DISSERTATION/ DOCTORAL THESIS

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The effect of human socialisation on problem solving abilities of canines: are dogs socially more dependent than wolves?

verfasst von / submitted by

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To Cluni

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Summary

2. Author's contributions

Article 1:

Lazzaroni M, Range F, Bernasconi L, Darc L, Holtsch M, Massimei R, Marshall-Pescini S (2019). The role of life experience in affecting persistence: A comparative study between free-ranging dogs, pet dogs and captive pack dogs. PloS one. 14.4: e0214806.

ML participated in the design of the study, collected field data, carried out the statistical analyses, the study and drafted the manuscript; FR participated in the design of the study and helped draft the manuscript; LB, LD, MH, MR collected field data, participated in data analysis; SMP participated in the design of the study, coordinated the data collection and helped draft the manuscript.

Article 2:

Lazzaroni M, Marshall-Pescini S, Manzenreiter H, Gosch S, Přibilová L, Darc L, McGetrick J, Range F (2020). Why do dogs look back at the human in an impossible task? Looking back behaviour may be over-interpreted. Animal Cognition.

ML participated in the design of the study, collected field data, carried out the statistical analyses, and drafted the manuscript; SMP participated in the design of the study, participated in the statistical analyses and helped draft the manuscript; HM, SG, LP collected field data and participated in data analysis; LD collected field data and participated in the design of the study; JMG participated in data analysis and statistical analyses and critically revised the manuscript; FR participated in the design of the study, coordinated the study and helped draft the manuscript.

Article 3:

Lazzaroni L, Range F, Backes J, Portele K, Scheck K, Marshall-Pescini S (accepted in Frontiers). The effect of domestication and experience on the social interaction of dogs and wolves with a human companion.

ML participated in the design of the study, collected field data, carried out the statistical analyses, and drafted the manuscript; FR participated in the design of the study, coordinated the study and helped draft the manuscript. JB, KP, LS collected field data, participated in data analysis and revised the manuscript. SMP participated in the design of the study, participated in the statistical analyses and helped draft the manuscript.

Publications not included in the thesis.

Article 5:

Rao A, Bernasconi L, Lazzaroni M, Marshall-Pescini S, & Range F (2018). Differences in persistence between dogs and wolves in an unsolvable task in the absence of humans. PeerJ, 6, e5944.

AR conceived and designed the experiments, performed the experiments, analyzed the data, prepared figures and/or tables, authored drafts of the paper; LB conceived and designed the experiments, performed the experiments, reviewed drafts of the paper; ML conceived and designed the experiments, coded videos for interobserver reliability, reviewed drafts of the paper; SMP conceived and designed the experiments, authored drafts of the paper; FR conceived and designed the experiments, contributed reagents/materials/analysis tools, authored drafts of the paper.

Article 6:

Lazzaroni M and Debottam B, Marshall-Pescini S, Darc L, Range F (in preparation, will be submitted in 2020). Dogs' and wolves' persistence in searching for human proximity.

Article 7:

Lazzaroni M, Range F, Marshall-Pescini S, Dale R (in preparation, will be submitted in 2020). The effect of experience in dogs' comprehension of human emotional expressions.

Book chapter:

Lazzaroni M, Marshall-Pescini S (2020). The "Missing link": free-ranging dogs' impact on our understanding of wolf-dog behavioural differences / Der streuner – Das fehlende bindeglied. Unterschiedliche soziokognitiven fähigkeiten. KOSMOS Verlag editor.

Other:

ML participated in conceptualizing other studies that will result in future publications but in some cases the studies are still ongoing or data are still to be processed:

- Social interactions between subjects in packs of free-ranging dogs and relatedness between pack members
- Spatial distribution of free-ranging dogs
- Humans attitude towards free-ranging dogs
- Investigating the genetic basis of different phenotypes in litters of free ranging dogs

3. General introduction

3.1 The effect of domestication: how are dogs different from wolves?

Studies on dogs' behaviour and cognition are quite recent because for a long time dogs have been considered as "artificial animals" created by humans (1), living in an unnatural environment and not worthy of being studied. Since the turn of the twenty-first century, this view started to change when most researchers began to consider dogs as 'real animals', adapted to life in an urbanized environment as domestic pets. This determined an explosion of behavioural studies on pet dogs (2), which mainly focused on investigating dogs' social skills when it comes to interacting with humans.

These initial studies found that pet dogs had rather extraordinary skills in understanding human forms of communication (for a complete review, see 3). For example, they could comprehend the referential nature of human pointing (4, 5), as well as recognize and follow social rules (6), distinguish and respond to different facial expressions of emotion (7) with some authors' suggesting that dogs' skills in these tasks were superior to those of humans' closest living relatives, chimpanzees (8).

To better comprehend dogs' peculiarity in understanding human forms of communication, one approach has been to compare dogs with their closest living relatives, wolves (9-15), with the idea that dogs may have acquired some of these abilities during the domestication process, adapting to life in close contact with humans.

The initial comparative studies found that dogs outperformed human-socialized wolves when it comes to reading subtle communicative cues (9-11). Moreover, in a number of studies, human raised wolves were slower or more reluctant than dogs to establish eye contact with a human partner (11-13). Wolves also appeared to be less likely than dogs to adapt their behaviour following a human's change in attitude from threatening to friendly (14) and less inclined to develop attachment bonds to humans (6).

Fewer studies instead investigated dogs' performance in physical (and asocial) cognition tasks. Contrary to socio-cognitive tasks, in asocial cognition tasks dogs performed rather poorly. For instance, dogs solved the invisible displacement task in object permanence studies by using simple local rules, like the adjacency rule (16-18). Similarly, they showed gravity bias (19), failed to infer the location of food if only indirect causal information was available (20) and were not very good in most means-end understanding tasks (21 but see 22). Dogs showed difficulties in encoding a complex sequence of events and representing a position change that was signalled but not directly perceived (23). Moreover, the use of a displacement device impaired the performance of dogs also in visible displacement tasks (24). Dogs did not understand the solidity principle (25), and male dogs did not respond to the size constancy violation with a significant increase in looking time (26).

Interestingly, in studies that directly compared dogs and wolves in physical cognition tasks, wolves often showed better performances than dogs. For example, wolves were more successful than dogs in different problem-solving and manipulation tasks (27-29), suggesting a better understanding of rudimentary means-ends relations (30, but see 31) and outperformed dogs in their ability to follow causal cues (32). When interacting with a puzzle box, wolves were more persistent than dogs (33) and performed a greater variety of behaviours in their attempt to solve the task (33, 34). In a quantity discrimination task, Range et al (35) found that despite both dogs and wolves being able to distinguish between two different amounts of food, wolves performed above chance even with high ratios of food, differently from dogs that performed at chance level in these conditions. Finally, in a study on inhibitory control, Marshall-Pescini et al. (36) found that wolves outperformed dogs in a detour task, suggesting a better capacity in tasks requiring spatial cognition.

Many authors suggested that the differences observed between dogs and wolves in both social and asocial cognition tasks were the result of the domestication process that allowed dogs to adapt specifically to life with humans (8-10, 30). It was suggested that dogs evolved special social cognitive skills functionally equivalent to those of humans (9, 10, 37), and that domestication reduced dogs' fearfulness towards humans (38, 39), made dogs more attentive to humans (10, 11) or socially more tolerant in general (40) than wolves, facilitating their cohabitation with humans. Additionally, due to dogs' poor performance in asocial cognition tasks, it has been hypothesised that domestication had a detrimental effect on their physical cognition (30). In fact, since in dogs environmental effects on feeding and mating are buffered by humans, natural selection might have relaxed their problem-solving abilities (30, 41).

These hypotheses are in line with the idea that, as for other domestic species such as farm animals, dogs' domestication was an artificial process actively controlled by humans. This process resulted in the evolution of pet dogs that are 'saved' from the natural selective forces thanks to the care of their human companions (42).

However, it seems more likely that dogs underwent a process of 'self-domestication' by which their morphology and behaviour changed to adapt to the human-created niche (43). Indeed the beginning of dogs' domestication appears to coincide with the late Pleistocene megafauna extinction (44), which dramatically reduced wolves' prey accompanied by a drastic fall in their population size (45). It is thus not unlikely, that, coinciding with this prey crisis, some wolves discovered and slowly started to rely upon refuses found around human encampments. Another possibility is that some wolves switched their feeding niche from scavenging on wild animal carcasses to scavenging on human leftovers. In fact, it has been observed that before the Pleistocene megafauna extinction, wolf populations showed a higher morphological and ecological diversity than extant wolves (46, 47) and analyses of fossil records' skull shape, tooth wear, and isotopic data suggest that some of these populations may have been specialized scavengers (46). The subsequent rise in refuse availability, which accompanied the development of sedentary human communities associated with the agricultural revolution might have functioned as a significant catalyst for the dogs' domestication process (48) (as well as giving rise to multiple other species' domestication events, see 49, 50).

Thus, rather than being selected to become an useful human companion, dogs evolved under natural selective forces (still acting on modern free-ranging dogs 51), which selected in dogs specific adaptations for a scavenging diet. Comparative studies on wolves and dogs should indeed take into account that the adaptation to a new feeding niche may have played a significant role in shaping dogs' behavioural and cognitive profile and that the results might be affected by dogs and wolves' differences in feeding and socio-ecology (52).

3.2 Differences in dogs' and wolves' socio-feeding ecology and implications for comparative studies.

Wolves and dogs show marked differences regarding their feeding ecology, mating system and social organization (43, 52).

Wolves are independent from humans and live in natural environments. Their home range may overlap with the one of humans in highly dense populated areas but interactions between humans and wolves are rare since in these areas wolves tend to avoid human contact. Wolves form family groups with a complex social structure composed of the breeding pair and their offspring from different generations (53, 54). Although wolves may behave as facultative scavengers on human waste (55) they are mainly hunters, strongly relying on cooperation among pack members to succeed in hunting (56-58) and defend the prey from other competitors (59). Wolves seem to exhibit the most highly evolved, complex parental behaviour in the carnivore world (43). In fact, all family members participate in rearing the offspring, bringing food to the puppies and playing with them, other than guarding them and defending the territory (57). The investment in the offspring is high because juveniles cannot feed autonomously and have to learn how to hunt from other individuals (43).

Despite dogs are classically considered as pet dogs, they are best represented by free-ranging dogs that are estimated to be almost 80% of the total dog world population (60-62). Since free-ranging dogs are not under direct human control, they are free to move and reproduce and thus are also defined as free-breeding dogs (62). Indeed, pure-breed dogs and free-ranging dogs are genetically distinct populations with the latter representing the ancient dog population from which pure-breed dogs have been selected (51).

Contrary to wolves, dogs (free-ranging dogs) tend to live and reproduce around human settlements, both in urban environments as well as in suburban and rural environments (63, 64). In order to adapt to such different and variable environments dogs show quite a flexible social structure. In fact, individuals living in urban areas are often solitary or form only small temporary associations with conspecifics (usually 2–3 individuals) (64-68). On the contrary, in suburban and rural areas dogs tend to form bigger groups (64) with a well-defined social structure (69, 70), but where transients members as well as temporary emigration from the pack of one or more individuals ('pack splitting', 64) are frequent. It has been suggested that to more successfully exploit their feeding niche (i.e. human refuses), dogs' developed an r-selected reproductive strategy (43) characterized by promiscuity, early maturity onset, high reproductive rates and mortality rates (especially among puppies)(65, 71), other than reduced parental care, which is almost absent after the weaning since puppies can feed autonomously on refuses (43, 64). Furthermore, it has been suggested that free-ranging dogs forage mostly solitary even when living in related packs (72).

Such marked differences in wolves and dogs social and feeding ecology likely affect many of the differences observed between the two species when tested in cognitive and behavioural studies (52). For instance, in line with wolves' more dangerous and complex foraging strategy, they appear more risk-prone than dogs when it comes to choose between a safe low quality reward and a high quality but less certain one (73) and are also more neophobic, yet more explorative than dogs (74, 75). In line with the need to be highly persistent in order to follow and catch their preys (58), wolves are more persistent than dogs in different tasks (33, 76). Moreover, since persistence is positively correlated with subjects' problem-solving performance (77-80), it likely affected wolves better performance in different problem-solving and manipulation tasks compared to dogs (27, 28, 76, 81).

In the social domain, in line with dogs' reduced reliance on cooperation among pack' members, dogs avoid each other rather than reconcile (as wolves do) after conflicts (82). Additionally, dogs show less accuracy in imitative learning from conspecifics compared to wolves (83) and are much less successful in intraspecific cooperative tasks (84, 85 but see 86). Interestingly, despite dogs performing rather poorly when tested with conspecifics in cooperative tasks, their performance improves when tested with humans and no differences between wolves and dogs were observed when cooperating with human partners (87, 88). Thus, contrary to what has been previously suggested (40), it has been hypothesised that dog-human cooperation might be largely based on wolves' capacity for conspecific cooperation (Canine Cooperation Hypothesis, 89). For the first time, the Canine Cooperation Hypothesis took into account the species' ecology as a potentially quite important factor in shaping dogs' domestication process and thus affecting wolves' and dogs' performance in behavioural studies.

3.3 The role of life experience and implications for comparative studies.

As previously highlighted, numerous hypotheses on the effect of domestication in dogs have been put forward. Some suggested that humans selected human-like social skills (9-11) in dogs or that humans might have selected less fearful (38, 39) or more tolerant subjects (40), hypersocial individuals (hypersociability hypothesis, 90) or more submissive subjects (deferential hypothesis, 87). All of these potential changes in dogs' behaviour compared to wolves, would have indeed facilitated their cohabitation with humans.

Some of these hypotheses were based on the results of studies that compared pet dogs with human-socialized captive wolves, populations that had very different levels of experience with humans. Such differences in life experience might have played a crucial role in determining differences in behaviours observed and thus might have been wrongly attributed to the effect of domestication.

Consequently, some authors highlighted that experiential factors could be of equal if not greater importance than domestication in affecting results on wolf-dog differences in socio-cognitive tests (91). Indeed, Udell et al. (92) comparing the behaviour of hand-raised wolves, pet dogs and former street dogs, found that the hand-raised wolves outperformed the former street dogs supporting the hypothesis that ontogeny might have affected individuals more than selection during domestication. These findings raised a debate regarding the roles of domestication vs. experience (e.g., 8 vs 93; 94 vs 95; 96 vs 97) on dog-wolf differences in human-related socio-cognitive abilities.

In order to clearly investigate the role of domestication on wolf-dog behavioural differences one approach has been to compare wolves and dogs raised in the same manner and thus equally socialized with humans. The majority of these studies were conducted at the Wolf Science Center (Austria) and showed that, when highly socialized with humans, wolves' social abilities are similar to those of dogs. For example, both species used 'showing' behaviour to indicate a food location to humans and adjusted their communication to the cooperativeness of the experimenter (98). They both benefited from a training session with a known trainer, showing a reduction in cortisol levels which is a physiological index of stress, although dogs did show more gazing behaviour towards the trainer (99). Both wolves and dogs were shown to cooperate equally well with humans in a string pulling test, although wolves tended to take the leading role, whereas dogs' more often waited for the human to take the initiative (87). Additionally, in the same task, both species showed to fully understand the partner's role, waiting for the human before commencing the test and recruiting her when necessary to solve the task (88).

These findings highlight the controversy still surrounding what has in fact changed during domestication, in that they are in contrast with the implications of most domestication hypotheses previously cited, but are in line with suggestions that domestication could have acted directly on human-directed behaviours of dogs for example by reducing fear of humans facilitating socialization with them (38, 39), by increasing subjects' sociability (90) or submissive attitude towards humans (87).

In fact, the most likely scenario is that both the domestication process and life experiences play important roles in the emergence of dogs' socio-cognitive skills (100). Miklósi and Topal (101) pointed out that to properly compare different species at the level of complex social skills, it is necessary to compare different populations of both dogs and wolves. Due to an effect of the major evolutionary processes, species may differ (be constrained) in the degree to which they are able to react to challenges of the social environment showing a difference in their phenotypic plasticity. More specifically, due to domestication, dogs may display human-like behaviours in the anthropogenic environment following a lower intensity of social stimulation than wolves. However, this does not exclude that wolves are able to display human-like social skills if socialized in an exceptionally intensive manner. In conclusion, as pointed out by Miklósi and Topal (101) to have a better understanding of the effects of domestication and experience on the socio-cognitive abilities of wolves and dogs it is necessary to include populations with differing experience as regards human socialization, allowing us to take this variable into account when testing wolf-dog differences in socio-cognitive tasks.

3.4 Research aim and research questions

The **aim** of the current research was to test the effect of domestication comparing groups of wolves and dogs raised in the same manner, but importantly, also to assess the role of experience with humans by comparing groups of subjects from a number of dog populations differing in their social experience with humans, i.e. free-ranging dogs socialized with humans (village dogs) and pet dogs living constantly with their owner.

Although at present, an estimated 80% of the world dog population lives outside of human control (60), free-ranging dogs have started only recently to be tested in cognitive tasks (28, 102-108). Indeed, the current dog-wolf comparisons are based largely on pet dogs (9, 109), a few studies on shelter dogs (92), and finally dogs raised by humans in peer groups and kept in packs in large enclosures in a game park setting (for example 11, 35, 36, 75). Although comparing equally raised, and highly socialized, wolves and dogs is important since it can answer questions about whether (but not to what extent) domestication has affected the behaviours observed, to address the possible role of experience and its impact on dogs' behaviours, it is important to compare dogs from more diverse backgrounds. Among these dog populations, free-ranging dogs should indeed be included since: 1. they have a reduced experience of humans compared to pet dogs and shelter dogs; 2. they are the main representatives of the dog species; and 3. they are still nowadays affected by natural selective forces and should thus show behavioural adaptations to their living environment and feeding niche.

Our **research questions** aimed to investigate:

1. Whether domestication has affected both dogs' socio-cognitive skills and their independent problem-solving skills by comparing wolves and dogs raised in the same manner at the WSC

2. To what extent these skills are affected by dogs' social experience with humans by comparing dogs differing on this factor: i.e. free-ranging dogs with scarce contact with humans but well socialized (village dogs), WSC dogs with daily contact with humans but living in packs, and pet dogs living constantly with their human partners.

Based on the relative importance of domestication and experience in affecting dogs' behaviours we formulated three general predictions:

- Prediction 1:

  If *experience* (i.e. the learned dependency on humans during their life) plays a major role in dogs enhanced socio-cognitive abilities towards humans and their poor performance in independent problem solving, we would expect pet dogs living in close contact with the owner to excel in the former and show the least capacities in the latter compared to less socially dependant dogs (i.e. village dogs). Furthermore, wolves and dogs raised in the same way (WSC dogs and wolves) should largely show similar patterns of results.

- Prediction 2:

  If *domestication* plays a major role in these differences, we would expect free-ranging dogs, WSC dogs and pet dogs to perform relatively similarly, and show large differences compared to wolves (e.g. all groups of dogs are better in social tasks and worse in independent problem solving tasks than wolves).
- Prediction 3:

  Finally if both aspects are important, in that *domestication predisposes dogs for social dependency* making them more sensitive to it, then we expect dogs with more experience of human contact to perform better in socio-cognitive tasks than dogs with less experience of human contact (Pet dogs> free-ranging dogs), and vice versa be less proficient in independent problem solving. Importantly, we also expect dogs that are raised with the same high level of human contact as wolves (WSC dogs), to show a better performance in social tasks and poorer performance in independent ones.

3.5 Overall experimental design and methods

Subjects.

Identically-raised wolves and dogs (Wolf Science Centre, Austria)

Five dog packs (ranging from 2 to 6 individuals) composed of a total of 15 dogs (9M, 6F)(WSC dogs) and 4 wolf packs (ranging from 2 to 5 individuals)(WSC wolves) composed of a total of 12 wolves (8M, 4F), were tested at the Wolf Science Centre (WSC; www.wolfscience.at, Ernstbrunn, Austria). WSC wolves are timber wolves acquired from zoos. WSC dogs are mixed breed individuals (which were born at the WSC) and mongrels, representative of free-ranging dogs of Eastern Europe (acquired from shelters in Hungary).

All animals were hand-raised in peer groups at the WSC after being separated from their mothers during the first 10 days after birth. They were bottle-fed and later hand-fed by humans and had continuous access to humans the first 5 months of their life. At month 5, they were introduced to their respective packs, but continued to have daily social contact with humans during training and/or cognitive and behavioural experiments. The enclosures (2000-8000 m^2) are equipped with trees, bushes, and shelters. Water for drinking is permanently available. All animals receive a diet of meat, fruits, milk products and dry food. During the first months of their lives, they were fed several times per day, which was slowly reduced to being fed major meals daily.

Pet dogs (Vienna, Austria)

Pet dogs were either selected from a database of the Clever Dod Lab (Messerli research Institute, Veterinary University of Vienna) containing over 3000 dogs or recruited around dog areas in Vienna. Dogs were tested in dog areas and in their homes.

Free-ranging dogs (Taghazout, Morocco)

The study on free ranging dogs was conducted in Morocco, in the area of Taghazout. This territory is characterized by the presence of a large number of free-ranging dogs that are structured in packs of different sizes, from small packs of two to three individuals to big packs of up to 10 individuals. Initial genetic analyses on these populations showed that these dogs are largely genetically similar to free-ranging dogs in Eastern Europe (Pilot, unpublished data). Subjects were recruited and tested on the streets.

Moroccan free-ranging dogs and our study population in Taghazout.

In Morocco, the dog population is estimated to be about two million (110). A census of 1993 estimated that sixty percent of dogs were completely free to move while twenty percent were partially free either during the day or night (111). In both cases, they were not under strict supervision or care of humans and thus can be considered as free-ranging dogs. Nevertheless, a great number of these dogs are considered to be owned by the local population (95% of people declare to own at least one dog) and serve as guardian dogs (66%) or guard flocks (31.4%). However, they completely differ from our (i.e. Western) concept of pet dog. In fact, these dogs are free to move and reproduce, the majority do not receive veterinary care or treatments and they do not live inside the houses. They settle in a specific territory because they can find some sources of food directly or often indirectly provided by the “owners” through waste and leftovers. Thus, they protect those territories and families from intruders and, if living around livestock as puppies, they naturally tend to follow the herds without any kind of specific training.

Our study population is largely centred in the town of Taghazout and the surrounding area (approx. 0.5 km^2). Taghazout is a Berber fishing village of approximately 5000 people close to Agadir on the Atlantic coast of Morocco. The Taghazout bay attracts 60.000 tourists every year both from Morocco (especially in the summer) and from the Western countries (especially in the winter). In fact, Taghazout has become quite famous all over the world for surfing and it is indeed full of surfers from October to April. This is also the time when it is possible to see the highest number of dogs roaming around.

