genetic changes have resulted in a human analogue attachment system that has probably strongly contributed to the successful 'adoption' of the dog into the human social system.

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