From 2016 to 2018 we have monitored the area of Taghazout between October and February and observed between 110-130 adult dogs each year (considering only dogs that were seen at least 3 times). In 2017, we found 42% of dogs that were present in 2016, suggesting that about half of the population was stable. In 2018, we found only 26% of the dogs observed in 2017. The reason for this large drop between 2017 and 2018 was due to a dog-culling event initiated by the local authorities, that took place in April 2018 aimed at reducing the population. Many dogs were protected and hidden by the local population and tourists, but a lot did not survive. Probably due to this event, only 15.5% of the dogs found in 2018 were the same that were observed in 2016. However, interestingly, already by the end of 2018 and beginning of 2019, the total number of dogs was back again to 111 individuals, suggesting that this is the carrying capacity of the area and importantly demonstrating that killing or removing dogs (e.g. to shelters or adoption) as a measure to reduce the population is rather ineffective.

Like other free-ranging dogs, dogs in Taghazout live mostly of scavenging on human garbage produced by the local population and the touristic activities (restaurants, hotels etc.). Garbage can be found in stable places (such as bins) and at predictable times of the day (for example when the restaurants throw the garbage out late in the evening). However, a lot of garbage is also spread around in unpredictable locations. Furthermore, we observed dogs feeding on human faeces, as already observed in other studies (112), and this is likely an important source of food since Taghazout does not have a complete sewer system. Both locals and tourists also feed the dogs directly, offering another source of food by placing food in specific locations, following a fixed schedule (and more or less stable groups of dogs tend to form around these). Finally, despite these dogs being mainly scavenger, locals observed dogs chasing wild boars entering the village and in one case we were told that a dog managed to kill a boar. Finally, we observed a dog killing and eating a kitten.

In terms of migration patterns, we observed dogs arriving in the village in different ways. The majority of dogs appeared to arrive spontaneously from the surrounding areas. But some dogs are brought to the village by tourists or locals from other towns because they know that in Taghazout dogs are well accepted. Many are born in town and will just stay.

Free-ranging dogs can vary enormously in terms of how shy or friendly they are towards people, and initial observations in different Moroccan towns showed quite some variability when trying to approach different dogs. A peculiarity of Taghazout dogs is that many of them, especially the ones that live in the centre of the village, are extremely friendly. Preliminary results of an observational study showed that the majority of interactions initiated by the dogs (73%) were friendly independently if directed towards locals or tourists. Similarly, 80% of the human-initiated interactions towards the dogs were also positive (such as playing, petting and feeding). Interestingly, we also did not find a large difference in the behaviour of people, with 90% of Western tourists initiating positive interactions and 76% of locals interacting positively with the dogs.

Early comparisons of pet dogs to captive zoo wolves (9-14) were rightly criticized, because any form of test involving humans may ‘penalize’ wolves, since they may be more scared and hence less attentive or relaxed during the experimental procedure. Because our aim was to present different types of behavioural and cognitive tests to the free-ranging dogs, and as much as possible compare them to pet and WSC dogs, it was similarly important for us to select a population that would not show fear towards us, and hence voluntarily and in a relaxed manner participate in our tests. For this reason we chose the Taghazout dogs. The main differences aside from the levels of experience with human interactions of course, was that WSC wolves and dogs as well as pet dogs are always confined to a limited space, while free-ranging dogs are completely free and are tested on the streets.

The difficulties of testing free-ranging dogs.

Testing free-ranging dogs require a substantial change in perspective in comparison with testing pet dogs and captive animals in general which can be restrained. The tests need to be designed differently, considering dogs are free and cannot be confined. Moreover, testing the same dogs more than once turned out to be quite difficult, since, as we discovered, although some individuals appear to be quite stable in a specific territory, many roam far and wide, and therefore there is no guarantee that the same dogs can be found on repeated occasions. Finally, testing a dog alone and with no distracting events is quite complex and many tests needed to be disregarded because of procedural errors.

We adopted early mornings as our preferred testing time (to reduce the number of distractions), and in many cases we worked in teams of two or three people. The latter allowed us to adopt 'distracting' techniques to lure some dogs away from the subject we wanted to test. We also tried to design tests that could accommodate the peculiarities of our populations, yet still be applicable to all dogs including pet dogs in Vienna, and WSC dogs and wolves.

Procedures.

To fully answer the research questions outlined above it would have been necessary to tests all groups in numerous, social and physical cognition tasks, this is an ongoing research program. In the current dissertation, I report three studies that we conducted on specific aspects (but see the general discussion for a broader discussion including other comparative studies on dogs and wolves).

Study 1. A number of studies have shown that wolves are more persistent than dogs in object manipulation tasks. Dogs' lower persistence compared to wolves' has been attributed to their adaptation to a scavenging niche (33), to their reliance on humans' help (ref), or to their experience of being inhibited by humans to interact with objects (81). To clarify the role of life experience with humans in affecting subjects' persistence, we investigated how free-ranging dogs (who are considerably less reliant on humans and possibly more motivated to obtain food), would compare to other dog populations on their persistence in obtaining food hidden in different objects. We presented subjects with two objects (a big rigid plastic ball and a big rigid bottle) baited with food which was impossible to reach. All subjects were tested alone and in the absence of humans.

Study 2. The aim of the present study was to investigate whether the 'looking-back' behaviour of dogs in an impossible task paradigm functions indeed as a help-seeking request as widely suggested. We tested pet dogs (who have a wide experience of receiving human help) with free ranging dogs (who do not experience receiving help) with a modified version of the classic impossible task, in which the subjects simultaneously faced three possible and one impossible trial. Additionally, subjects were tested in four different conditions: social condition (with an unknown experimenter); asocial condition (subject alone); 'dummy' human condition (with a 'dummy' human); object condition (with a big sheet of cardboard).

Study 3. The aim of the present study was to investigate the relative roles of both domestication and experience on the value that dogs attribute to human social contact. We tested WSC wolves, WSC dogs, free-ranging dogs and pet dogs in a choice task were subjects had the possibility to choose between a human that previously provided them food and a human that previously provided them social contact.

4. Publications

4.1 Article 1: The role of life experience in affecting persistence: a comparative study between free-ranging dogs, pet dogs and captive pack dogs.

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Abstract

Persistence in object manipulation has been consistently associated with problem-solving success and it is known to be affected, at the individual level, by life experience. Differences in life experiences are particularly poorly studied in the problem-solving context and mainly refer to the comparison between wild and captive animals. Dogs represent interesting study subjects, since dog populations differ widely in their life experiences. In this comparative study we investigated subjects' persistence when presenting a novel object containing food that could not be accessed (impossible task) to three dog populations with very diverse life experiences: free-ranging village dogs (in Morocco), pet dogs (in Vienna) and captive pack living dogs (Wolf Science Center-WSC). We found that pet dogs and captive dogs (WSC) were more manipulative and persistent than free-ranging dogs. The low persistence of free ranging-dogs is unlikely the effect of a lack of exposure to objects, since they are confronted with many human’ artefacts in their environment daily. Instead, we suggest that the higher persistence of captive dogs and pet dogs in comparison to free-ranging dogs might be due to their increased experience of human-mediated object interaction. This provides subjects with a socially guided experience in manipulating and interacting with objects increasing their motivation to engage in such tasks.

Keywords: persistence, free-ranging dogs, captivity.

Introduction

Problem solving performance is a cognitive trait which is an accepted measure of general cognitive ability [1] and has been observed to variably influence subjects' fitness [2-5]. Studies investigating the factors that influence individuals' problem-solving performance focus on both intra-specific (for review see [6]) and inter-specific [7-11] comparison. In both cases, subjects' performance has been observed to be determined by a combination of numerous factors, i.e. innovation [8, 12-14], neophobia [7, 12-14], behavioural flexibility [12, 15], and persistence or task-directed motivation [8, 12-14]. Moreover, in intra-specific comparisons, problem solving performance seems to be additionally influenced by factors such as personality [14, 16], social rank [14], sex [12, 17], age [8, 12, 14, 18, 19], and individual life experience [20-22].

Differences in life experiences are particularly poorly studied in the problem-solving context and mainly refer to the comparison between wild and captive animals. Here, captive animals have been found to outperform their wild counterparts when presented with problem-solving tasks [20-22], which could be due to them having a safer and more enriched environment (i.e. material conditions). This may allow them more opportunities to practice object-manipulation and be less neophobic towards human artefacts. Another possible explanation is that experience with humans leads to an increase in socially guided exploration opportunities that enhance captive animals’ problem-solving performance [23, 24].

Since the life experience of the individual may influence problem-solving performance, dogs represent interesting study subjects. In fact, dog populations differ widely in their life experiences. In terms of their socio-ecology, dogs are an anthrodependent species [25] that have adapted to live and reproduce around human settlements [26]. Classically, they are considered 'pets', despite this category representing only 20-30% of the world dog population [27]. Pet dogs are restricted dogs that fully depend on humans for food provisioning, reproduction, and movements [28, 29]. Their social lives are deeply interconnected with those of their human companions [30] with whom they establish complex social relationships [31]. The other 70 - 80% of the world dog population is represented by free-ranging dogs [27, 32, 33]. Despite being self-sustaining and self-regulating populations, without any [major] human constraints on their activities [34], free-ranging dogs mostly live around humans settlements in urban, suburban, and rural environments [35, 36]. Although 'feral' dogs that live removed from humans and base their survival on hunting small prey exist [27, 36-38], the majority of free-ranging dogs are largely scavengers [39-45] that rely on resources provided by human activity [45]. Free-ranging dogs living in urban areas have a close association with humans and tend to be solitary or form smaller groups compared to those living in rural areas that are more independent from humans and tend to form bigger groups [35, 36] with a well-defined social structure [46, 47].

Despite the evidence that life experience may influence individuals' problem-solving performance, only a few studies have investigated problem-solving abilities across dog populations with different experiences. Many of these studies focused on pet dogs, comparing trained and untrained dogs [48-52]. The main finding of these studies is that training (i.e. experience in interacting with objects with human guidance) improves subject's persistence and problem-solving success (but see [52]).

In a study on problem-solving performance in dogs and wolves, Udell et al. [53] additionally compared two dog populations with different life experiences: shelter dogs and pet dogs. The authors did not find differences between the two dog groups, which both showed low persistence and problem-solving success. Interestingly, they found that for both groups the subject's persistence to interact with the puzzle box was higher when encouraged by the human than when tested alone. They suggested that the low persistence showed by the subjects when tested alone was due to the experience of being inhibited by the owners in interacting with the objects. In fact, it is commonly assumed that the poor performance of dogs in problem-solving tasks is a consequence of the fact that dogs' day-to-day behaviours are often regulated by their owners [53]. Thus, dogs may be inhibited to interact with the objects or just avoid to solving problems because they are used to receiving help from the human partner [54]. However, shelter dogs and pet dogs behaved similarly in this task, which was explained by the authors as social inhibition being rather generalized. In contrast to this hypothesis are the findings of another study also comparing problem-solving performance between shelter dogs and pet dogs [55]. In this study, Barrera et al. [55] found that pet dogs where more persistent in looking for a reward than shelter dogs. Moreover, they did not observe differences in persistence between dogs tested alone or with the experimenter. This would exclude that the lower persistence of shelter dogs was due their higher needs to socially interact with a human instead of focusing on the task.

The contrasting results observed in these studies may be due to the fact that the past experience of shelter dogs with humans could be extremely variable. This could be due to different shelter-management styles or a difference in dogs' experiences, since some may have lived for years as pet dogs and others as free-ranging dogs. Thus, to properly test the effect of the experience with humans it would be necessary to compare dogs that strictly depend on humans (i.e. pet dogs and captive dogs) with unrestricted free-ranging dogs.

To our knowledge, only one study has investigated differences in problem-solving between pet dogs and free-ranging dogs [56]. Interestingly, the study found that free-ranging dogs were less persistent (i.e. they interacted with the apparatus for a shorter duration) than pet dogs. This is in line with what was observed in other species where captive animals outperform their wild counterparts [20-22]. However, this result was restricted to the condition when the pet dogs were tested indoors; when they were tested outdoors no difference emerged between pet and free-ranging dogs due to a decrease in the pet dogs' persistence, probably because of lower motivation in this context. Furthermore, the experimenter's/owner's presence during the test may have influenced the behaviour of the subjects differently, with free-ranging dogs potentially being more nervous in the presence of the human than pets.

In the current study we investigated differences in persistence between dog groups differing in their experience with humans. We tested free-ranging dogs and pet dogs in an impossible task (i.e. an object containing food that could not be accessed), in their home environment. We used the same paradigm used by a previous study conducted on captive dogs and wolves at the Wolf Science Center (WSC) [57]. Additionally, we compared our data from pet and free-ranging dogs with the previous data on enclosure-kept dogs that differ in their experience from pet dogs. We investigated whether persistence is affected by the subject's experience and hypothesised that the experience interacting with humans and their artefacts would increase subjects' persistence.

All subjects were tested with a big rigid plastic ball that they had never encountered before (however, all dogs might have been exposed to ball-like objects before). Additionally, as neophobia (defined as 'the avoidance of an object solely because it has never been experienced and is dissimilar from what has been experienced in the individual's past' [58]) has often been shown to negatively correlate with persistence ([12, 14, 59] but see [60]), we also tested both free-ranging dogs and pet dogs with a plastic bottle – a familiar object that all subjects have considerable experience with. This allowed us to assess the potentially different effect of neophobia on persistence in the two dog populations. All tests were performed in the absence of conspecifics and humans.

We predicted that if persistence is influenced by different life experiences with humans as observed in other species [20-22], WSC dogs and pet dogs should be more persistent with the ball than free-ranging dogs.

Additionally, pet dogs (that live in constant contact with humans) should be more persistent with the ball than WSC (and free-ranging) dogs.

Finally, since the population of free-ranging dogs that we tested has been observed to live around a wide variety of human artefacts, we expected neither free-ranging dogs nor pets to act differently when tested with the ball compared to the plastic bottle.

Materials and methods

Ethical statement

Ethical approval for this study was obtained from the 'Ethik und Tierschutzkommission' of the University of Veterinary Medicine (Protocol number ETK-15/05/2016). Informed consent was obtained by all owners of the pet dogs. The authorization to test the free-ranging dogs was provided by the municipality of Taghazout (Morocco).

Subjects

Free-ranging dogs (FRd). Free-ranging dogs were tested in their natural environment in the municipality of Taghazout, Agadir, Morocco. The experimenters (ML, LD and RM) travelled by car to look for solitary dogs (solitary dogs were chosen to avoid interference by conspecifics). Only adult dogs (appearing to be over 1 year of age) were tested. A total of 35 free-ranging dogs were tested, 32 (20 F, 12 M) were included in the analyses (10 dogs were tested with both the ball and the bottle, 13 with only the ball and 12 with only the bottle). Three dogs were excluded because did not approach the apparatus. The tested free-ranging dogs were village-dogs living around human settlements. Their main source of food is derived from human waste that is both concentrated in specific spots (i.e. bins) and scattered around, especially during the tourist seasons (Fig 1).

Pet dogs (Pd). Mixed-breed pet dogs were tested in private gardens in Austria. A total of 25 pet dogs were tested; 24 were included in the analyses (15F, 9M mean age: 7 years; range: 1 to 15). One dog was excluded because did not approach the apparatus. Four tests with the bottle were stopped before the end due to the owner's request (but were kept for analyses, see the result section). Twenty-two dogs were tested with both the ball and the bottle, 2 with only the ball and 1 with only the bottle.

Enclosure kept, pack-living dogs (WSCd). 16 mixed-breed dogs (8F, 8M: mean age in years: 4, range: 2 to 6) housed at the Wolf Science Center (www.wolfscience.at) were tested. Dogs live in conspecific packs and are hand raised. The animals are trained and participate in behavioural tests (for further information on this population see [61]). All animals were presented with the ball only.

Fig 1. Free ranging dog looking for food in the garbage.

In the study area the experience of finding food in the garbage, surrounded by human's artefacts (such as plastic bottles, boxes, bags, etc..) is common since early age.

Apparatus

Ball test. A Lion Feeder Ball (a perforated, hard plastic sphere 24 cm in diameter, weighing 1.5 kg, commercially available “Lion Feeder Ball” from www.ottoenvironmental.com; Fig 2) baited with food impossible to reach was fixed on the ground with a 30 cm chain or a rope.

Bottle test. An opaque and rigid plastic bottle (a perforated, hard plastic bottle 30 cm length, weighing 0.25 kg; Fig 3) baited with food impossible to reach was fixed on the ground with a 30 cm rope.

The apparatuses were baited with sausage and meat for WSCd and sausage and cheese for Pd and FRd. The order of the two tests that were performed with the same subjects was randomized.

Fig 2. Ball.

Fig 3. Bottle.

Test procedure

We defined persistence as task-directed motivation. We were interested in measuring and comparing subjects' persistence in their specific familiar home environment. To achieve this, we tested each dog population in their home territory, without other dogs, and in the absence of any salient stimuli (i.e. unusual for that population) (for additional statistical comparisons of the effect of testing location in Pd see S1 File).

Free-ranging dogs (FRd). Free-ranging dogs were tested in the streets and on the beaches of Taghazout. The tests were done mainly in the early morning, reducing the likelihood of salient stimuli and possible interference with the test. Once a subject was located alone, the experimenter placed the apparatus on the ground, taking care to not be seen by the subject. The apparatus was anchored using a 30-cm long rope to a stone. The experimenter then hid in the car and waited for the dog to independently find the object. If after five minutes, the dog did not find the apparatus (12 dogs did not find the ball and 12 did not find the bottle), a second experimenter went to the dog, greeted it for a few seconds and then walked towards the apparatus with the subject following her. The experimenter did not indicate the apparatus to the dog but simply walked past it and then got into the car. The test started when the dog approached the apparatus. The tests were filmed from the car (S1 video and S2 video).

Pet dogs (Pd). Pet dogs were tested in their home gardens in Austria. Once the experimenter arrived at the house, the animals were taken inside. Then the experimenter placed two cameras and the apparatus on the ground in the garden without being seen by the subject. The apparatus was anchored using a 30-cm long rope to a camping peg driven into the ground. Once the object was in place, the experimenter left, and the dogs were allowed into the garden. The owner and the experimenter remained in the house and were out of sight of the test subject, but able to observe the test from the house and therefore end the test at the appropriate moment.

WSC dogs (WSCd). WSC dogs were tested in their home enclosures at the Wolf Science Centre, Austria. The subjects and their pack were first shifted out from their home enclosure. Before a test session began, we anchored the ball using a 30-cm long metal chain to a camping peg driven into the ground in the subjects' home enclosure. This was done out of sight of the test subject. The peg was positioned such that we could record any interactions the subject had with the object from two different angles without any visual obstructions. We mounted two video cameras (one remote-controlled) on tripods outside the enclosures. Once the apparatus was in place, the focal subject was shifted back into the enclosure. No humans or other animals were present in the area or visible to the test subject. WSC animals are used to being shifted daily from their home enclosure and to be momentarily separated from other pack members. We tested the animals in their home enclosure where they are usually not tested to reduce the possibility that expecting human presence would interfere with their behaviour.

In all tests the subject was left to find the object on its own to avoid a potentially different effect of human behaviour/presence on the subjects' behaviour in the three groups. In fact, observing the placing of the object on the ground might have increased subjects' motivation to interact with the apparatus for Pd and WSCd, which are used to being tested and/or playing with objects presented by humans. On the contrary, free-ranging dogs might have been inhibited by the humans' contact with the object, in their approach and interaction with it.

For Pd and WSCd a circle of two-body-lengths radius around the apparatus was drawn on the ground, while for FRd it was drawn on the videos (it was not possible to draw on the ground since this process risked the dog leaving the area or seeing the experimenter).

The subject was given 5 minutes to approach the object (defined as approaching the object within 10 cm). In case the subject did not approach within five minutes, the test session was terminated. The subjects were free to interact with the object for as long as they wanted and the test was considered finished when the animal left the two-body-lengths radius from the apparatus.

Analyses

All the videos were coded using the software Solomon coder® (100926 developed by András Péter, Dept. of Ethology, Budapest, www.solomoncoder.com). See Table 1 for definitions of the coded behaviours.

Table 1. Ethogram of the behaviours analysed.

Contact latency	Time the subject takes to reach the object (less than 10 cm distance) from a 2-body length circle.
Interaction with the object	
duration of sniffing	Time (seconds) the animal spends sniffing the object from less than 10 cm distance (without touching it).
duration of manipulation (persistence)	Time (seconds) the animal spends touching the object with either snout or paw.

The sum of the durations of sniffing and manipulating is defined as interaction with the object.

Inter-observer reliability was carried out with a second observer coding 20% of video data (Intra-class correlation coefficient: duration of manipulation ICC = 0.99, *F*= 4409, *p* < 0.0001; duration of sniffing ICC = 0.99, *F*= 232, *p* < 0.0001).

To investigate possible effects of neophobia, we analysed if the contact latency varied when subjects were tested with the ball (unfamiliar object) or with the bottle (familiar object). For Pd and FRd we ran the analyses on the subjects that performed both the ball and the bottle test (22 Pd, 10 FRd), comparing contact latency for the two objects for each group. Two GAMLSS models were used to evaluate the effects of object type on the contact latency in Pd and FRd. The subject ID was included as random factor. The model on contact latency in Pd was fitted with Box-Cox t distribution and validated with Inverse Gamma, Generalized Gamma and Generalized Inversed Gaussian distributions. The model on contact latency in FRd was fitted with a Generalized Beta type II distribution and validated with Gamma, ex-Gaussian and Weibull distributions. We additionally compared Pd with WSCd that were tested with the ball, since the two groups could be compared for this analysis since both were tested with the same procedure. We included in this analysis only Pd that did the ball test as the first test (13 Pd) to allow for a proper comparison with the WSCd that performed only the ball test and not the bottle test. A GAMLSS model was used to evaluate the effect of group (Pd vs WSCd) on the contact latency for the ball test. The model was fitted with an Inverse Gamma distribution and validated with Box-Cox Power Exponential, Inverse Gamma and Box-Cox Cole and Green distributions.

We then investigated differences in interaction time and persistence between the groups. A GAMLSS model was used to evaluate the effect of group (FRd, Pd, WSCd) on the interaction time with the ball (sum of duration of sniffing and manipulation). To compare Pd and FRd with WSCd that were tested only with the ball, we included in this model Pd and FRd that did the ball test as the first test or that were only tested with the ball (13 Pd and 13 FRd). The model was fitted with a Box-Cox t distribution and validated with Inversed Gamma, Generalized Gamma and Generalized Beta type 2 distributions.

We investigated the difference in the occurrence of manipulating the ball between groups with a general linear model (GLM) with a quasibinomial distribution. The occurrence of manipulating the ball (manipulating vs non-manipulating) was included as the response variable and group as the explanatory factor. In this analysis, we included all subjects tested with the ball that approached and sniffed the object (23 Pd, 22 FRd, 16 WSCd). Since as a group FRd were not manipulative with the ball (only 3 dogs manipulated the object), we excluded them from further analyses on the persistence in manipulating the ball and compared only Pd and WSCd. A GAMLSS model was used to evaluate the effects of the explanatory factor group (Pd, WSCd) on persistence in manipulating the ball. Since WSCd were only tested with the ball, to compare the two groups, we included in this model only Pd that did the ball test as the first test (13 Pd). We excluded the subjects that did not manipulate the ball (2 WSCd). The model was fitted with an Inverse Gamma distribution and validated with Generalized Gamma, Generalized Inverse Gaussian and Box-Cox t distributions.

We finally investigated differences in interaction time and persistence between Pd and FRd between ball and bottle test. These analyses were run on all subjects, including those that performed only one test (32 FRd: 20 ball tests and 22 bottle tests; 25 Pd: 23 ball and 23 bottle tests). In fact, a preliminary analysis showed no effect of the order of presentation or number of objects presented on the animals' interaction time (S2 File). We excluded 1 Pd and 1 FRd that in the bottle test managed to open the object and eat the content. A GAMLSS model was run to evaluate the effects of the explanatory factors group (Pd-FRd) and object type (ball-bottle) on the response variable interaction time. We included the subject as a random factor. The model was fitted with a Box-Cox t distribution and validated with Gamma, Generalized Beta type II, Generalized Gamma distributions. We investigated the differences in the occurrence of manipulating the bottle between Pd and FRd with a general linear model (GLM) with a binomial distribution. The occurrence of manipulating the bottle (manipulating vs non-manipulating) was include as the response variable and group as the explanatory factor. In this analysis we included all subjects tested with the ball that approached and sniffed the object (23 Pd, 22 FRd). In contrast to the ball, the majority of FRd manipulated the bottle. Thus, we investigated differences in persistence between Pd and FRd for the bottle test only. A GAMLSS model was run to evaluate the effects of group (Pd-FRd) on the response variable persistence. We excluded the subjects that did not manipulate the bottle (3 Pd, 7 FRd). The model was fitted with an Exponential distribution and validated with Weibull, Pareto Type 2 and Generalized Inverse Gaussian distributions.

All models were run in the program R (version 3.4.4). We used generalized linear models (GLM) and generalized linear mixed models (GLMM). The models were fitted using the functions glm (R package stats) and glmer (R package lme4) [62, 63]. P values for the individual effects were based on likelihood ratio tests comparing the full model with the respective reduced models [64]. We additionally used the package GAMLSS ("gamlss" version 5.0-6) [65]). We used the "gamlss.Dist" package version 5.0-4 to fit distributions to our data. We validated our models' results by fitting identical models with other probable distributions. We evaluated all models fit both by their generalised Akaike information criteria [66] and by the distribution of the model residual quantile-quantile plots. This approach enabled us to analyse the data without major transformations, which could have affected the interpretation of results [67, 68].

Results

There was no significant effect of object type (GAMLSS: $t = 0.09$, $p = 0.92$) on the contact latency in Pd (ball: mean 1.76 s, range 0.6-8.4 s; bottle: 2.06 s, range 0.6-10.2 s). There was also no significant effect of object type (GAMLSS: $t = -1.44$, $p = 0.17$) on the contact latency in FRd (ball: mean 2.64 s, range 0.2-7.6 s; bottle: mean 2.08 s, range 1-5.2 s). WSCd were found to be faster than Pd in approaching the ball (GAMLSS: $t = -4.3$, $p < 0.001$) (WSCd mean 0.98 s, range 0.6-1.2 s; Pd mean 2.38 s, range 0.6-8.4 s).

The three groups did not differ in the interaction time with the ball (i.e. interacting: sum of sniffing and manipulating) (GAMLSS: FRd-Pd $t = 1.2$, $p = 0.23$; FRd-WSCd $t = 0.34$, $p = 0.73$; Pd-WSCd $t = -0.91$, $p = 0.36$) (FRd mean 15.64 s, range 5.6-39 s; Pd mean 30.04 s, range 3.4-147.6 s; WSCd mean 32.4 s, range 6-337 s). Despite all FRd that approached the ball also sniffed it, only 3 manipulated it. Thus, analysing whether the subjects manipulated the ball or not, we found significant difference between FRd and Pd (GLM: $z = 4.02$, $p < 0.001$) and FRd and WSCd (GLM: $z = 3.6$, $p < 0.001$), while no differences were observed between Pd and WSCd (GLM: $z = 0.05$, $p = 0.9$), Fig 4. We did not find differences in persistence in manipulating the ball between Pd and WSCd (GAMLSS: $t = -0.56$, $p = 0.58$) (Pd mean 13.9 s, range 0.8-129.4 s; WSCd mean 26.18 s, range 0.8-316.8 s), Fig 5.

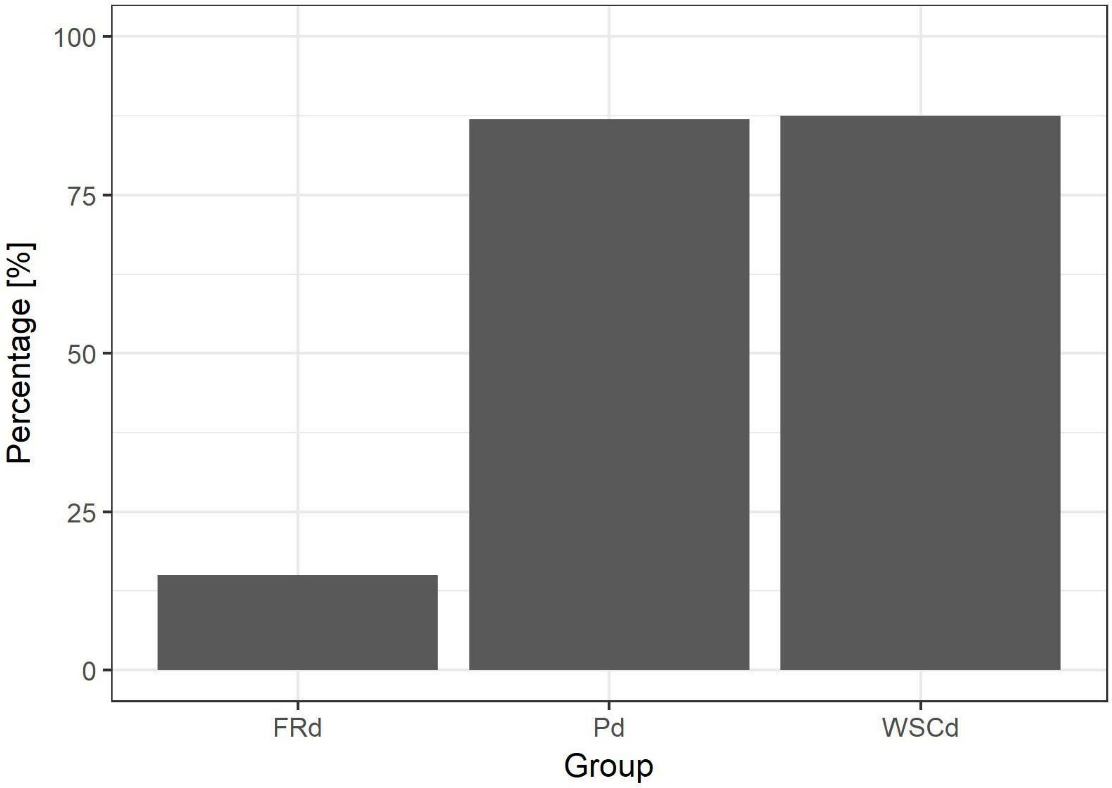

Fig 4. Manipulation of the ball. Proportion of individuals that manipulated the ball in the three groups (Pd: pet dogs, FRd: free-ranging dogs, WSCd: WSC dogs)

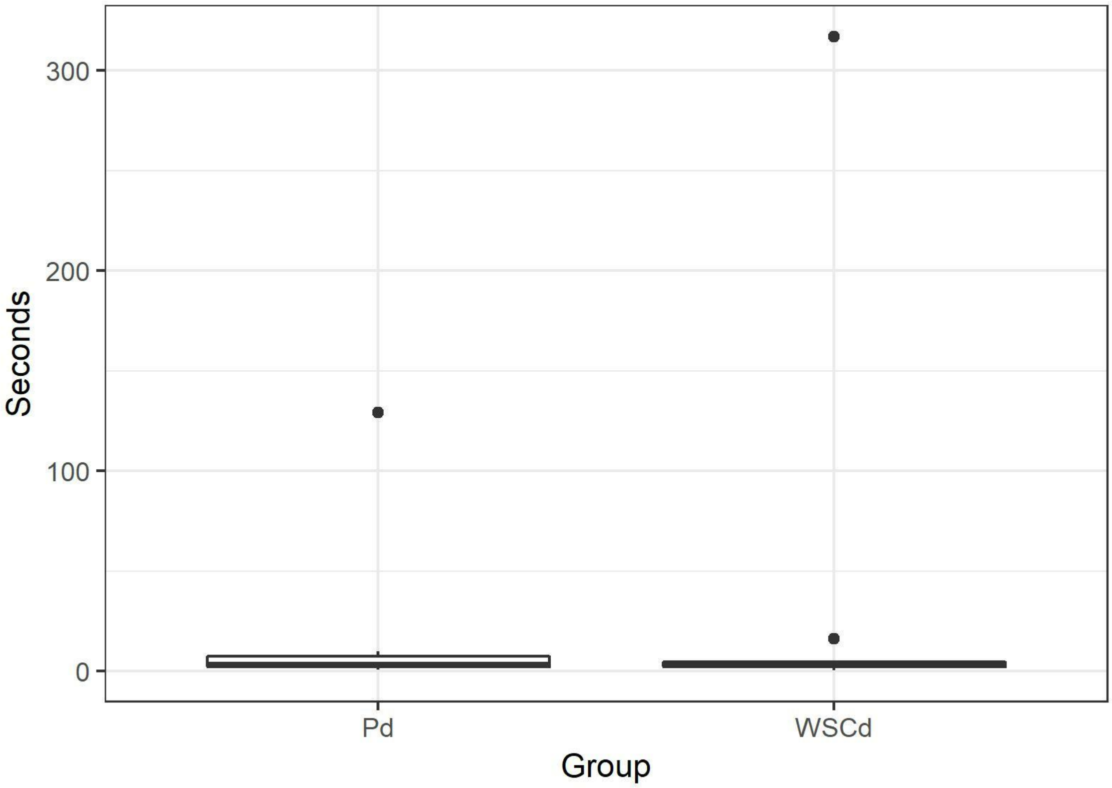

Fig 5. Duration of manipulation of the ball for pet dogs (Pd) and WSC dogs (WSCd).

Pd and FRd were additionally tested with a bottle representing a familiar object for these two populations. There was no significant effect of group (Pd-FRd) (GAMLSS: t = 0.86, p = 0.4) or object type (ball-bottle) (GAMLSS: t = 0.57, p = 0.57) on interaction time (ball: Pd mean 33.97 s, range 2-147.6 s; FRd mean 15.14 sec, range 3.8-44.8 s; bottle: Pd mean 33.78 s, range 2.4-112.8 s; FRd mean 15.61 s, range 6-64.6 s). The interaction between group and object type was not significant (t = 0.5, p = 0.62). Differently from the ball test, in the bottle test FRd manipulated the object and did not differ from Pd (GLM: z = 1.47, p = 0.14). However, FRd were less persistent than Pd in manipulating the bottle (GAMLSS: z = 3.17, p = 0.003), (Pd mean 42.5 s, range 0.8-230.2 s; FRd mean 10.8 s, range 1-47.8 s), Fig 6.

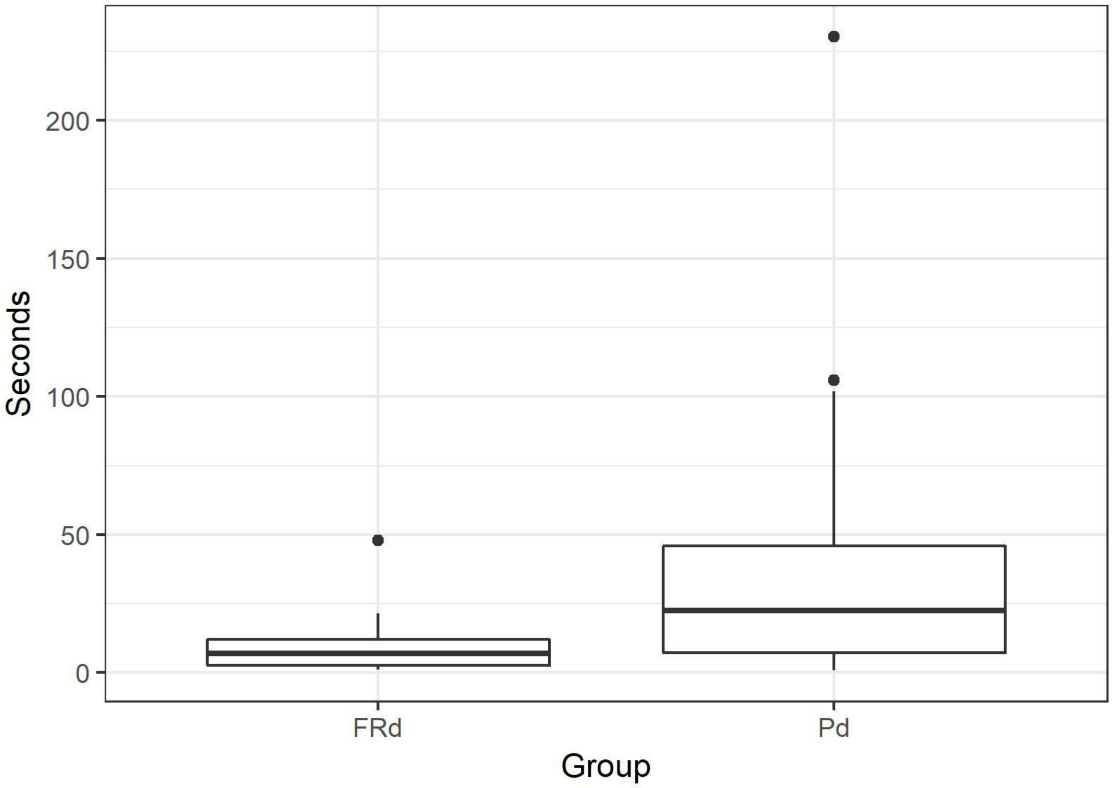

Fig 6. Duration of manipulation of the bottle for free-ranging dogs (FRd) and pet dogs (Pd).

Discussion

We investigated differences in persistence in an impossible task in three groups of dogs with different life experiences. We found that pet dogs and captive dogs were more manipulative and persistent than free-ranging dogs. This is in contrast with the common thinking that pet dogs are bad problem solvers due to owners training them to inhibit object manipulations and/or the lack of needing to independently solve tasks. We suggest that the lower manipulation and persistence of free-ranging dogs compared to pet dogs and WSC dogs cannot be attributed to greater neophobia towards the objects. In fact, for free-ranging dogs we could not find differences in latency to approach a novel object (ball) and a familiar object (bottle). Unfortunately, we could not directly compare the latency to approach the ball between free-ranging dogs and the other groups, since they were tested with different procedures (random starting point for free-ranging dogs compared to a fixed starting point for the other groups). Free-ranging dogs usually roam around slowly looking for food, while WSC dogs or pet dogs usually run into their enclosures/gardens engaging in exploration activities (pet dogs) or looking for a reward (WSC dogs). However, we did compare pet dogs and WSC dogs and found that the latter were faster in approaching the object despite being equally persistent. This was probably because WSC animals are used to being shifted out from their home enclosures and then receive treats or enrichment once shifted back in, which might increase their motivation and speed in moving back into the enclosure.

Despite free-ranging dogs being particularly less manipulative than pet dogs, the two groups did not differ in their overall interest toward the objects, interacting similarly with the bottle and the ball. This additionally supports the absence of neophobia in free-ranging dogs towards the objects, compared to pet dogs. However, both groups were more persistent when manipulating the bottle than the ball. These results are likely due to different features of the objects that could have affected subjects' persistence, since the bottle appeared to be easier to manipulate than the ball [69].

We suggest two possible explanations as to why free-ranging dogs were less persistent than pet dogs and WSC dogs: 1) free-ranging dogs may be less willing to persist in a difficult task than pet dogs and WSC dogs to conserve energy [70]; 2) experiential factors differing between groups may have influenced subjects' persistence in the task, e.g., different training experiences with objects – both the WSC dogs and pet dogs are encouraged by the trainers/owners to interact with objects in certain situations (i.e. experiments, dog toys).

In regard to the first explanation, we observed that in the study area, where we tested free-ranging dogs, the food distribution is variable. Thus, in some locations the food sources are predictable, either concentrated or scattered, while in other locations the food sources are unpredictable, which is likely connected to the variability of human activity. This food distribution results in solitary dogs roaming around looking for food, moving from one spot to another to eat scattered garbage. In accordance with the optimal foraging strategy, since the subjects might perceive our task as extremely difficult if not impossible, the best foraging strategy would result in ignoring the task and looking for other food sources [71]. This strategy would be additionally supported by the fact that the other food sources are easy to locate and consume and have high energetic value. While free-ranging dogs are used to finding scattered food, pet dogs and WSC dogs are used to predicable food located in a single spot. Thus, free-ranging dogs may not waste energy in trying to obtain food in one location but decide to move to the next spot because other food resources are usually available. Moreover, they may have learned that if they cannot get access to food within human artefacts easily, it is more energy efficient to move on and look for other sources of food, which might otherwise be found by competing scavengers. However, in contrast with this interpretation is the observation that many subjects

(21.7 %) laid down close to the apparatus or continued standing in the area without looking for other food sources. Moreover, the presence of other dogs increased the subjects' interaction time with the ball. In fact, an additional 13 dogs where tested for this study, but excluded because another dog appeared either at the start or during the test. Comparing these dogs to the study sample of 23 dogs tested alone we found that dogs tested with another dog present interacted with the ball longer. Furthermore, when testing the time spent interacting with the ball before compared to after the second dogs' arrival, we found that the arrival of a dog tended to increase subjects' interaction time with the object (S3 File).

Another possible factor that might have determined the differences in persistence between dog groups is their different experiences with humans. Interestingly, the comparison between the three dog groups allowed us to refute the hypothesis that dogs' low persistence may be due to a conditioned inhibition of problem-solving behaviour [53]. In fact, neither free-ranging dogs nor WSC dogs experience the inhibitory influence of a human companion controlling their potentially destructive tendencies in a home environment. Yet WSC dogs were just as persistent as pet dogs and free-ranging dogs were less persistent than the other groups. Rather, our results are in line with findings from other studies that compared subjects in captivity and in the wild and found contact with humans to increase problem-solving success [20-22]. Although these studies did not measure persistence per se, problem-solving success and persistence have often been observed to be positively correlated [12-14, 72-75]. Though the increased success of captive animals is commonly attributed to their greater chances to interact with human objects during their lifetime, this was not so in our case. In fact, in our study area, free-ranging dogs live around human settlements and are always in contact with garbage disposed in the streets and open-air dumps. This often includes discarded containers of various kinds and provides dogs with many opportunities to interact with human artefacts. Additionally, the presence of food around or inside the variety of objects that can be found, points to the possibility that free-ranging dogs may have associated human artefacts with food just as much as the other two dog groups. Thus, we suggest that a possible factor influencing the difference in persistence observed between free-ranging dogs and pet dogs-WSC dogs could be the experience of humans mediating the animals' interaction with the objects around them. In fact, although it has been observed that the mere presence of a human does not increase the dog's persistence [53], the human's encouragement does [52, 53]. Thus, the life experience of object-interaction mediated by human encouragement (through play and/or positive social response) may increase the subjects' overall motivation to interact with objects. This would also explain why pet dogs and WSC dogs showed similar persistence levels: despite living in such different environments, both groups experience human-guided interactions with objects. In support with this interpretation are the findings of studies comparing trained and untrained pet dogs in problem-solving tasks (belong to the same pet dog population, having similar food motivation and health conditions) that have consistently found trained dogs, regardless of the training discipline (agility, search and rescue, dog dancing etc.), to be more persistent and have higher problem-solving success than untrained subjects ([48-51] but see [52]).

To sum up, we observed that free-ranging dogs were less persistent than pet dogs and pack dogs living in enclosures. This is in contrast with the common thinking that pet dogs are inhibited to interact with objects and/or do not need to do it because they are used receiving help from a human partner. Although further studies are necessary to deepen our understanding of the reason underlying these differences, we suggest that a possible explanation for this finding is the different human-mediated object interaction between groups. Humans may provide subjects with a socially guided experience in manipulating and interacting with objects, which could increase their motivation to engage in such tasks (even in their absence). Thus, pet dogs as well as pack-living captive dogs, both with ample experience of human-mediated object interaction, spent significantly longer manipulating the object than free-ranging dogs. This is in line with observations in other species when comparing captive and wild subjects. Finally, these results support the findings of a previous study focusing on a wolf-dog comparison suggesting that the lower persistence of dogs when compared to wolves, is a consequence of the different foraging ecologies of the two species (hunting vs scavenging) rather than the effect of humans inhibiting dogs' interactiveness with objects [57].

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SUPPLEMENTARY MATERIALS

S1 File. Additional analyses in pet dogs on the possible effect of testing location on interaction time and persistence.

We initially ran a pilot study on 10 Pd in an outdoor area with both the ball and the bottle. The test procedure was identical to the one used for Pd in the current study, except for the fact that the owner was present in the dog area, sitting on a chair hidden behind a tree. No other dogs were present in the dog area or in sight of the subject. All the subjects were left in the dog area for 5 minutes before the test started. We did not include these subjects in the main study because the presence of the owner might have strongly affected the persistence of the subjects [1], thus possibly affecting the comparison between Pd tested with the owner and FRd and WSCd tested alone.

However, we investigated a possible effect of the test location (garden vs dog area) on interaction time and persistence in Pd. We run two GAMLSS models to evaluate the effects of the explanatory factors test location and object type (ball and bottle) on the interaction time or on persistence. The subject was included as a random factor. We included in these analyses only Pd that were tested in their home gardens with both the ball and the bottle test (22 Pd) and 10 different Pd tested in an outdoor area with both objects. We removed from the analyses one Pd in the bottle test, tested in the garden, that opened the bottle eating the content. We additionally excluded the subjects that did not manipulate the ball (4 subjects tested with the ball in the dog area, 3 subjects tested with the ball and 3 subjects tested with the bottle in the gardens). The model on interaction time was fitted with an Inversed Gamma distribution and validated with Log Normal, Generalized Inverse Gaussian and Generalized Gamma distributions. The model on persistence was fitted with a Generalized Inverse Gaussian distribution and validated with Log Normal, Pareto type 2 and Generalized Gamma distributions.

There was no difference in the interaction time with the objects between Pd tested in the gardens and Pd tested in the outdoor area (GAMLSS: $t = 0.08$, $p = 0.93$) nor difference in the interaction time with the two objects (GAMLSS: $t = 1.78$, $p = 0.08$). There was no difference in persistence with the objects between Pd tested in the gardens and Pd tested in the outdoor area (GAMLSS: $t = 0.89$, $p = 0.37$), but independently from the area where the dogs were tested, subjects were more persistent in manipulating the bottle than the ball (GAMLSS: $t = 2.36$, $p = 0.02$).

These results suggest that the testing location did not have an influence on subjects' interaction time and persistence with the objects. However, we could not exclude that the presence of the owner might have differently influenced subjects' behaviours. Anyhow, in this case we would have expected that the presence of the owner would have reduced subjects' persistence as suggested in previous studies [1, 2].

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S2 File. Additional statistics comparing Pd and FRd that carried out both ball and bottle test.

We investigated if the test order (test done as first or as second) influenced the interaction time with the objects in both Pd and FRd. For this statistic we considered only the subjects that did both tests (10 FRd, 22 Pd). We run a GAMLSS model to evaluate the effects of the explanatory factor test order (test done as first or as second) on the response variable interaction time. We included the animal ID as a random factor. The model was fitted with a Box-Cox-t distribution and validated with Gamma, Generalized Beta type II, Generalized Gamma distributions. We found that the order in which the subjects performed the tests did not influence the time spent interacting with the objects (GAMLSS: t = -1.02, p = 0.312) (the interaction group*tests order was not significant (GAMLSS: t = 0.43, p = 0.668). We additionally investigated whether the number of tests performed by the subjects influenced the time spent in interacting with the objects in FRd. For this statistic we considered all 32 FRd tested. We run a GAMLSS model with test number (1 or 2 tests) as explanatory factor and interaction time as response variable. The model was fitted with a Box-Cox-t distribution and validated with Gamma, Generalized Beta type II, Generalized Gamma distributions. We found that the number of tests performed by the subjects (1 or 2 tests) did not influence the time spent interacting with the object (GAMLSS: t = -1.36, p = 0.18).

S3 File. Additional statistics comparing free-ranging dogs tested alone and in the presence of other dogs, in the ball test.S1 Video. Free-ranging dog tested with the ball.

While running the test with free-ranging dogs, we tested 13 additional dogs with the ball, which were excluded from the main study because during the test another dog (initially not present) approached. Although we did not specifically design the study to test the differences in the interaction time with the object between dogs tested alone and dogs tested in the presence of other dogs, we analysed these data, since it may help clarify the motivation for the reduced persistence in free-ranging dogs. Nevertheless, these results should be considered carefully, and further studies should be run to properly test differences in interaction with objects in the presence or absence of other dogs.

We investigated if the presence of other dogs influenced the overall interaction time with the ball. For this statistic we considered 23 FRd tested alone and 13 FRd tested with the presence of other dogs. We run a GAMLSS model to evaluate the effects of the explanatory factor presence of other dogs on the response variable interaction time. The model was fitted with Zaga distribution. We found that subject tested with other dogs interacted significantly longer with the ball than subjects tested alone (GAMLSS: $t = 2.24$, $p = 0.03$).

We additionally investigated whether the arrival of the other dogs influenced the time spent in interacting with the ball. For this statistic we considered the 13 FRd tested in the presence of other dogs. We run a GAMLSS model with before/after the arrival of the other dog as explanatory factor and interaction time as response variable. Subject was included as random factor. The model was fitted with a Zaga distribution. We found that after the arrival of another dog, subjects tended to increase their interaction time with the object (GAMLSS: t = -1.9, p = 0.06).

4.2 Article 2: Why do dogs look back at the human in an impossible task? Looking back behaviour may be over-interpreted.

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Animal Cognition

Abstract

The impossible task paradigm has been extensively used to study the looking back behaviour in dogs. This behaviour is commonly considered a social problem-solving strategy: dogs facing an unsolvable task soon give up and look back at the experimenter to ask for help. We aimed to test if the looking back in an impossible task does indeed represent a social problem-solving strategy. We used a modified version of the classic impossible task, in which the subjects simultaneously faced three possible and one impossible trials. Additionally, subjects were tested in four different conditions: social condition (with an unknown experimenter); asocial condition (subject alone); 'dummy' human condition (with a ‘dummy’ human); object condition (with a big sheet of cardboard). Finally, we compared two populations of dogs differing in their experience of receiving help from humans: 20 pet dogs tested in their houses and 31 free-ranging dogs tested in Morocco.

We found that the pet dogs and free-ranging dogs had similar persistence in interacting with the impossible task in all conditions. Moreover, subjects looked back with similar latencies at the human, at the dummy human and at the object. Overall, pet dogs looked back longer at the human than free-ranging dogs. This could be interpreted as pet dogs being more attracted to humans and/or having a stronger association between humans and food than free-ranging dogs. Concluding, the looking back in an impossible task does not represent a problem-solving strategy. This behaviour seems rather linked to the subject’s persistence, to the salience of the stimuli presented, and potentially to the past reinforcement history.

Keywords: looking back, impossible task, persistence, free-ranging dogs.

Introduction

Humans look at each other in many situations and often directly at each other’s faces to collect information about others’ intentions and mental states. This ability allows for a complex social communication (Bruce and Young 1998). Interestingly, dogs also gaze at their human partners in many different situations, which is often interpreted as serving similar functions as in humans (Hare and Tomasello 2005). This propensity to look at us has been suggested to have evolved during the domestication process enabling the close dog-human communication characterizing our relationship (Hare and Tomasello 2005; Hare et al. 2002). In their seminal study, Miklósi et al (Miklósi et al. 2003) compared the looking behaviour towards humans in an impossible task paradigm between dogs and human-socialized wolves, which likely resemble dogs’ closest non-domesticated ancestors (Lindblad-Toh et al. 2005). In this paradigm, the subject is faced with a series of possible trials, in which the animal can independently solve the problem to obtain a food reward. Following the possible trials, an impossible trial is presented, which is identical to the prior ones but it is no longer solvable. When facing the impossible trial, dogs looked back at the human sooner and for longer than the wolves, which instead persisted in the attempt to reach the reward. Since the two groups showed similar food motivations, the authors suggested that dogs “were bound to a lesser degree to the ‘attracting’ effects of the food”, being instead more attracted by the human and thus facilitating dog-human communication (Miklósi et al. 2003).

Since then, the impossible task paradigm has been extensively used to study the looking back behaviour in many different contexts: domestication (Miklósi et al. 2003; Marshall-Pescini et al. 2017; Smith and Litchfield 2013); training (Marshall-Pescini et al. 2009; D’Aniello et al. 2015; Marshall-Pescini et al. 2016); breed differences (Konno et al. 2016; Brodd 2014; Marshall-Pescini et al. 2016); genetic bases and heritability (Hori et al. 2013; Persson et al. 2015); aging (Passalacqua et al. 2011; Brodd 2014); effect of experience (D’Aniello and Scandurra 2016; Marshall-Pescini et al. 2017); reputation (Piotti et al. 2017) and comprehension of the other's attentional stance (Marshall-Pescini et al. 2013). In quite a number of these studies (Piotti et al. 2017; Brodd 2014; Passalacqua et al. 2011; Hori et al. 2013; Konno et al. 2016; Marshall-Pescini et al. 2016; Persson et al. 2015; D’Aniello and Scandurra 2016), the authors hypothesised that the looking back was not only determined by ‘human’s attractiveness’ to dogs, but that dogs might use this looking behaviour as an alternative problem-solving strategy (i.e. asking the human for help). It has been investigated whether dogs assess the skilfulness of the human, enlisting her help specifically (Piotti et al. 2017), and whether primitive breeds (wolf-like) were less prone to use this behaviour than other breeds (Passalacqua et al. 2011). Other studies have shown that experience of living in close contact with humans strongly affects some aspects of the looking back behaviour. In fact, it has been found that adult dogs looked longer at the experimenter than juvenile dogs (Passalacqua et al. 2011; Brodd 2014) and that pet dogs looked back longer than dogs living in kennels and thus had far less experiences with human interactions (D’Aniello and Scandurra 2016).

The results of these studies using the impossible task paradigm suggest a selection for a tendency to look at the human in dogs during the domestication process, which would facilitate the development of complex socio-communicative skills given the right experience. This could include requesting help in specific situations and would be in line with the hypothesis that both domestication and subjects’ experience play a role in the emergence of dogs’ socio-cognitive skills (Reid 2009; Miklósi and Topál 2013).

Whether this looking behaviour in these situations indeed functions as a communicative signal that can be interpreted as a request for help has never been properly tested. Indeed, two studies have recently questioned the interpretation of the looking back behaviour in the impossible task paradigm (Marshall-Pescini et al. 2017; Udell 2015). Both studies suggested that the shorter latency in the looking back behaviour of dogs in comparison with wolves might be due to a lower persistence in dogs compared to wolves in their interaction with the object. Udell et al. (2015) suggested that such lower persistence in dogs may be determined by a degree of social inhibition enforced by humans on dogs in their everyday life. Marshall-Pescini et al. (2017) found that indeed subjects' persistence (i.e. duration of interaction with the object during the impossible trial) emerged as the best explanatory variable to account for differences between wolves and dogs, suggesting that their differential looking behaviour did not reflect different problem-solving strategies or attraction to the human face. Moreover, contrary to what was expected, the authors did not find any difference in the latency to look back, among populations of dogs with different experiences of human help (i.e. free-ranging dogs, captive pack-living dogs and pet dogs). The authors suggested that the looking-back behaviour may be the direct consequence of giving up and then turning to the most salient stimulus (the human) in the environment rather than a 'social/communicative' strategy aimed at solving the problem (Hall 2017). However, based on these results alone it could still be argued that dogs may voluntarily give up the task sooner to ask for help, while wolves try to solve the task independently from the human (Udell 2015; Marshall-Pescini et al. 2017).

Another problem with the task that has not been considered so far is in the procedure itself: in the majority of studies the experimenter manipulates the apparatus, refilling it with the food and presenting the possible trials consecutively one after the other, ending with the impossible trial (but see Persson et al. 2015; Brodd 2014). This procedure might influence subjects' perception of the experimenter's role, leading the dogs to look back at the experimenter just because they associate the experimenter with refilling the empty apparatus with food (Horn et al. 2009). Moreover, in some studies, subjects were kept on the leash while tested and the coercion to face the trials might have induced subjects' looking back at the handler (Smith and Litchfield 2013).

The aim of the current study was to test if the looking back behaviour in an impossible task represents a social problem-solving strategy and if experience with human helping affects the occurrence of this behaviour. We used a modified version of the impossible task, in which the subjects simultaneously faced three possible and one impossible apparatuses, but never observed a person interacting with the apparatus and handling the rewards. Furthermore, the subjects were tested in 4 different conditions (one social condition and three control conditions): social condition (the experimenter was present); asocial condition (the subject was alone); 'dummy' human condition (a cardboard shaped as a human and with a human painted on it was present); object condition (a non-human-shaped cardboard was present). Furthermore, we compared two populations of dogs differing in their experiences with humans: pet dogs (Pd), which have ample experience of human's help, and a free-ranging dog (FRd) population, which have no experience of humans helping but are well socialized to humans and are likely to have associated humans with food, given their daily experiences. Indeed, our study population of free-ranging dogs consists of scavengers whose main source of food is represented by human waste and that predominately obtain food autonomously. Although they are occasionally directly fed by the human population, in two 6-month-long field seasons we never observed any form of 'helping' whereby a person would aid a dog in obtaining food. The closest observation of this type of interaction occurred on only a few occasions, in which we observed dogs obtaining food from a man who was rummaging in a bin (inaccessible to dogs) and accidentally dropped some food, which the dogs quickly obtained.

Our predictions (see Table 1) are based on the main hypotheses of whether the looking back functions as a problem-solving strategy: 1. Looking back is an acquired problem-solving strategy, which might be either favoured by an effect of domestication on dogs' overall tendency to look at the humans (1a) or only be determined by subjects' experience (1b). 2. Alternatively, looking back behaviour is either a consequence of a reduced persistence resulting in dogs ceasing the interaction with an apparatus and then looking at the most salient stimulus in the environment – usually the human (2a) or dogs looking at the human because of selection for this behaviour, but it does not function as a problem-solving strategy, but rather occurs in all situations (2b). Aside from the usual behavioural measures (persistence in manipulating the task and latency, frequency and duration of looking behaviour towards the human), we also analysed the dog's tail position and wagging behaviour. Since the behaviour of free-ranging dogs towards people can vary widely across populations, we used tail-wagging as a proxy for positive arousal and assessed it in both the pet and free-ranging population.

	Predictions		
	Persistence*	Latency and frequency of looking back when manipulating the impossible bowl	Overall duration of looking back
1. Looking back is a problem-solving strategy			
1a. Domestication has selected in dogs the tendency to look at the human, which favoured the development of looking back as a problem-solving strategy.	Pd should be less persistent in the social condition than in the control conditions and less persistent than FRd in the social condition.	All subjects should look back sooner and more frequently in the social condition than in the control conditions but Pd should look back more frequently after attempting the impossible bowl than the possible bowls.	All subjects should look longer at the human than at the objects, but Pd should look longer at the human than FRd.
1b. Domestication did not have a selective effect on dogs' tendency to look at the human but looking back represents an acquired problem-solving strategy	Pd should be less persistent in the social condition than in the control conditions and less persistent than FRd in the social condition	Pd should look back sooner and more frequently in the social condition than in the control conditions and more frequently after attempting the impossible bowl than the possible bowls. FRd should look back with similar latency and frequency in all conditions.	Pd should look longer at the human than at the objects and should look longer at the human than do FRd. FRd may look longer at the human than at the object due to the higher saliency of the human or they may not look at the human at all.
2. Looking back is not a problem-solving strategy			
2a. Looking back is only driven by the dogs giving up and then looking at the most salient object.	Subjects should be equally persistent in all conditions.	Subjects should look back with similar latency and frequency in all conditions.	Subjects should look longer at the human than at the objects and longer at the human shape than at the cardboard. Pd should look longer at the experimenter than FRd due to their stronger relationship with the humans.
	No differences between pet dogs and free-ranging dogs.		
2b. Domestication has selected in dogs the tendency to look at the human face independently of the situation.	Subjects should be equally persistent in all conditions.	Subjects should look with a shorter latency and more frequently at the human than at the objects but with similar frequency after attempting the impossible bowl or the possible ones.	Subjects should look longer at the human than at the objects and longer at the human shape than at the cardboard.
	Overall no differences between pet dogs and free-ranging dogs.		

Table 1. List of the hypotheses and predictions. *Persistence refers to the total duration of interaction with the impossible bowl. Pd: Pet dogs; FRd: free-ranging dogs.

Materials and methods

Ethical statement

Ethical approval for this study was obtained from the ‘Ethik und Tierschutzkommission’ of the University of Veterinary Medicine Vienna (Protocol number ETK-16/09/2017, ETK-20/09/2017). Informed consent was obtained by all owners of the pet dogs. The authorization to test the free-ranging dogs was provided by the municipality of Taghazout (Morocco).

Subjects

Pet dogs (Pd). Mixed-breed pet dogs were tested in private homes in Austria. The subjects were recruited from both the Clever Dog Lab database and via social media. A total of 20 pet dogs were tested (13 F, 7 M; mean age in years: 6.3 ± 0.6 SE).

Free-ranging dogs (FRd). Free-ranging dogs were tested in their natural environment in the municipality of Taghazout, Agadir, Morocco. The experimenters (ML, LD and RM) travelled by car to look for solitary dogs (solitary dogs were chosen to avoid interference by conspecifics). Only adult dogs (appearing to be over 1 year of age) were tested. A total of 62 dogs performed at least one test condition. A total of 31 dogs were excluded from the analyses because other dogs interfered during the test. Hence, a total of 31 free-ranging dogs (12 F, 19 M) were included in the analyses. The tested free-ranging dogs were village-dogs living around human settlements. They were well socialized with humans and had daily experience of humans near their food sources (mainly garbage). Many of them also experienced receiving food directly from humans. However, while the dogs might relate humans to food, they did not receive help from humans in obtaining food.

Apparatus.

The apparatus consisted of a wooden board (length: 1m, width: 0.5m) with four overturned transparent and perforated containers baited with three types of food simultaneously (dry food, sausage and cheese). Three out of the four containers could be moved (possible bowls), whereas the fourth one was attached to the board (impossible bowl). To avoid habituation to the apparatus, we used different shapes of containers for each condition (bottom of a rigid plastic bottle, top of a rigid plastic bottle, or Tupperware box) that were counterbalanced across dogs and conditions (e.g. a subject experienced the Tupperware box as the container in condition 1, and the rigid plastic bottle top as the container in condition 2, whereas another subject might have experienced the rigid plastic bottle bottom in their condition 1 etc.). The objects were chosen to be at least somewhat familiar to the free-ranging dogs.

Testing Procedure

All pet dogs were tested in all four test conditions: 1. social; 2. dummy; 3. object; 4. alone (80 tests in total with Pd). 14 of the free-ranging dogs were tested in the social and alone conditions, while 17 naïve dogs were tested only in the 'dummy' human condition) (45 tests in total with FRd). Depending on the test condition (social, dummy, object), the experimenter, a 'dummy' human (Han Solo figure, width: 59cm, height: 186cm) or a 'dummy' object (width: 64cm, height: 188cm) were standing at 1.5 meters behind the apparatus. Both the objects and the experimenter were unknown to the dogs (see Fig. 1). Where we were able to test the same dogs twice the conditions were counterbalanced across dogs.

Fig. 1 The four conditions presented to the subjects: social (a human present); dummy (a dummy human present); object (a big cardboard present); alone (the dog is alone). Three pictures of free-ranging dogs and one of a pet dog are shown.

Pet dogs (Pd). Subjects were tested in their owner's homes in Vienna. The animals were initially moved to a different room before the apparatus was placed in the testing room. Once the apparatus, cameras and where applicable, the human, the human shaped cardboard and the object were in place, the dog was led into the room. For the social condition, the experimenter stood at a distance of 1.5 meters from the apparatus looking at her phone during the entire test, while the owner was waiting in a separate room. For the other conditions, both the owner and the experimenter left the house after giving a 'goodbye' signal to the dog according to the usual routine of the specific dog-human dyad. . All tests were recorded using two cameras with one camera being remotely controlled to observe the subject in the three conditions in which it was left alone in the room.

Free-ranging dogs (FRd). Free-ranging dogs were tested in the streets and on the beaches of Taghazout. Once a subject was located alone, the experimenter placed the apparatus on the ground, taking care not to be seen by the subject. The experimenter then stood at 1.5 meters behind/next to the apparatus (for the social condition) or hid in the car (control conditions). A second experimenter went to the dog, petted it for a few seconds and then walked towards the apparatus making sure that the dog followed. The experimenter did not show the apparatus to the dog, but simply walked past it and then got into the car. The test started when the dog approached the apparatus. All tests were filmed from the car or from the experimenter standing in front the apparatus (social condition).

The tests started when the dog approached the apparatus (i.e. when they were within 10 cm of the apparatus) and ended if the subject stopped interacting with the apparatus (sniffing it or manipulating it) for 5 minutes. Thus, the whole test duration was not fixed but determined by the behaviour of the subject (Online Resource 2). We tested pet dogs and free-ranging dogs in different environments (indoor and outdoor), because the common and most important feature was that both groups were tested in their most familiar environment, where it was assumed they would feel most comfortable.

Analyses

All the videos were coded using the software Solomon coder (developed by András Péter, Dept. of Ethology, Budapest, www.solomoncoder.com). See Table 2 for definitions of the coded behaviours.

Persistence	The subject sniffs and/or manipulates, either with the paw or the nose, the impossible bowl (duration*).
Looking back	The subject turns/lifts its head towards any part of the experimenter's body, the 'dummy' human or the object (duration*, latency**, frequency***).
Looking up	The subject raises its head up from the ground soon after (max 2 sec) interacting with the bowl (frequency).
Emotional arousal	Tail wagging: the subject moves rapidly the tail from side to side. The tail may be perpendicular to or below the plane of the back (duration*).

Table 2 Detailed description of the coded behaviours. * The duration of persistence, looking back and tail wagging is collected for the whole test duration. The latency of looking back is the interval of time that elapses between the first time that the subject sniffs or touches the impossible bowl - once all the reachable food is eaten - to the first time the subject looks back. *** The frequency of looking back is the number of times the subject looks back after interacting with the impossible or the possible bowls (it is counted only if it occurs within a two second frame from the end of the interaction with the bowl).**

Inter-observer reliability was carried out between three observers each coding 20% of the video data (Intra-class correlation coefficient: persistence ICC = 0.99, look back frequency ICC = 0.81, look back duration ICC = 0.82, look back latency ICC = 0.96).

For statistical analyses, we used Generalized Linear Models (GLM) and Generalized Linear Mixed Models (GLMM). All models were fitted in R (version 3.6.1; R Core Team 2019) using the functions lm (R package stats), lmer (R package lme4) (Bates et al. 2014), glmmTMB (Brooks et al. 2017) and coxme (Terry M. Therneau 2019). Model residuals of Gaussian models were tested for normality and homogeneity using diagnostic plots. Where the initial model did not fit the assumption of normally distributed residuals (models P1, P2, P3, L2, L3) we applied the Box-Cox transformation method, using the package MASS (Venables et al. 2002), and the appropriate transformation was applied to the response variable to achieve normally distributed residuals (log-transformation for models P1, P2, P3, L3 and sqrt-transformation for model L2) (Vernables and Ripley 2002). However, we decided to show in the graphs non-transformed data. Collinearity of predictors, assessed applying the function vif of the R package car (Fox et al. 2012), appeared not to be an issue (Quinn and Keough 2002). Overdispersion appeared not to be an issue (range of dispersion parameters 0.19 – 1.17) except for models DL2, DL3, W2, W3 where we applied a function kindly provided by Roger Mundry to correct SE, z-, and P-values for individual predictors. We assessed model stability on the level of the estimated coefficients and standard deviations by excluding the levels of the random effects one at a time (Nieuwenhuis et al. 2012). Overall, all models except model-F1, model-F2 and model-F4 were of moderate or good stability (Online Resource 1). For models including more than one predictors, P values for the individual effects were based on likelihood ratio tests comparing the full model with the respective reduced models lacking the model predictors (R function 'anova') (Barr 2013).

Results were supplemented with Bayes Factors, which were computed with the BayesFactor package (Morey and Rouder 2018) using the functions anovaBF and lmBF. For models DL1, DL2, DL3, W1, W2, W3 Bayes Factors were manually calculated using the BIC approximation (Wagenmakers 2007). Whenever non-significant results were found using frequentist inference statistics, the null-hypothesis cannot be rejected. Bayesian statistics allow a determination of whether the data provide stronger evidence for H1 or the null-hypothesis (H0). The value of the Bayes factor (BF) indicates the number of times the data are more likely under the H1 hypothesis than under the H0 null-hypothesis. A BF higher than 1 gives stronger support to the H1 hypothesis than the H0 hypothesis, while a BF smaller than 1 is in support of the H0 hypothesis rather than the H1 hypothesis. Conventionally, a BF > 3 can be interpreted as substantial evidence, whereas a BF > 10 is considered strong evidence (Rouder et al. 2018; Lee and Wagenmakers 2014). Plots were created in R using the package ggplot2 (Wickham 2009).

Persistence. The subjects that did not interact with the impossible bowl (Pd: object 1; FRd: social 1, alone 1) were excluded from the analyses of persistence, as persistence refers specifically to the duration of interacting with the impossible bowl. Two Generalized Linear Mixed Models (model-P1 for Pd and model-P2 for FRd) were run with persistence as the response variable, test order and condition (social, alone, object, dummy for Pd; social and alone for FRd) as explanatory factors and subject ID as random factor. To investigate differences in persistence between Pd and FRd in the presence of the human experimenter (social condition), a linear model (model-P3) was run with persistence as the response variable and group (Pd, FRd) as explanatory factor. The null models lacked the predictor condition for the comparison with model-P1 and model-P2. We calculated Bayes factors for condition in model-P1 and model-P2 and for group in model-P3.

Latency of looking back. In these analyses we considered the latency to look back after attempting the impossible bowl once all the reachable food was eaten (see Table 2). The subjects that did not interact with the impossible bowl after the food was eaten were excluded from these analyses (1 Pd, 5 FRd). To investigate the differences in the latency of looking back between conditions (social, dummy and object) in Pd, we ran a Cox mixed-effects model (model-L1). A survival response variable was constructed using the Surv function (Therneau 2015), considering the latency to look back (or termination of the experiment) and whether this event occurred or not. Subject was included in the model as a random factor. Given that in the social condition all Pd looked back, to ensure model convergence we considered one subject in the social condition (with the longest latency to look back) as not having performed the behaviour. All FRd that finished the food and attempted the impossible bowl (10 social, 9 dummy) looked back at the experimenter or at the dummy human, except one, which was excluded from the next analysis. To investigate the differences, in the latency to look back, between conditions in FRd, we ran a linear model (model-L2) with latency to look back as the response variable and condition (social, dummy) as the explanatory factor. To investigate differences in the latency to look back between Pd and FRd in the presence of the human experimenter, we ran a linear model (model-L3) with latency to look back as the response variable and group (Pd, FRd) as the explanatory factor. We calculated Bayes factors for condition in model-L1 and model-L2 and for group in model-L3, excluding the subjects that did not look back.

Effect of condition and group on the frequency of looking back after attempting the impossible bowl. The subjects that never attempted the impossible bowl were exclude from these analyses (Pd: object 1; FRd: dummy 3). To investigate the differences in the frequencies of looking back after attempting the impossible bowl between conditions in Pd and FRd, a Generalized Linear Mixed Model for Pd (model-F1) and a Generalized Linear Model for FRd (model-F2) with a quasibinomial distribution were run with the occurrence of looking back (see Table 2) as the response variable, normalized by the total number of times the subject attempted the impossible bowl, condition (social, dummy, object for Pd; social and dummy for FRd) as the explanatory factor and subject as the random factor (only for model-F2). To investigate the differences in the frequencies of looking back at the experimenter after attempting the impossible bowl between pet dogs and free-ranging dogs, a binomial model with a quasibinomial distribution (model-F3) was run with the occurrence of looking back as the response variable, normalized by the total number of times the subject attempted the impossible bowl, and group as explanatory factor (this analysis was run only for the social condition). The null models lacked the predictor condition for the comparison with model-F1.

Effect of group and the obtainability of food (possible vs. impossible bowl) on the frequency of looking back. These analyses were run on the whole test duration, only for the social condition. We investigated the differences in the frequencies of looking back between Pd and FRd, after attempting either the possible or the impossible bowl. We ran a Generalized Linear Mixed Model (model-F4) with a binomial distribution with the occurrence of looking back (see Table 2) as the response variable, normalized by the total number of times the subject looked up (see Table 2) after attempting the bowl. The group, the attempted bowl (possible or impossible) and their interaction were included as explanatory factors. The null model lacked both predictors.

Duration of looking back and emotional arousal. These analyses were run on the whole test duration. All tested subjects were included in these analyses. To investigate whether the proportion of time individuals looked back or tail wagged at the experimenter differed between conditions, we ran two Generalized Linear Mixed Models for Pd (model-DL1 and model-W1) and two Generalised Linear Models for FRd (model-DL2 and model-W2) with beta error structure and logit link function. We included condition (social, object, dummy for Pd; social, dummy for FRd) as explanatory factor and subject as a random factor (only for model-DL1 and model-W1).

To investigate whether the proportion of time individuals looked back or tail wagged at the experimenter differed between Pd and FRd in the social condition, we ran two Generalised Linear Models (model-DL3 and model-W3) with beta error structure and logit link function. We included group (Pd, FRd) as an explanatory factor. For model-DL3, to account for possible more distractions in FRd than in Pd, which were tested outdoors, the response variable was the total time that the subjects looked at the experimenter divided by the total time the subjects looked up (see Table 2). For all the other models (model-DL1, model-W1, model-DL2, model-W2, model-W3) the response variable was the total time that the subjects looked or tail wagged divided by the total duration of the test.

The null models lacked the predictor condition for the comparison with model-DL1 and model-W1. We calculated Bayes factors for condition in model-DL1, model-W1, model-DL2, model-W2 and for group in model-DL3 and model-W3.

Results

Persistence of manipulating the impossible bowl. Both the mixed model analysis and the Bayes factor analysis indicated that there was no effect of condition on persistence in Pd and FRd and there was no difference in persistence between Pd and FRd in the social condition (see Table 3) (see Fig. 2) (Online Resource 1). (See also Online Resource 3 reporting all raw data and Online Resource 4 reporting a summary of all data used in the analyses).

Differences in persistence*	Model	Comparisons full-null model/ Tests	Bayes Factor (support for H1)	Bayes Factor (support for H0)
Across conditions in Pd	Model-P1	χ^2_3= 4.2, p=0.24	0.14	6.93
Across conditions in FRd	Model-P2	χ^2_1= 0.43, p=0.51	0.38	2.59
Between Pd and FRd (social condition)	Model-P3	t=0.34, p=0.73	0.35	2.89

Table 3 Differences in persistence, summary of statistics. * Pd: pet dogs, FRd: free-ranging dogs.

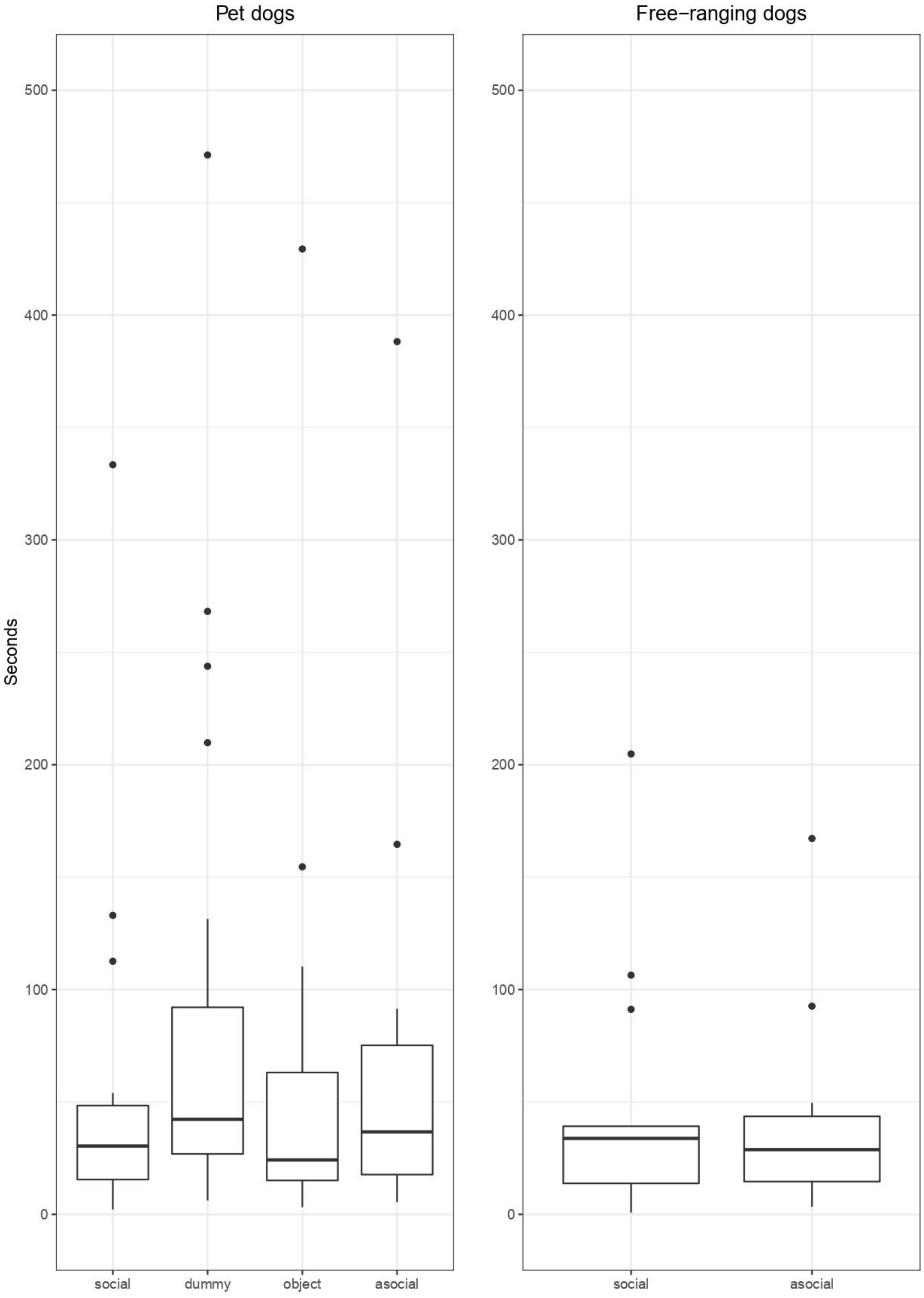

Fig. 2 Persistence of interacting with the impossible bowl for pet dogs (N=20) and free-ranging dogs (N=14). One pet dog tested in the asocial condition, with a value of 806.2 sec, is not shown in the graph.

Latency to look back after trying to solve the impossible bowl. Both the mixed model analysis and the Bayes factor analysis indicated that there was no effect of condition on latency to look back in both Pd and FRd and there was no difference in latency to look back between Pd and FRd in the social condition (see Table 4) (see Fig. 3) (Online Resource 1).

Differences in latency*	Model	Comparisons full-null model/ Tests	Bayes Factor (support for H1)	Bayes Factor (support for H0)
Across conditions in Pd	Model-L1	χ^2_2= 2.98, p=0.22	0.18	5.42
Across conditions in FRd	Model-L2	t=0.01, p=0.93	0.41	2.42
Between Pd and FRd (social condition)	Model-L3	t=-0.32, p=0.75	0.37	2.67

Table 4 Differences in latency, summary of statistics. * Pd: pet dogs, FRd: free-ranging dogs.

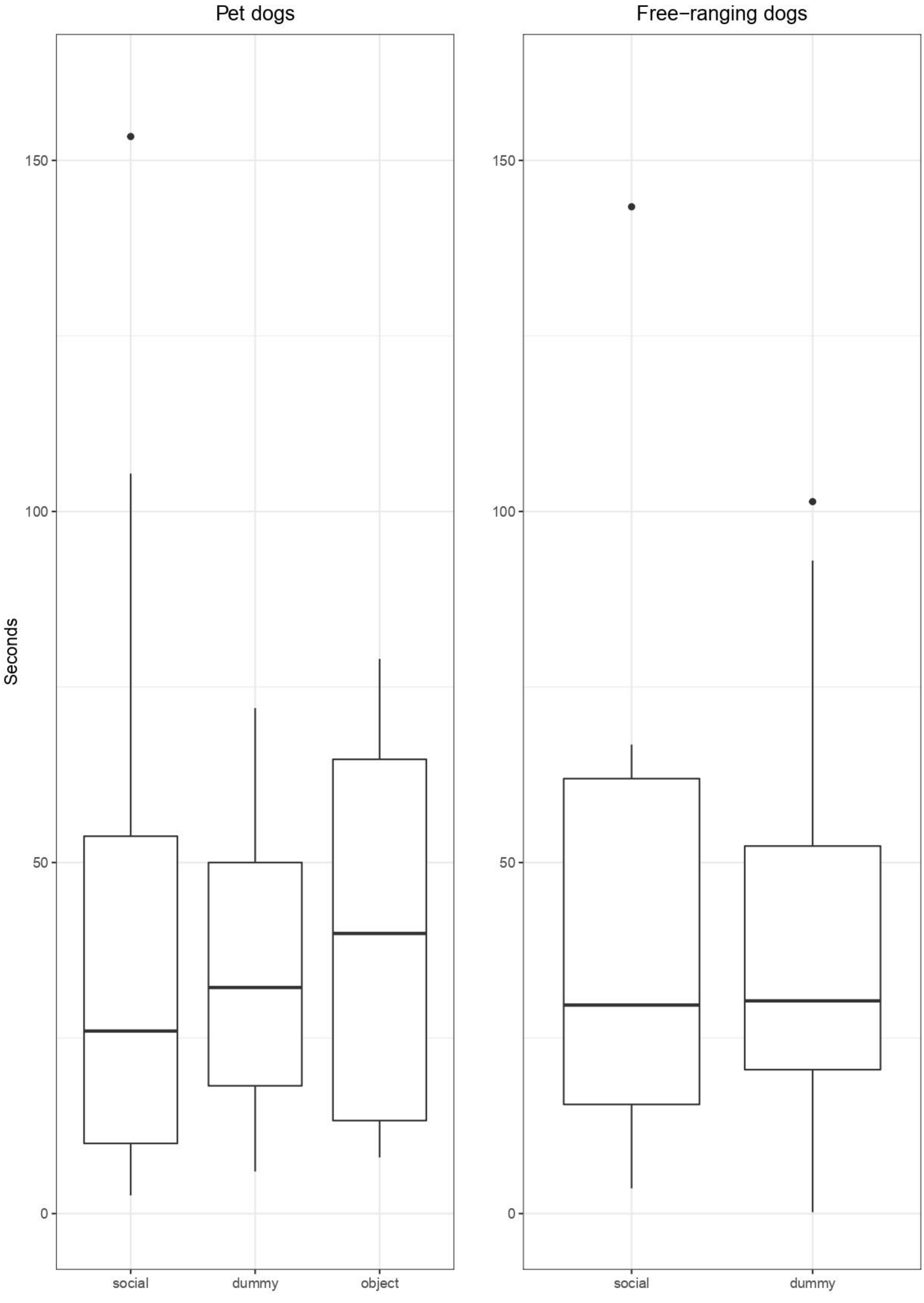

Fig. 3 Latency to look back after interacting with the impossible bowl for pet dogs (N=20) and free-ranging dogs (N=26). One pet dog tested in the dummy condition, with a value of 332.2, is not shown in the graph.

Frequency of looking back. We found that the frequency of looking back after attempting the impossible bowl differed between conditions in Pd (model-F1) (comparisons between the full and the null model, likelihood ratio test: χ^2_2=15.5, p<0.001). Pd looked more frequently at the human than at the 'dummy' human and object (social-object: z=3.25, p=0.001; social-dummy: z=-2.66, p=0.007), with no difference between the frequency of looking at the 'dummy' human and at the object (dummy-object: z=1.2, p=0.23) (Online Resource 1). In FRd, there were no difference between conditions (social and dummy) in the frequency of looking back after attempting the impossible bowl (model-F2) (z=0.32, p=0.74) (Online Resource 1). Furthermore, there was no difference in the frequency of looking back at the experimenter after attempting the impossible bowl between Pd and FRd (model-F3) (z=-0.5, p=0.56) (Online Resource 1). Finally, considering only the social condition in which the experimenter was present, Pd and FRd did not differ in the frequency of looking back when attempting either the possible or the impossible bowl (model-F4) (comparisons between the full and the null model, likelihood ratio test: χ^2_2=0.87, p=0.64) (Online Resource 1).

Duration of looking back over the entire test. We found that the duration of looking back differed between the three conditions in Pd (see Table 5). Pd looked longer at the human than at the 'dummy' human and object (social-object: z=4.8, p<0.0001; social-dummy: z=3.4, p<0.001) and longer at the 'dummy' human than at the object (dummy-object: z=-2.39, p=0.01). In contrast, no difference in the duration of looking back was found between the social and the dummy condition in FRd (see Table 5) (see Fig. 4). We found that Pd tended to look back at the experimenter for longer than did FRd (see Table 5) (see Fig. 5) (Online Resource 1).

Differences in duration of looking back*	Model	Comparisons full-null model/ Tests	Bayes Factor (support for H1)	Bayes Factor (support for H0)
Across conditions in Pd	Model-DL1	χ^2_2= 21.75, p<0.001	897.88	0.001
Across conditions in FRd	Model-DL2	z= -0.8, p=0.42	0.34	2.87
Between Pd and FRd (social condition)	Model-DL3	z=1.87, p=0.06	2.19	0.45

Table 5 Differences in the overall duration of looking back, summary of statistics. * Pd: pet dogs, FRd: free-ranging dogs.

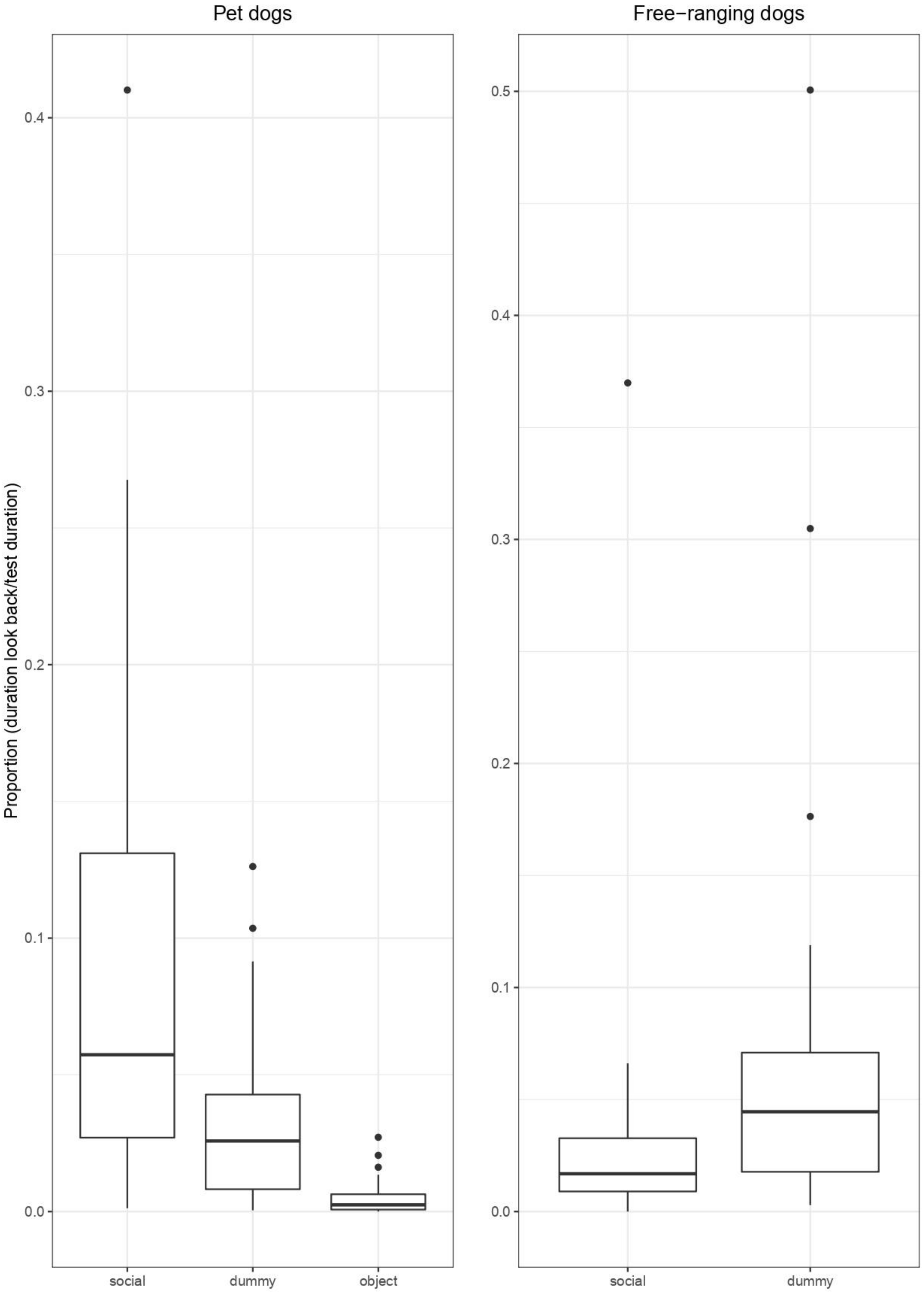

Fig. 4 Proportion of time subjects looked back over the entire test in 3 test conditions (object, dummy, social) for pet dogs (N=20) and in the 2 test conditions (dummy, social) for free-ranging dogs (N=31).

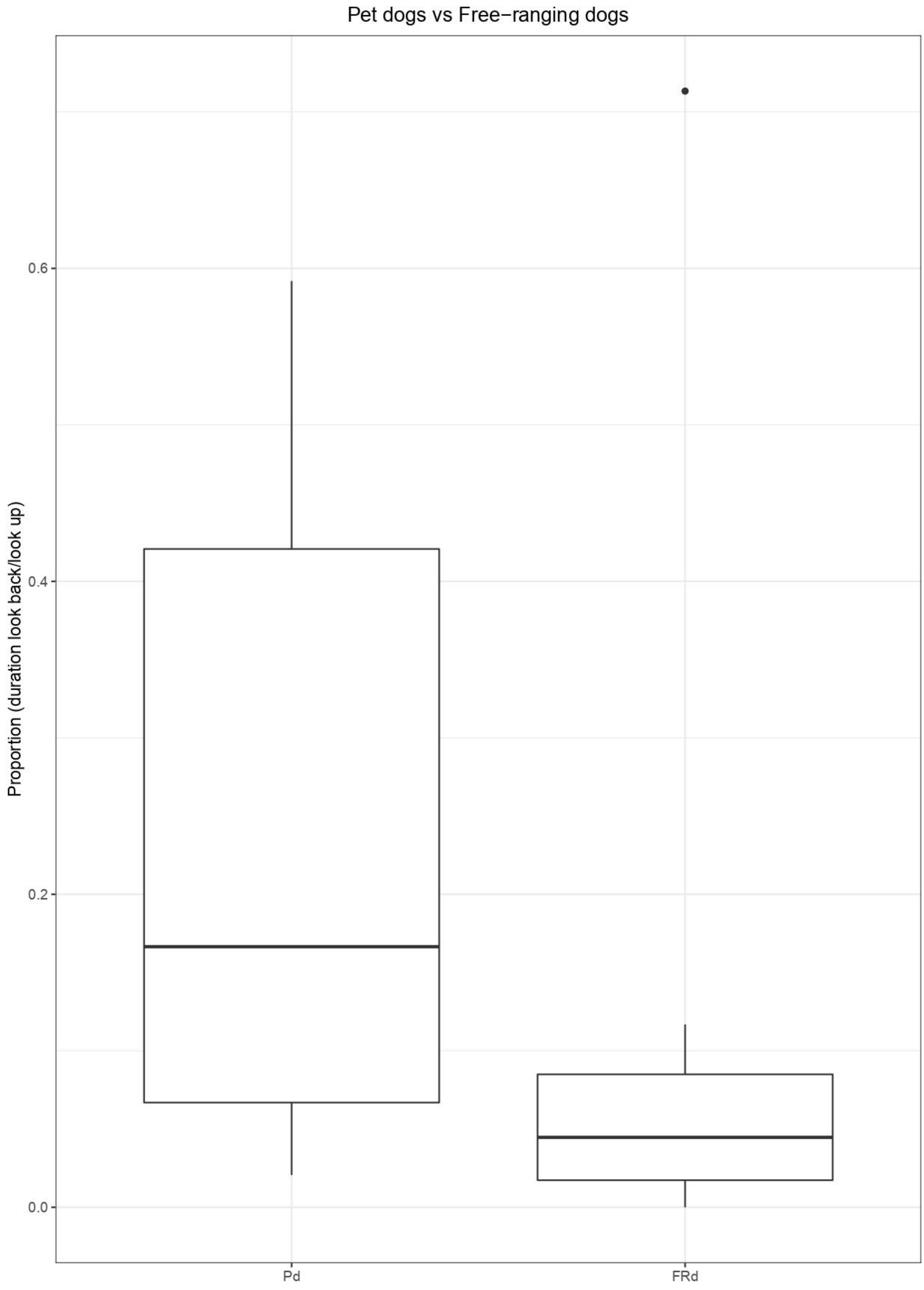

Fig. 5 Time spent looking back as a proportion of time spent looking up (in the social condition) for pet dogs (N=19) and free-ranging dogs (N=14).

Duration of tail wagging during the entire test. The duration of tail wagging was positively correlated with the duration of looking back behaviour for both groups (Pearson's correlation: Pd Cor.coeff=0.83; p<0.0001; FRd Cor.coeff=0.78; p<0.0001). We found that the duration of tail wagging differed between the three conditions in Pd (see Table 6). Pd performed tail wagging for longer in the social condition than in the 'dummy' human condition and in the object condition (social-dummy: z=3.68, p<0.0001; social-object: z=4.14, p<0.0001) and for longer in the 'dummy' human condition than the object condition (dummy-object: z=2.39, p=0.02) (see Table 6). Overall, there were no differences in the duration of tail wagging between the social and dummy condition in FRd (see Table 6). There were no differences between Pd and FRd in the duration of tail wagging in the social condition (see Table 6) (see Fig. 6) (Online Resource 1).

Differences in duration of tail wagging*	Model	Comparisons full-null model, likelihood ratio test	Bayes Factor (support for H1)	Bayes Factor (support for H0)
Across conditions in Pd	Model-W1	χ^2_2= 10.15, p=0.006	2.7	0.37
Across conditions in FRd	Model-W2	z= -0.03, p=0.97	0.18	5.56
Between Pd and FRd (social condition)	Model-W3	z=0.97, p=0.32	0.44	2.23

Table 6 Differences in duration of tail wagging, summary of statistics. * Pd: pet dogs, FRd: free-ranging dogs.

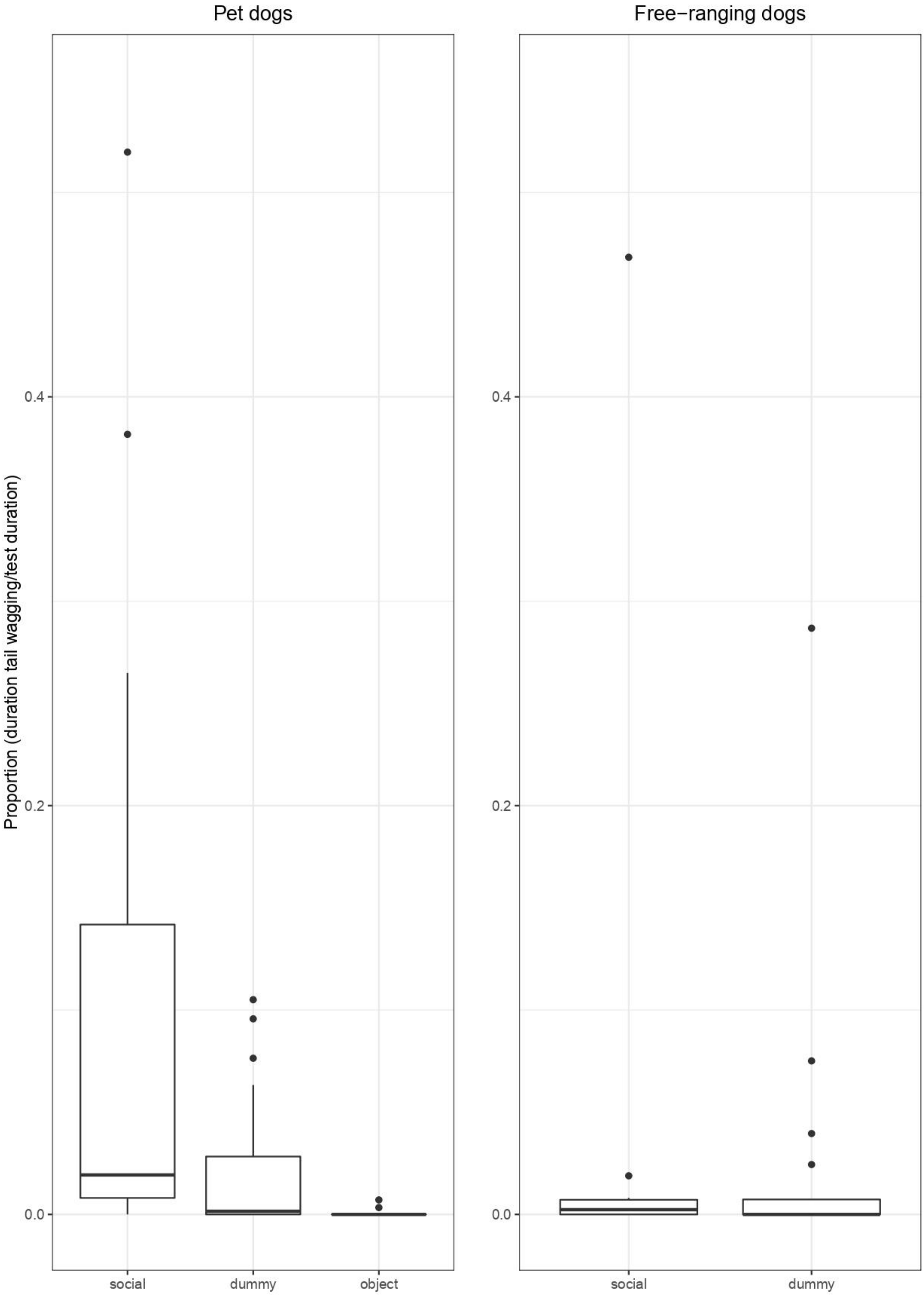

Fig. 6 Proportion of time subjects wagged their tails over the entire test in 3 test conditions (dummy, object, social) for pet dogs (N=20) and in the 2 test conditions (dummy, social) for free-ranging dogs (N=31).

Discussion

Overall, the results indicate that the looking back behaviour in an impossible task is not a problem-solving strategy (i.e. the dogs do not look back to ask for help) but is rather a consequence of giving up and looking at the most salient object in the environment (hypothesis 2a).

If looking back was a social strategy, then dogs should have tried to solve the task by themselves for less time when in the presence of a human that could help them, than in the absence of a human. But this was not the case. Furthermore, if looking back was a social strategy, then pet dogs, used to humans helping them in various ways, should have shown this pattern of results more strongly than free-ranging dogs that have never experienced human 'help'. Contrary to this, we found that pet dogs and free-ranging dogs had a similar persistence in the social condition and non-social conditions and we found no difference between free-ranging and pet dogs in their latency to look back at the human. Interestingly, dogs in this study showed a similar persistence (social condition: Pd mean 53.1 s; FRd mean 42.74 s) to different groups of dogs from a previous study (i.e. Indian free-ranging dogs: mean 60 s, captive dogs living in packs: mean 46.5 s). This suggests that persistence is rather constant across different dog populations in this test paradigm and independent of the human presence and the subject's past experience (Marshall-Pescini et al. 2017). Furthermore, as suggested by Marshall-Pescini and Rao (Marshall-Pescini et al. 2017), the latency to look back in this testing paradigm seems to be mainly determined by subject's persistence: the animals give up trying to solve the apparatus after a certain amount of time and then look around at the most salient object in their environment - either the experimenter or any other object that stands out. Considering the current results and the suggested link between latency and persistence, observed differences in latency to look back in previous studies (Hori et al. 2013; Passalacqua et al. 2011; Miklósi et al. 2003), might have been determined by differences in persistence between subjects (but see Konno et al. 2016; D'Aniello and Scandurra 2016) as has already been found in dogs and wolves (Rao et al. 2018; Marshall-Pescini et al. 2017). The previous studies mainly focused on latency, rarely analysing persistence which should instead be considered one of the main factors influencing subjects' looking behaviour in similar testing paradigms.

One partial limitation of the study is that whereas pet dogs carried out all test conditions, in free-ranging dogs we were able to re-test only a subsample of dogs. However, it is important to note that the comparison between free-ranging dogs and pet dogs was carried out on this sub-population and only in the social condition, and in both populations the order of presentation was counterbalanced.

Interestingly, a few differences in the looking back behaviour between free-ranging and pet dogs did emerge. Whereas free-ranging dogs looked back as frequently (and for as long) at the human and at the 'dummy' human, pet dogs looked back more frequently (and for longer) at the human than at the control objects. The fact that free-ranging dogs looked for a similar duration at the human and at the 'dummy' human may suggest that free-ranging dogs were a bit fearful of the human shape (a novel object in their environment), or perhaps needed a bit more time to figure out what this stimuli was (video V1). Interestingly, based on their tail-wagging behaviour being of similar duration for both human and dummy-human, it would appear that the dogs, at least to begin with, may have approached the dummy human in a 'social' manner (Quaranta et al. 2007). Pet dogs, on the other hand differentiated more between the social and control stimuli, looking and tail-wagging more towards the experimenter, than the dummy human, while they also looked and tail-wagged more towards the dummy than the cardboard. This gradient is interesting, since it would suggest they at least initially, treated the 'Han Solo' cut-out as more 'human-like' than the cardboard. These results may suggest that pet dogs are in general better at quickly discriminating between humans and other odd objects in their environment than free-ranging dogs. However, they do not support the idea of looking back as a problem solving strategy: if looking back was a problem solving strategy we would have expected pet dogs to look back more often specifically after attempting the impossible bowl (and not when manipulating the possible bowls), but this was not the case.

Finally, we found that in the social condition pet dogs tended to look longer (during the whole test) at the experimenter than did free-ranging dogs. This difference could not be attributed to free-ranging dogs being scared of humans since the tested population had a friendly attitude towards humans (they are not feral dogs that have 'dishabituated' to the presence of humans). These 'village' dog populations are commonly observed all over the world and have already been tested in different cognitive studies investigating dog-human interactions (Bhattacharjee et al. 2017a, 2017b, 2018; Brubaker et al. 2017, 2019; Marshall-Pescini et al. 2017). Rather, we suggest that the greater duration of the looking behaviour in pet dogs, may simply be because they are more attracted to humans, potentially because they form stronger, more long-lasting bonds with humans than the free-ranging dogs in our population and/or because of their long history of associating humans (and potentially looking at humans) with food (Bentosela et al. 2008, 2009; D'Aniello and Scandurra 2016; Hall 2017).

The results of the previous studies on the impossible task also highlight the importance of previous reinforcement history. Trained dogs looked for longer at the human than untrained dogs (Marshall-Pescini et al. 2009; D'Aniello et al. 2015), and dogs trained for 'agility' (i.e. trained to specifically look at the human) looked for longer at the owner than untrained dogs and dogs trained for 'search and rescue' (Marshall-Pescini et al. 2009). Additionally, dogs living in kennels, with limited contact with humans, looked back for a shorter duration than untrained pet dogs (D'Aniello and Scandurra 2016). Finally, older dogs, which indeed have a longer experience of associating food with looking at humans, looked for longer at the human than did younger dogs (Hori et al. 2013; Passalacqua et al. 2011). It is worth noting that in some of these studies the authors expected to find exactly the opposite results: the more experienced the dogs were, the less they should have looked back at the human if asking for help. Overall, pet dogs' experience, whereby looking is likely to be both intentionally and inadvertently reinforced by humans, strongly affects looking patterns in such experimental settings, highlighting the importance of subjects' previous ontogenic background.

In conclusion, our results show that dogs' looking back behaviour in an impossible task does not represent a social 'help-seeking' strategy. The latency of looking back is rather linked to the subject's persistence, whereas the frequency and duration of looking back are rather linked to the salience of the stimuli presented, and potentially to the past reinforcement history of the study population. This behaviour has been widely over-interpreted and more caution should be exercised in future studies.

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SUPPLEMENTARY MATERIALS

Online resource 1.

The following are reported for all models: the estimates, together with standard errors, tests, confidence limits, as well as minimum and maximum of estimates derived after excluding individuals one at a time (model stability).

Table 1. Results of the model-P1: differences in persistence across conditions in pet dogs.

term	Estimate	SE	χ^2	p	lower CI	upper CI	min	max
(Intercept)	4.018	0.358	(1)	(1)	-0.366	0.913	3.824	4.241
condition (dummy) (2)	0.273	0.321	(1)	(1)	-0.978	0.325	-0.137	-0.395
condition (object) (2)	-0.328	0.327	(1)	(1)	-0.952	0.349	-0.481	-0.162
condition (social) (2)	-0.303	0.326	(1)	(1)	-0.342	0.079	-0.420	-0.097
test	-0.131	0.106	1.51	0.218	-0.366	0.913	-0.177	-0.093

(1) not indicated because of having a very limited interpretation

(2) condition ‘alone’ is the reference category

Table 2. Results of the model-P2: differences in persistence across conditions in free-ranging dogs.

term	Estimate	SE	χ^2	p	lower CI	upper CI	min	max
(Intercept)	4.401	0.711	(1)	(1)	2.941	5.866	4.069	4.889
condition (social) (2)	0.302	0.459	0.430	0.512	-0.639	1.255	0.073	0.523
test	-0.871	0.461	3.284	0.069	-1.824	0.077	-1.077	-0.644

(1) not indicated because of having a very limited interpretation

(2) condition ‘alone’ is the reference category

Table 3. Results of the model-P3: differences in persistence between pet dogs and free-ranging dogs in the social condition .

term	Estimate	SE	t	p	lower CI	upper CI	min	max
(Intercept)	3.233	0.339	(1)	(1)	2.538	3.927	2.945	3.406
group (pet dogs) (2)	0.151	0.441	0.342	0.735	- 0.750	1.052	-0.023	0.439

(1) not indicated because of having a very limited interpretation

(2) group ‘free-ranging dogs’ is the reference category

Table 4. Results of the model-L1: differences in latency to look back across conditions in pet dogs.

term	Estimate	SE	z	p	lower CI	upper CI
condition (dummy) (1)	-0.737	0.890	-0.83	0.410	-26.796	1.398
condition (social) (1)	-1.928	1.161	-1.66	0.097	-22.969	-0.989

(1) condition ‘object’ is the reference category

Table 5. Results of the model-L2: differences in latency to look back across conditions in free-ranging dogs.

term	Estimate	SE	t	p	lower CI	upper CI	min	max
(Intercept)	5.729	1.088	(1)	(1)	3.422	8.036	4.975	6.349
condition (social) (2)	0.133	1.459	0.091	0.929	-2.962	3.227	-0.487	0.887

(1) not indicated because of having a very limited interpretation

(2) condition ‘dummy’ is the reference category

Table 6. Results of the model-L3: differences in latency to look back between pet dogs and free-ranging dogs in the social condition.

term	Estimate	SE	t	p	lower CI	upper CI	min	max
(Intercept)	3.272	0.351	(1)	(1)	2.550	3.994	3.051	3.461
group (pet dogs) (2)	- 0.141	0.438	-0.322	0.75	- 1.041	0.759	- 0.329	0.080

(1) not indicated because of having a very limited interpretation

(2) group ‘free-ranging dogs’ is the reference category

Table 7. Results of the model-F1: differences in frequency of looking back across conditions in pet dogs.

term	Estimate	SE	z	p	lower CI	upper CI	min	max
(Intercept)	-3.146	0.466	(1)	(1)	-4.205	-2.335	-4.014	-2.959
condition(dummy) (2)	0.658	0.548	1.201(3)	0.229(3)	-0.363	1.835	0.405	1.565
condition (social) (2)	1.643	0.506	3.250(3)	0.001(3)	0.727	2.755	1.477	2.588

(1) not indicated because of having a very limited interpretation

(2) condition ‘object’ is the reference category

Table 8. Results of the model-F2: differences in frequency of looking back across conditions in free-ranging dogs.

term	Estimate	SE	z	p	lower CI	upper CI	min	max
(Intercept)	-1.408	0.336	(1)	(1)	-2.119	-0.787	-1.663	-1.293
condition (social) (2)	0.146	0.446	0.329	0.742	-0.722	1.039	-0.018	0.401

(1) not indicated because of having a very limited interpretation

(2) condition ‘dummy’ is the reference category

Table 9. Results of the model-F3: differences in frequency of looking back at the human between pet dogs and free-ranging dogs.

term	Estimate	SE	z	p	lower CI	upper CI	min	max
(Intercept)	-1.262	0.292	(1)	(1)	- 1.871	- 0.715	- 1.427	- 1.156
group (pet dogs) (2)	- 0.209	0.359	- 0.583	0.56	- 0.904	0.514	- 0.353	- 0.045

(1) not indicated because of having a very limited interpretation

(2) group ‘free-ranging dogs’ is the reference category

Table 10. Results of the model-F4: differences between pet dogs and free-ranging dogs in frequency of looking back at the human after attempting the possible or the impossible bowls.

term	Estimate	SE	z	p	lower CI	upper CI	min	max
(Intercept)	0.449	0.356	(1)	(1)	-0.215	1.218	0.294	0.608
group (pet dogs) (2)	0.187	0.449	0.416	0.678	-0.765	1.105	-0.013	0.482
poss-imp	-0.379	0.494	- 0.767	0.443	-1.411	0.668	-0.546	-0.085

(1) not indicated because of having a very limited interpretation

(2) group ‘free-ranging dogs’ is the reference category

Table 11. Results of the model-DL1: differences in duration of looking back across conditions in pet dogs.

term	Estimate	SE	z	p	lower CI	upper CI	min	max
(Intercept)	-3.116	0.215	(1)	(1)	- 3.536	- 2.695	- 3.296	- 3.049
condition (object) (2)	- 0.615	0.257	- 2.395	0.017	- 1.118	- 0.112	- 0.697	- 0.534
condition (social) (2)	0.800	0.235	3.404	<0.001	0.339	1.261	0.712	1.022

(1) not indicated because of having a very limited interpretation

(2) condition ‘dummy’ is the reference category

Table 12. Results of the model-DL2: differences in duration of looking back across conditions in free-ranging dogs.

term	Estimate	SE	z	p	lower CI	upper CI	min	max
(Intercept)	-2.196	0.304	(1)	(1)	-2.614	-1.779	-2.447	-2.142
condition (social) (2)	-0.346	0.430	-0.805	0.421	-0.936	0.244	-0.499	-0.268

(1) not indicated because of having a very limited interpretation

(2) condition 'dummy' is the reference category

Table 13. Results of the model-DL3: differences between pet dogs and free-ranging dogs in duration of looking back at the experimenter.

term	Estimate	SE	z	p	lower CI	upper CI	min	max
(Intercept)	-1.885	0.279	(1)	(1)	-2.432	-1.339	-2.176	-1.821
group (pet dogs) (2)	0.744	0.396	1.876	0.06	0.104	1.384	0.681	0.962

(1) not indicated because of having a very limited interpretation

(2) group 'free-ranging dogs' is the reference category

Table 14. Results of the model-W1: differences in duration of tail wagging across conditions in pet dogs.

Term	Estimate	SE	z	p	lower CI	upper CI	min	max
(Intercept)	-3.576	0.343	(1)	(1)	- 4.249	- 2.903	- 3.852	- 3.127
condition (object) (2)	- 0.723	0.308	- 2.349	0.018	-1.326	- 0.119	-0.890	- 0.277
condition (social) (2)	1.050	0.285	3.678	<0.001	0.490	1.609	- 0.511	1.328

(1) not indicated because of having a very limited interpretation

(2) condition 'dummy' is the reference category

Table 15. Results of the model-W2: differences in duration of tail wagging across conditions in free-ranging dogs.

Term	Estimate	SE	z	p	lower CI	upper CI	min	max
(Intercept)	-2.923	0.441	(1)	(1)	-3.399	-2.448	-3.279	-2.893
condition (social) (2)	-0.019	0.561	-0.033	0.97	-0.624	0.586	-0.215	0.082

(1) not indicated because of having a very limited interpretation

(2) condition 'dummy' is the reference category

Table 16. Results of the model-W3: differences between pet dogs and free-ranging dogs in duration of tail wagging at the experimenter.

Term	Estimate	SE	z	p	lower CI	upper CI	min	max
(Intercept)	-2.577	0.417	(1)	(1)	-3.159	-1.995	-2.867	-2.546
group (pet dogs) (2)	0.449	0.459	0.977	0.328	-0.193	1.092	0.393	0.617

(1) not indicated because of having a very limited interpretation

(2) group 'free-ranging dogs' is the reference category

Online resource 2.

Additional analyses on test duration.

Since the test ended when the subject did not interact with the apparatus for more than five minutes, the test duration varied across subjects. To investigate differences in test duration between conditions we ran a generalized linear mixed model for Pd and a generalized linear model for FRd with test duration as the response variable, condition (social, dummy, object for Pd; social, dummy for FRd) as the explanatory factor and subject as a random factor (only for Pd). To investigate differences in test duration between Pd and FRd in the social condition we ran a generalized linear model with test duration as the response variable and group (Pd, FRd) as the explanatory factor. All models fitted the assumption of normally distributed residuals and were of moderate or good stability.

Overall there were no differences in the test duration across different conditions in Pd (comparisons between the full and the null model, likelihood ratio test: χ^2_2= 0.83, p=0.66). However, we found that the test duration differed between the two conditions in FRd (t= 2.92, p=0.006), where the social condition lasted significantly longer than the 'dummy' human condition. We found that the social condition tests lasted longer in Pd than in FRd (t=2.64, p=0.013) (Pd: mean 498.16 s, range 305-644.4 s; FRd: mean 411.04 s, range 319-472.6 s).

Following are reported for all models the estimates, together with standard errors, tests, confidence limits, as well as minimum and maximum of estimates derived after excluding individuals one at a time (model stability).

Table 1. Differences in test duration for social, dummy and object conditions in pet dogs.

term	Estimate	SE	χ^2	p	lower CI	upper CI	min	max
(Intercept)	499.44	45.699	(1)	(1)	408.39	590.48	462.87	521.04
condition (object) (2)	-52.020	64.628	(1)	(1)	-180.78	76.738	-96.579	-15.231
condition (social) (2)	-1.277	65.473	(1)	(1)	-131.72	129.16	-24.371	38.809

(1) not indicated because of having a very limited interpretation

(2) condition 'dummy' is the reference category

Table 2. Differences in test duration for social and dummy conditions in pet dogs.

term	Estimate	SE	t	p	lower CI	upper CI	min	max
(Intercept)	288.53	28.16	(1)	(1)	230.93	346.13	106.88	304.16
condition (social) (2)	122.51	41.91	2.92	0.006	36.805	208.22	106.88	134.09

(1) not indicated because of having a very limited interpretation

(2) condition 'dummy' is the reference category

Table 2. Differences in test duration for the social condition between pet dogs and free-ranging dogs.

term	Estimate	SE	t	p	lower CI	upper CI	min	max
(Intercept)	411.04	24.97	(1)	(1)	360.11	461.97	403.96	416.18
group (pet dogs) (2)	87.12	32.91	2.647	0.013	20.004	154.24	76.389	100.03

(1) not indicated because of having a very limited interpretation

(2) group 'free-ranging dogs' is the reference category

Online resource 4.

Summary tables of data used in the analyses.

Group	Condition	Persistence (sec)	Latency of looking back (sec)	Duration of looking back (sec)	Duration of tail wagging (sec)	Test duration (sec)
pet dogs	social	53.1 ± 77.44	38.31 ± 39.81	46.93 ± 47.74	43.27 ± 63.34	498.16 ± 112.04
	dummy	94.91 ± 117.24	49.73 ± 73.33	15.54 ± 21.17	7.83 ± 13.28	499.44 ± 271.5
	object	60 ± 97.65	39.78 ± 27.03	2.37 ± 3.12	0.29 ± 0.939	447.42 ± 209.9
free-ranging dogs	asocial	100.49 ± 186.89	*	*	*	459.52 ± 299.8
	social	48.38 ± 56.2	42.7 ± 42.09	18.58 ± 37.55	14.76 ± 48.94	411.04 ± 58.60

Table 2. Mean and standard deviation of durations, in pet dogs and free-ranging dogs.

Group	Condition	Frequency of looking back imp (1)	Frequency of looking back poss (2)	Frequency of attempting the imp	Frequency of look up poss (2)	Frequency of look up imp (1)
pet dogs	social	1.47 ± 1.26	0.26 ± 0.47	7.89 ± 3.43	0.6 ± 0.63	2.93 ± 1.67
	dummy	0.65 ± 0.74	*	8.65 ± 6.58	*	*
	object	0.26 ± 0.73	*	6.26 ± 4.28	*	*
free-ranging dogs	social	1.07 ± 0.83	0.85 ± 0.77	4.86 ± 3.06	1.57 ± 1.74	3.14 ± 2.21
	dummy	0.78 ± 0.67	*	4 ± 3.23	*	*

Table 3. Mean and standard deviation of frequencies (number of times a behaviour was performed), in pet dogs and free-ranging dogs; imp: impossible bowl, poss: possible bowls. (1) number of times the subjects looked back or looked up after attempting the impossible bowl; (2) number of times the subjects looked back or looked up after attempting the possible bowls (note that looking back in this case is considered only if it happened in the two second period after the subject stopped interacting with the bowl. Additionally, note that after interacting with the possible bowls subjects where busy eating the food on the ground while this did not happen after interacting with the impossible bowl).

4.3 Article 3: The effect of domestication and experience on the social interaction of dogs and wolves with a human companion

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Abstract

The results of current wolf-dog studies on human-directed behaviours seem to suggest that domestication has acted on dogs' general attitudes and not on specific socio-cognitive skills. A recent hypothesis suggests that domestication may have increased dogs' overall sociability (hypersociability hypothesis). The aim of the present study was to test one aspect of the hypersociability hypothesis, whereby dogs should be more interested in social human contact compared to wolves, and to investigate the relative roles of both domestication and experience on the value that dogs attribute to human social contact. We compared equally raised wolves and dogs kept at the Wolf Science Center (WSCw, WSCd) but also dogs with different human socialization experiences i.e. pet dogs and free-ranging dogs. We presented subjects with a simple test, divided in two phases: in the Pre-test phase animals were exposed to two people in succession. One person invited the animal for a social/cuddle session (contact provider) and the other fed the animal (food provider). In the Test phase, animals could choose which of the two persons to approach, when both stood in a neutral posture. We directly compared WSCd with WSCw and free-ranging dogs with pet dogs. We found that in the Pre-test, WSCd and free-ranging dogs spent more time with the contact provider than WSCw and pet dogs, respectively. The results regarding the free-ranging dog and pet dog comparison were surprising, hence we conducted a follow-up testing pet dogs in a familiar, distraction-free area. Free-ranging dogs and this group of pet dogs did not differ in the time spent cuddling. In the test phase, WSCd were more likely than WSCw to approach the two experimenters. However, neither for the WSCd-WSCw comparison nor for the free-ranging dogs-pet dogs comparison, we could find a clear preference for one person over the other. Our findings support the idea that domestication has affected dogs' behaviour in terms of their overall interest in being in proximity with a human partner also in case of dogs with a relatively sparse socialization experience (free-ranging dogs). However, it remains unclear what the driving motivation to interact with the human may be.

Introduction

Based on comparative studies of dogs and wolves (e.g. Frank and Frank, 1982, 1985; Frank et al., 1989; vonHoldt et al., 2017; Range et al., 2019) a number of hypotheses have been proposed regarding the role

The results of current wolf-dog studies on human-directed behaviours seem to suggest that domestication has acted on dogs' general attitudes and not on specific socio-cognitive skills. A recent hypothesis suggests that domestication may have increased dogs' overall sociability (hypersociability hypothesis). The aim of the present study was to test one aspect of the hypersociability hypothesis, whereby dogs should be more interested in social human contact compared to wolves, and to investigate the relative roles of both domestication and experience on the value that dogs attribute to human social contact. We compared equally raised wolves and dogs kept at the Wolf Science Center (WSCw, WSCd) but also dogs with different

human socialization experiences i.e. pet dogs and free-ranging dogs. We presented subjects with a simple test, divided in two phases: in the Pre-test phase animals were exposed to two people in succession. One person invited the animal for a social/cuddle session (contact provider) and the other fed the animal (food provider). In the Test phase, animals could choose which of the two persons to approach, when both stood in a neutral posture. We directly compared WSCd with WSCw and free-ranging dogs with pet dogs. We found that in the Pre-test, WSCd and free-ranging dogs spent more time with the contact provider than WSCw and pet dogs, respectively. The results regarding the free-ranging dog and pet dog comparison were surprising, hence we conducted a follow-up testing pet dogs in a familiar, distraction-free area. Free-ranging dogs and this group of pet dogs did not differ in the time spent cuddling. In the test phase, WSCd were more likely than WSCw to approach the two experimenters. However, neither for the WSCd-WSCw comparison nor for the free-ranging dogs-pet dogs comparison, we could find a clear preference for one person over the other. Our findings support the idea that domestication has affected dogs' behaviour in terms of their overall interest in being in proximity with a human partner also in case of dogs with a relatively sparse socialization experience (free-ranging dogs). However, it remains unclear what the driving motivation to interact with the human may be.

Materials and methods

Ethical statement

Ethical approval for this study was obtained from the 'Ethik und Tierschutzkommission' of the University of Veterinary Medicine of Vienna (Protocol number: ETK-28/07/2017, ETK-05/11/2018, ETK-022/01/2020). Informed consent was obtained by all owners of the pet dogs. The authorization to test the free-ranging dogs was provided by the municipality of Taghazout (Morocco).

Subjects

Similarly raised and kept wolves and dogs (WSCw and WSCd). 16 wolves (6F, 10M; mean age in years: 6.3 ± 3.22 SE) and 13 mixed-breed dogs (6F, 7M: mean age in years: 5.8 ± 1.63 SE) housed at the Wolf Science Center (www.wolfscience.at) were tested. All wolves and dogs live in conspecific packs and are raised and kept in the same way. The animals are trained and participate in behavioural tests on a regular basis (for further information on this population (see (Range and Virányi 2014).

Pet dogs tested in dog areas (PdA). Mixed-breed pet dogs were tested in outdoor areas in Vienna. Subjects were recruited randomly by asking owners walking around with their dogs if they were willing to participate in the study. A total of 53 pet dogs were tested (22 F; 31 M; mean age in years: 4.34 ± 3.3 SE).

Free-ranging dogs (FRd). Free-ranging dogs were tested in their natural environment in the municipality of Taghazout, Agadir, Morocco. The experimenters (ML, LD, KT, LS) travelled by car to look for solitary dogs (solitary dogs were chosen to avoid interference by conspecifics). Only adult dogs (appearing to be over 1 year of age) were tested. Subjects that appeared uncomfortable with being approached (7 dogs) were not tested. A dog was considered uncomfortable if it showed aggressive behaviours toward the handler (i.e. growling, barking and stiff posture) or an avoidance behaviour. A total of 46 dogs were tested (18 F; 28 M). The tested free-ranging dogs were village-dogs living around human settlements and socialized with humans. Despite being socialized with humans and occasionally receiving food by the local people as well as tourists, they are mainly scavengers that feed on garbage and are completely free to move and reproduce.

Follow-up group: Pet dogs tested in a dog day care facility (PdC). Following statistical analyses comparing pet dogs tested in dog areas and free-ranging dogs (see results), an additional group of pet dogs was tested to clarify the obtained results. The group consisted of a total of 31 pet dogs (18 F; 13 M; mean age in years: 4.68 ± 2.94), that regularly frequented an outdoor dog day care facility located in a private garden, which was isolated from possible disturbances. The tests were conducted in this area, which was therefore highly familiar to the dogs.

Testing Procedure

The procedure varied slightly for the different groups according to the specific environments, where the subjects were tested and the characteristics of the group subjects. All tests consisted of a Pre-test phase and a Test phase. In the Pre-test, the subject received either food or social contact from two different experimenters appearing in sequence. In the Test phase, the subject was free to choose between the two of them. We randomized both the order, in which the subject was exposed to the two experimenters providing food or social contact in the Pre-test phase, as well as the locations in which the two experimenters stood (left or right) in the Test phase.

WSCw and WSCd. WSC animals were tested in an outdoor test enclosure at the Wolf Science Center. Before starting the test, the subject was free to explore the enclosure for 10 minutes. However, if after 10 minutes the subject was still moving and sniffing around, we gave it more time prior to starting the test.

Pre-test. The Food Person (FP) entered the area and stood one metre from the entrance. The subject was in the enclosure free to move and the pre-test started once the subject approached the FP (i.e. the subject looked at the experimenter while approaching her in a 4-metre radius). The FP did not call the subject, and once the subject itself approached her, she fed it 5 pieces of dry food (Royal Canin–German Shepherd) within 30 seconds, by dropping dry food on the ground in front of the subject and avoiding eye contact. After 30 seconds the FP left the area and hid out of sight of the subject. The subject remained free to move in the enclosure. Then, the Cuddle Person (CP) entered the area and stood one metre from the entrance. Once the subject approached the CP, she made eye contact, squatted down and if the animal came within reach, petted the subject for 30 seconds speaking nicely with it. After 30 seconds the CP left the enclosure and hid out of sight of the subject. Then, a third experimenter (henceforth referred to as “handler” and positioned 20 metre from the entrance on the opposite side of the testing enclosure) called the subject and fed it with a maximum of 3 pieces of low value dry food (Royal Canin–Medium Adult) once the subject reached her to allow the other persons to enter the test enclosure. The handler was hidden from the subject during the demonstration of the FP and CP. Differently from the test procedure of pet dogs and free-ranging dogs (see below), the handler directed the subject through the fence for safety reasons. Furthermore, to guarantee the animals’ collaboration also in future tests, the subjects were rewarded for coming when called.

Test phase. Once the subject was close to the handler and distracted, both the FP and CP re-entered the enclosure without making eye contact with the subject and stood 2 metre apart, at a distance of 16 metres from the subject. The handler hid once the FP and CP were in the established position. The subject was free to choose to go to either the CP or to the FP. The test started once the subject had seen the experimenters re-entering the enclosure and ended after 1 minute. A fourth experimenter, hidden from the subjects’ sight, recorded the trial durations.

Based on previous studies, we have observed that animals at the WSC (in particular wolves) can become uncomfortable when ignored by the trainers (from whom they expect engagement and/or food). Thus, to ensure both trainers and animals were comfortable with the test procedure, the Test phase lasted the maximum duration of one minute, which was enough time to allow animals to make a clear choice. Additionally, it was not possible to conduct the test with WSC animals with unknown people as was done with pet and free-ranging dogs. Therefore, the experimenters were all people who had a close relationship with the animals, such as trainers or hand raisers. For each animal, we chose two trainers that had a similarly close relationship with the subject. However, to take the possible effect of the relationship of the subject with the trainers into account, each subject was tested twice with the same experimenters alternating their roles as FP and CP. However, the order of entrance and the relative positioning of the two experimenters remained stable across the 2 sessions.

WSC animals were fed the day before testing and did not interact with the experimenters acting as FP or CP during the entire day prior to the test being conducted. We kept the same procedure used with WSC animals for pet dogs (PdA and PdC) with the following differences:

1. Pet dogs were tested in an outdoor fenced area in the absence of other dogs. PdA were tested in three different dog areas, while PdC were tested in a familiar fenced area located inside a private garden. All enclosures had different sizes, but in all tests the distances of the experimenters and owners from the entrance of the fenced area were the same.

2. The owner had the role of the handler and was present during the whole test inside the enclosure 6 metres from the entrance used by the FP and CP. The owner was always faced away from the entrance except when calling the subject at the end of the pre-test. Once the subject reached the owner, h/she turned facing the opposite site of the entrance and the FP and CP entered the enclosure.

3. The test phase lasted 2 minutes.

Analyses

All the videos were coded using the software Solomon coder (developed by András Péter, Dept. of Ethology, Budapest, www.solomoncoder.com). See Table 1 for definitions of the coded behaviours.

Behaviour	**Test Phas**	**Description**
Contact	Pre-test	Occurrence (yes/no) and duration of CP touching/stroking the subject.
Choice	test	The subject touches or approaches to within 20 cm of the experimenter. The first experimenter touched or approached is considered the animal's choice.
Proximity	test	The time the subject spends within a half body-length radius of the experimenter.

TABLE 1. Description of the coded behaviours.

Inter-observer reliability was carried out between three observers each coding 20% of the video data (Intra-class correlation coefficient: proximity ICC=0.97; contact ICC=0.9).

Initial analyses were conducted on WSC animals, free-ranging dogs and pet dogs tested in dog areas (PdA). These analyses were run separately for WSC and non WSC animals, because of the unavoidable procedural differences; for example, the repeated testing at the WSC required different statistical analyses (see below).

To clarify whether the potentially higher distraction and lower familiarity of dog areas affected pet dog's behaviour, we tested a follow-up group of pet dogs in a dog day care facility (PdC), which dogs frequented regularly. We re-ran all the analyses comparing FrD, PdC and PdA, and report them separately in the results section.

Analyses of Pre-test phase: duration of contact with the CP

We first tested whether the proportion of time individuals spent in contact with the CP in the pre-test differed between groups (WSCd vs. WSCw, PdA vs. FRd, respectively). To this end we used a Generalized Linear Mixed Model (GLMM) (Baayen, 2008) with beta error structure and logit link function (McCullagh and Nelder, 1989; Bolker, 2008) for the WSCd-WSCw comparison. We included group (dog or wolf) and the side at which the

CP was presented as fixed effects and individual ID as a random intercepts effect. For the FRd-PdA comparison we used a Generalized Linear Model (GLM) (Baayen, 2008) with beta error structure and logit link function with the same fixed effects but no random effect as each individual in this data set was tested only once. An identical model was used for the additionally analyses comparing FrD, PdC and PdA.

Analyses of the Test phase

To estimate the extent to which the tested groups (WSCd vs. WSCw or PdA vs. FRd) differed with regard to whether they approached (no or yes) either of the two experimenters (CP, FP) in the test phase, we fitted the same two models (a GLMM for WSCd-WSCd comparison and a GLM for PdA-FRd comparison), but this time with binomial error structure and logit link function (McCullagh and Nelder, 1989) as the response was binary. An identical model was used to additionally compare FrD, PdC and PdA.

In two further models we addressed the question whether individuals exhibited preferences for one of the two humans based on the choice of the CP or the FP and/or on the amount of time spent in proximity with the CP and FP. With regard to the predictors, these models were identical to those above. In one of these two models the response variable was which of the two humans (CP=1 or FP=0) the dog approached, and in the other, the response variable was the proportion of time individuals spent with the CP (out of the total time individuals spent with either of the two experimenters). Hence, the first model was fitted with a binomial error distribution and logit link function and the second with a beta error distribution and logit link function (Bolker 2008). As before, we fitted both models separately to the WSCd-WSCw data, PdA-FRd data, and subsequently to FrD-PdC-PdA data and again the models for the WSCd-WSCw data were mixed models.

We fitted the models in R (version 3.6.0) (R Team, 2019) using the functions glmer of the package lme4 (version 1.1-21; Bates et al., 2015; GLMM with binomial error distribution), glmmTMB of the identically named package (version 0.2.3; Brooks et al., 2017; GLMM with beta error distribution), glm of the R stats package (GLM with binomial error distribution), or betareg of the identically named package (Zeileis et al., 2010) (version 3.1-2; GLM with beta error distribution). We determined model stability by excluding individuals one at a time and comparing the estimates derived for these subsets of data with those obtained for the full data set. The fitted models appeared to be of moderate to good stability (for details see the results section). In the case of GLMMs, we determined confidence intervals of the estimated coefficients and the fitted model by means of parametric bootstraps (N=1000; functions bootMer of the package lme4 or simulate.glmmTMB of the package glmmTMB). For the beta GLM, we determined confidence intervals of model estimates using the R function confint and confidence intervals of the fitted model by means of a non-parametric bootstrap (N=1000). In the case of GLMMs we determined the significance of individual effects using likelihood ratio tests (Dobson, 2002), comparing the fit of the respective full model with that of reduced models lacking the fixed effects one at a time (Barr, 2013), otherwise we used Wald's z-approximation (Field, 2002). None of the models with beta error distribution were overdispersed (dispersion parameters: comparison WSCd-WSCw, contact model: 0.688 proximity model: 1.045; comparison PdA-FRd, contact model: 1.083; proximity model: 0.976; comparison FrD-PdC-PdA, contact model: 0.991; proximity model: 1.127). For sample sizes and the number of choices of the two experimenters in the case of logistic models, see the supplementary materials (Table 1).

Results

WSCd-WSCw comparison.

Pre-test phase. In the pre-test phase, all dogs in both tests accepted being cuddled by the trainer. Despite all wolves approached the trainer, then two subjects did not accept the contact in one of the two tests performed (one subject in the first test and one subject in the second test). There was a clear difference between WSC dogs and WSC wolves (see Table 2) whereby most dogs spent large fractions of their time in contact with the CP whereas wolves, on average, spent only about half the proportion of their time in contact with the CP. However, variation among wolves was large (WSCd, first test: mean=28.09, dev.st=5.95; second test: mean 28.72, dev.st=4.52. WSCw, first test: mean=19.28, dev.st 11.69; second test: mean=17.83, dev.st=12.28) (see Figure 1a).

TABLE 2. Results of the WSCd-WSCw comparison regarding the time spent in contact with the CP in the pre-test phase (estimates, together with standard errors, confidence limits, tests, as well as minimum and maximum of estimates derived after excluding individuals one at a time).

Term	Estimate	SE	Lower Cl	Upper Cl	χ^2	*df*	*P*	Min	Max
intercept	2.512	0.464	1.567	3.335			(1)	2.413	2.832
group(2)	-2.088	0.594	-3.172	-0.769	10.783	1	0.001	-2.349	-1.858

(1) not indicated because of having a very limited interpretation

(2) dummy coded with WSC dogs being the reference category

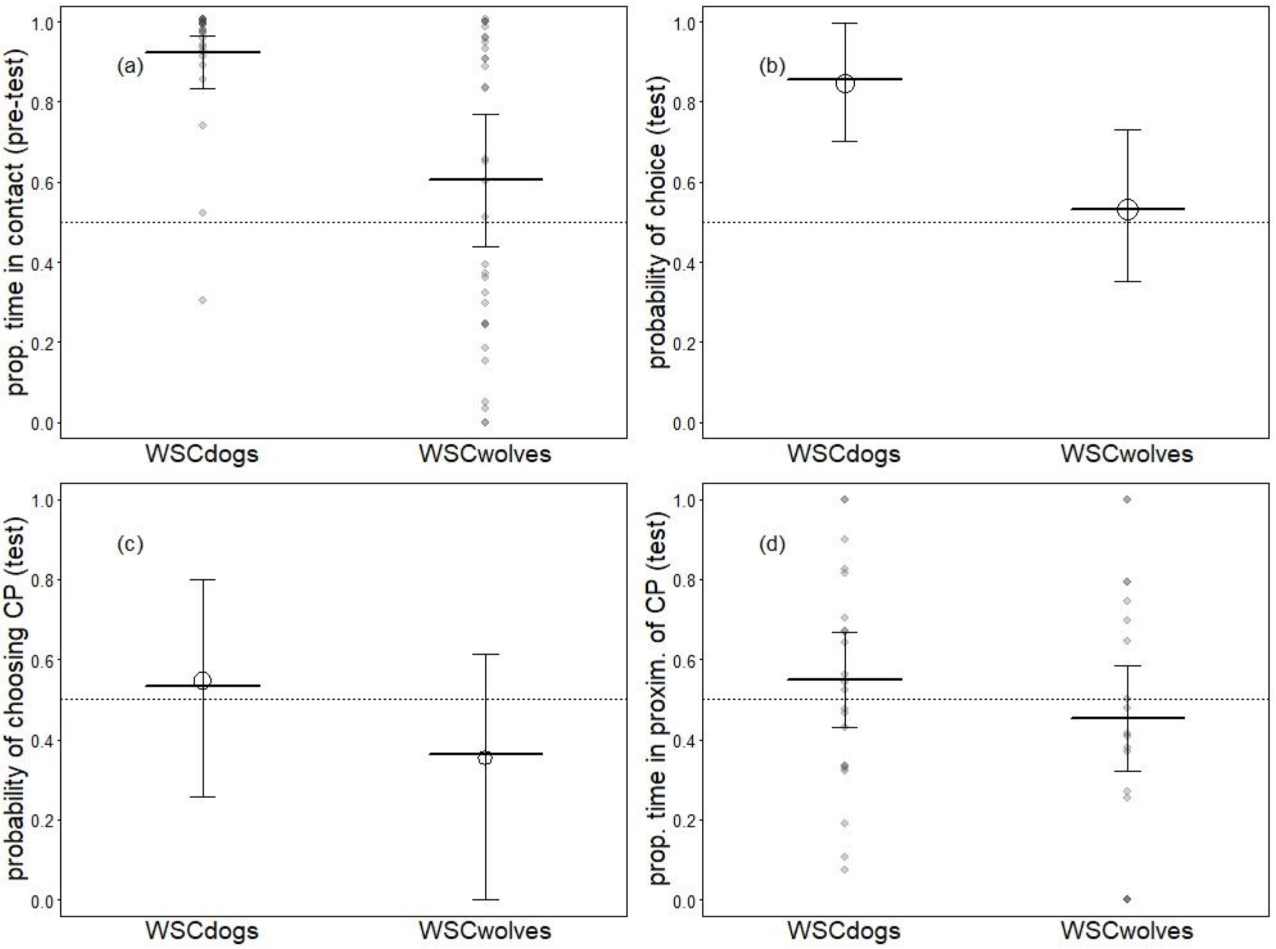

FIGURE 1. Results for the models comparing WSC dogs and WSC wolves. Indicated are the average response (circles in (b) and (c)) as well as the fitted model (thick horizontal lines) and its confidence intervals (error bars). Darker dots in (a) and (d) depict observations falling on top of one another.

<u>Test phase.</u> Overall, we found that WSC dogs were more likely to make a choice than WSC wolves (see Table 3; Figure 1b). In the first test, one WSC dog did not make a choice, whereas seven chose the FP and five chose the CP (exact binomial test: pet dogs p=0.38); six WSC wolves did not make a choice (just ignoring the people and sniffing/walking around); six individuals chose the FP and four individuals chose the CP (exact binomial test: p=0.37). In the second test, three WSC dogs did not make a choice, whereas three chose the FP and seven chose the CP (exact binomial test: pet dogs p=0.17); nine WSC wolves did not make a choice, five individuals chose the FP and two individuals chose the CP (exact binomial test: p=0.22). Thus, both groups did not show a significant preference for either person. Wolves and dogs did not differ in the probability to approach the CP (see Table 4; Figure 1c) nor in the time spent in her proximity (see Table 5; Figure 1d).

TABLE 3. Results of the WSCd-WSCw comparison regarding the willingness to approach the experimenters (estimates, together with standard errors, confidence limits, tests, as well as minimum and maximum of estimates derived after excluding individuals one at a time).

Term	**Estimate**	**SE**	**Lower Cl**	**Upper Cl**	χ^2	***df***	***P***	**Min**	**Max**
Intercept	1.545	0.669	0.583	4.961			(1)	1.442	2.163
group(2)	-1.659	0.736	-4.490	-0.615	6.679	1	0.009	-2.329	-1.473
social(3)	0.490	0.614	-0.709	2.176	0.650	1	0.419	0.325	0.767

(1) not indicated because of having a very limited interpretation

(2) dummy coded with WSC dogs being the reference category

(3) side at which the CP was placed; dummy coded with left being the reference category

TABLE 4. Results of the WSCd-WSCw comparison regarding the approach to the CP experimenter (estimates, together with standard errors, confidence limits, tests, as well as minimum and maximum of estimates derived after excluding individuals one at a time).

Term	**Estimate**	**SE**	**Lower Cl**	**Upper Cl**	χ^2	***df***	***P***	**Min**	**Max**
Intercept	0.585	0.540	-0.467	11.449			(1)	0.421	0.834
group(2)	-0.704	0.680	-20.487	0.665	1.090	1	0.296	-0.932	-0.478
social(3)	-0.871	0.670	-21.567	0.609	1.719	1	0.189	-1.162	-0.676

(1) not indicated because of having a very limited interpretation

(2) dummy coded with WSC dogs being the reference category

(3) side at which the CP was placed; dummy coded with left being the reference category

TABLE 5. Results of the WSCd-WSCw comparison regarding the proportion of time spent in proximity of the CP (estimates, together with standard errors, confidence limits, tests, as well as minimum and maximum of estimates derived after excluding individuals one at a time).

Term	**Estimate**	**SE**	**Lower Cl**	**Upper Cl**	χ^2	***df***	***P***	**Min**	**Max**
Intercept	0.484	0.299	-0.055	1.107			(1)	0.381	0.610
group(2)	-0.385	0.355	-1.124	0.274	1.162	1	0.281	-0.561	-0.266
social(3)	-0.595	0.357	-1.374	0.072	2.708	1	0.099	-0.820	-0.441

(1) not indicated because of having a very limited interpretation

(2) dummy coded with WSC dogs being the reference category

(3) side at which the CP was placed; dummy coded with left being the reference category

Free-ranging dogs-pet dogs comparison.

Pre-test phase. Although all dogs in both groups approached the experimenter in the pre-test, 90.56% (48 of 53) of pet dogs and 86% (39 of 45) of free-ranging dogs accepted cuddling. Pet dogs (tested in the dog areas) spent less time in contact with the CP than did free-ranging dogs (pet dogs: mean=15.28, dev.st=11.37; free-ranging dogs: mean=24.43, dev.st=11.32) (see Table 6, Figure 2a).

TABLE 6. Results of the FRd-Pd comparison regarding the duration of time spent in contact with the CP in the pre- test (estimates, together with standard errors, tests, confidence limits, as well as minimum and maximum of estimates derived after excluding individuals one at a time).

Term	Estimate	SE	*z*	*P*	Lower Cl	Upper Cl	Min	Max
(Intercept)	0.721	0.188		(1)	0.351	1.091	0.684	0.820
group(2)	-0.923	0.253	-3.639	<0.001	-1.419	-0.426	-1.030	-0.886

(1) not indicated because of having a very limited interpretation

(2) dummy coded with free-ranging dogs being the reference category

Test-phase. Both pet dogs and free-ranging dogs did not show a significant preference for the CP or the FP (see Tables 7 to 9, Figure 2). Fifteen pet dogs did not make a choice, whereas 21 chose the FP and 17 chose the CP (exact binomial test: pet dogs p=0.31). Fourteen free-ranging dogs did not make a choice, 20 individuals chose the FP and 12 individuals chose the CP (exact binomial test: p=0.10). The two groups did not differ in the probability to approach the CP nor in the time spent in its proximity (see Tables 7 to 9, Figure 2).

TABLE 7. Results of the FRd-Pd comparison regarding the willingness to approach the experimenters (estimates, together with standard errors, tests, confidence limits, as well as minimum and maximum of estimates derived after excluding individuals one at a time).

Term	Estimate	SE	*z*	*P*	Lower Cl	Upper Cl	Min	Max
intercept	1.240	0.434		(1)	0.431	2.152	1.099	1.298
group(2)	0.179	0.451	0.396	0.692	-0.710	1.069	0.101	0.256
social(3)	-0.780	0.469	-1.662	0.097	-1.738	0.118	-0.840	-0.671

(1) not indicated because of having a very limited interpretation

(2) dummy coded with free-ranging dogs being the reference category

(3) side at which the CP was placed; dummy coded with left being the reference category

TABLE 8. Results of the FRd-Pd comparison regarding the approach to the CP (estimates, together with standard errors, tests, confidence limits, as well as minimum and maximum of estimates derived after excluding individuals one at a time).

Term	Estimate	SE	*z*	*P*	Lower Cl	Upper Cl	Min	Max
intercept	-0.488	0.439		(1)	-1.381	0.360	-0.584	-0.352
group(2)	0.246	0.493	0.499	0.618	-0.718	1.225	0.147	0.320
social(3)	0.059	0.489	0.120	0.904	-0.904	1.024	-0.025	0.145

(1) not indicated because of having a very limited interpretation

(2) dummy coded with free-ranging dogs being the reference category

(3) side at which the CPH was placed; dummy coded with left being the reference category

TABLE 9. Results of the FRd-Pd comparison the proportion of time spent in proximity of the CP (estimates, together with standard errors, tests, confidence limits, as well as minimum and maximum of estimates derived after excluding individuals one at a time).

Term	Estimate	SE	*z*	*P*	Lower Cl	Upper Cl	Min	Max
intercept	0.222	0.279		(1)	-0.324	0.769	0.166	0.303
group(2)	0.079	0.342	0.232	0.817	-0.590	0.749	0.020	0.148
social(3)	-0.385	0.342	-1.125	0.260	-1.056	0.286	-0.450	-0.337

(1) not indicated because of having a very limited interpretation

(2) dummy coded with free ranging-dogs being the reference category

(3) side at which the CP was placed; dummy coded with left being the reference category

Additional analyses: FrD-PdC-PdA comparison.

Pre-test phase. In the pre-test phase, we found that pet dogs tested in dog areas (PdA) spent less time in contact with the CP than free-ranging dogs (FrD) and pet dogs tested in the dog care facility (PdC), and no difference was found between FrD and PdC (PdC: mean=18.05, dev.st 10.30) (see Table 10, Figure 2a).

TABLE 10. Results of the FrD-PdC-PdA comparison regarding the duration of time spent in contact with the CP in the pre- test (estimates, together with standard errors, tests, confidence limits, as well as minimum and maximum of estimates derived after excluding individuals one at a time).

Term	Estimate	SE	z	P	Lower Cl	Upper Cl	Min	Max
Intercept	0.715	0.187	3.814	(1)	0.348	1.083	0.675	0.811
group (PdC)(2)	-0.379	0.283	-1.339	0.180	-0.934	0.176	-0.464	-0.286
group (PdA)(2)	-0.980	0.254	-3.860	<0.001	-1.478	-0.482	-1.084	-0.941

(1) not indicated because of having a very limited interpretation

(2) dummy coded with FrD being the reference category; the difference between PdC and PdA was estimated as 0.601±0.274, z= -2.189, P= 0.028.

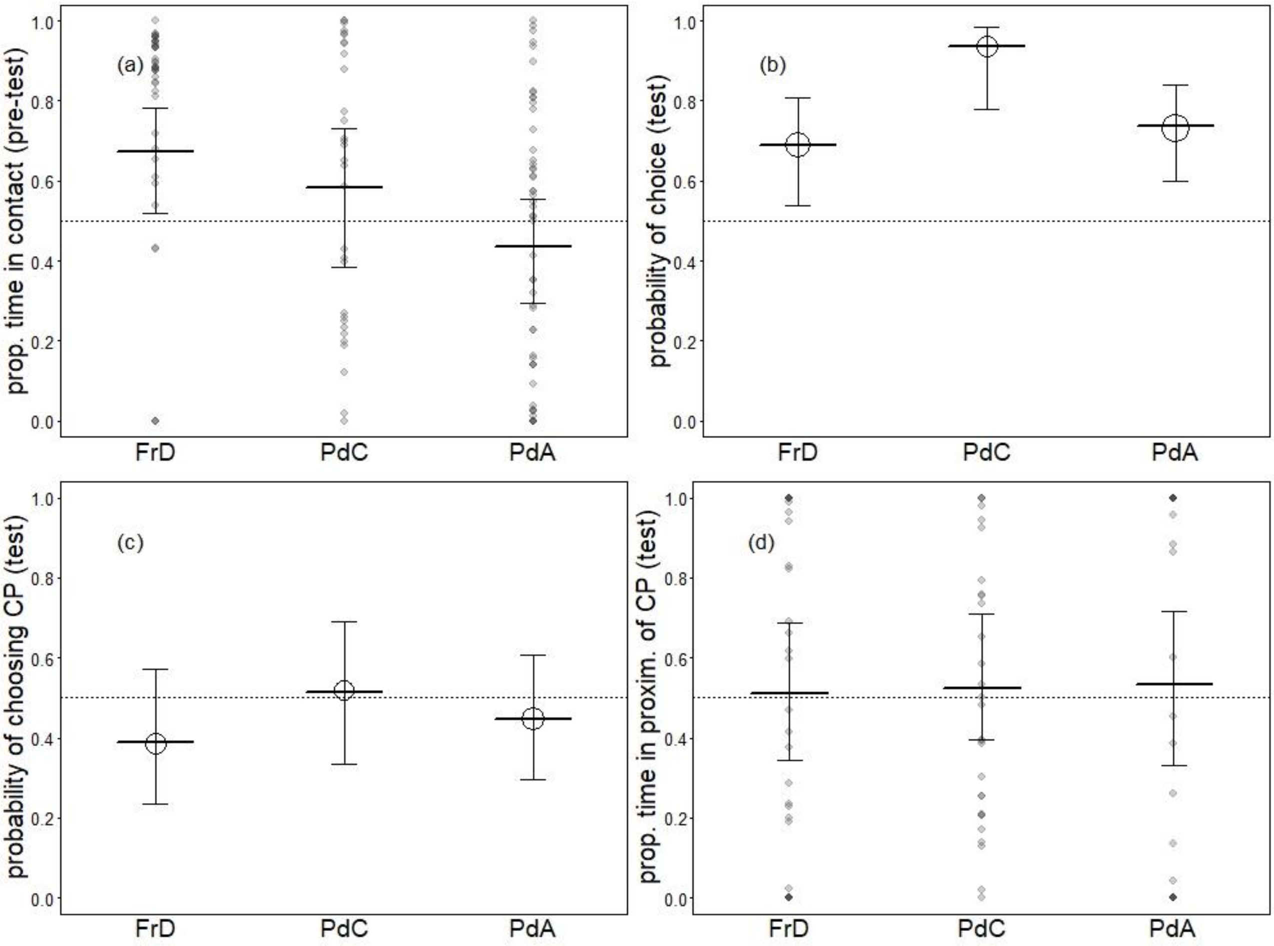

FIGURE 2. Results for the models comparing free-ranging dogs (FrD), pet dogs tested in the dog care facility (PdC) and pet dogs tested in dog areas (PdA). Indicated are the average response (circles in (b) and (c)) as well as the fitted model (thick horizontal lines) and its confidence intervals (error bars). Darker dots in (a) and (d) depict observations falling on top of one another.

Test phase. We found that pet dogs tested in the day care facility (PdC) were more likely to make a choice than pet dogs tested in dog areas (PdA) and free-ranging dogs (FrD) (see Table 11). Two PdC did not make a choice, whereas 14 individuals chose the FP and 15 individuals chose the CP (exact binomial test: p=0.48). Thus, as all other groups, PdC did not show a significant preference for either person. All groups did not differ in the probability to approach the CP (see Table 12) nor in the proportion of time spent in her proximity (time in proximity with CP: mean=16.73, dev.st=23.81; time in proximity with FP: mean=12.15, dev.st=14.18) (see Table 13).

TABLE 11. Results of the FrD-PdC-PdA comparison regarding the willingness to approach the experimenters (estimates, together with standard errors, tests, confidence limits, as well as minimum and maximum of estimates derived after excluding individuals one at a time).

Term	Estimate	SE	z	*P*	Lower Cl	Upper Cl	Min	Max
Intercept	1.160	0.421		(1)	0.371	2.039	1.027	1.217
group (PdC)(2)	1.913	0.803	2.382	0.017	0.520	3.825	1.573	1.992
group (PdA)(2)	0.236	0.454	0.519	0.604	-0.657	1.134	0.157	0.313
social(3)	-0.647	0.449	-1.440	0.150	-1.559	0.215	-0.704	-0.549

(1) not indicated because of having a very limited interpretation

(2) dummy coded with FrD being the reference category; the difference between PdC and PdA was estimated as 1.677±0.798, *z*= -2.101, *P*= 0.035.

(3) side at which the CP was placed; dummy coded with left being the reference category

TABLE 12. Results of the FrD-PdC-PdA comparison regarding the approach to the CP (estimates, together with standard errors, tests, confidence limits, as well as minimum and maximum of estimates derived after excluding individuals one at a time).

Term	Estimate	SE	*z*	*P*	Lower Cl	Upper Cl	Min	Max
Intercept	-0.623	0.423		(1)	-1.485	0.191	-0.705	-0.493
group (PdC)(2)	0.509	0.526	0.969	0.332	-0.516	1.556	0.414	0.602
group (PdA)(2)	0.236	0.494	0.477	0.633	-0.730	1.217	0.139	0.312
social(3)	0.331	0.411	0.805	0.420	-0.472	1.143	0.269	0.387

(1) not indicated because of having a very limited interpretation

(2) dummy coded with FrD being the reference category; the difference between PdC and PdA was estimated as 0.274±0.496, *z*= -0.552, *P*= 0.581

(3) side at which the CP was placed; dummy coded with left being the reference category

TABLE 13. Results of the FrD-PdC_PdA comparison the proportion of time spent in proximity of the CP (estimates, together with standard errors, tests, confidence limits, as well as minimum and maximum of estimates derived after excluding individuals one at a time).

Term	Estimate	SE	z	P	Lower Cl	Upper Cl	Min	Max
Intercept	0.072	0.263		(1)	-0.442	0.583	0.003	0.144
group (PdC)(2)	0.053	0.336	0.157	0.875	-0.607	0.702	-0.009	0.119
group (PdA)(2)	0.093	0.342	0.272	0.786	-0.576	0.756	0.029	0.163
social(3)	-0.061	0.280	-0.218	0.827	-0.600	0.492	-0.102	-0.009

(1) not indicated because of having a very limited interpretation

(2)dummy coded with FrD being the reference category; the difference between PdC and PdA was estimated as 0.040±0.355, *z*= 0.113, *P*= 0.910

(3) side at which the CP was placed; dummy coded with left being the reference category

Discussion

Overall, we found that human-socialized wolves seemed to be less attracted to humans (despite being closely bonded individuals) than similarly raised dogs, highlighting the important role of domestication in affecting dogs' social behaviours towards humans. Moreover, the results obtained from the comparison between highly socialized pet dogs and free-ranging dogs seem to suggest that even a limited/reduced socialization experience with humans is sufficient to elicit a strong social response in dogs. However, the subjects' motivation for interacting with humans remain unclear.

We found that while WSC dogs spent almost the entire duration of the Pre-test social phase being cuddled by the experimenter (medium 91.81%, range 30.43% – 100%, dev. Stand 16.27%), wolves spent only half of their available time in contact with the person (medium 57.76%, range 0% – 100%, dev. Stand 36.24%), although the variability in the response was much larger in wolves than dogs. Given that subjects were free to move and were never called by their names, we assume that their behaviours were not influenced by the test setting and/or their responsiveness to being asked to do something, but rather reflect their interest in socially interacting with the human or exploring the environment. When a subject was not in contact with the experimenter, it was typically moving around exploring the enclosure, thus the more explorative attitude of wolves compared to dogs (Moretti et al., 2015, Marshall-Pescini et al., 2017) might have taken precedence over their proximity-seeking towards the experimenter. However, contrary to wolves, dogs were attracted to the presence of the human, which for them seemed to be the most interesting stimulus in the environment. In any case, it is important to note that the experimenters were hand raisers, with whom both the wolves and the dogs have had a close bond. This might have increased wolves confidence in interacting with them since, as previously observed, wolves are less likely than dogs to generalize their social response to unknown humans (Gácsi et al., 2005), or on the contrary, might have decreased wolves' interest in the experimenters due to the lack of novelty.

Similarly, we found a significant difference between dogs and wolves in the likelihood of approaching either one of the two experimenters at the beginning of the Test-phase (92.3% of dogs approached in the first test and 77% in the second, 62.5% of wolves approached in the first test and 43.7% in the second). Thus, as well as having a greater tendency than wolves to accept the social contact of an 'active' human (Pre-test), dogs were also more likely to actively seek out human proximity than wolves when the two experimenters re-appearing in the Test phase maintained a neutral posture and completely ignored them. However, it is interesting to note that in the second test, in which animals already experience that the two people would not be doing much with them, we found a similar decrease in the number of subjects approaching the experimenters in both wolves and dogs.

Our results are in line with the findings of a previous study measuring sociability of pet dogs and captive hand-raised wolves, in which dogs spent more time in proximity to a human than wolves both when the human was 'active' (calling and touching the subject) and when s/he was ignoring the subject (Bentosela et al., 2016). Despite the authors acknowledging that differences in the experience of the two groups might have affected the results, in light of our own results on similarly raised groups, it seems that the experience with humans might have only modestly affected the differences observed between wolves and dogs regarding these behaviours. Considering these results, a more in depth investigation on differences in sociability between dogs and wolves is currently in progress at the Wolf Science Center on similarly raised populations.

Despite wolves showing less attraction to humans than dogs overall, the variance in the time spent accepting the social contact was large – from 0% to 100% – (see similar results also in Bentosela et al. (2016) with pet dogs vs. hand-raised wolves. The wolves' variability is likely to be the basis on which selection has acted during the domestication process (Persson et al., 2017) and the smaller variance observed in dogs compared to wolves supports the idea that dogs have undergone a strong selective process for higher sociability. Interestingly, we also found a wide variance in the time spent accepting the social contact in pet dogs tested in dog areas, suggesting that the role of life experience might be of great importance in affecting subjects' sociability.

As pointed out by Miklósi and Topál (2013), due to an effect of the major evolutionary processes, species may differ (be constrained) in the degree to which they are able to react to challenges of the social environment showing a difference in their phenotypic plasticity. Thus, due to domestication, dogs may require a lower intensity of social stimulation than wolves to display a similar social response towards human, but still life experience plays an important role in affecting subjects' behaviour.

Given the previous results, we would have expected WSC dogs to choose more often the 'social experimenter' than WSC wolves, however this was not the case, and additionally, also within species, no differences in their preferences emerged (overall 10 of 26 times dogs chose the FP and 12 of 26 the CP, while 11 of 32 times wolves chose the FP and 6 of 32 chose the CP). If dogs were more likely to approach than wolves because of a higher social or food motivation, in the test phase, we would have found a clear preference for either the 'social experimenter' or the 'food experimenter', respectively. Thus, the absence of a clear preference for one experimenter does not allow us to draw any conclusion regarding the subjects' motivation for approaching the humans. It is possible that subjects did not remember, which of the two experimenters provided food or social contact in the pre-test phase. Another possibility is that, since these animals are used to interacting with the trainers and receiving both food and social contact from them, it might be that they did not make a clear distinction between the possibilities of receiving food or social contact when approaching a trainer. This interpretation is supported by the findings that subjects were not consistent in their choice in the two tests overall. In fact, only four dogs and one wolf were consistent in choosing either food or social contact in both tests (2 dogs chose social contact and 2 dogs chose food; the wolf chose food). However, nine animals (6 of 13 dogs and 3 of 16 wolves) were consistent in their choice of the trainers (regardless of their role) across the tests. Thus, the possibility that the relationship with the trainer was affecting the subject's choice cannot be excluded.

Some of our findings relating to the wolf-dog comparison are in line with one aspect of the hypersociability hypothesis, which posits that the process of domestication has resulted in dogs showing a hypersocial response towards humans (and other species- although this aspect has not, as of yet, been tested) (vonHoldt et al., 2017). However, given that subjects' motivation for approaching the humans remains unclear, we suggest that other factors should also be taken into account, when explaining the wolf-dog differences in human-directed sociability. In fact, dogs' behaviours might have been determined by their more deferential attitude towards humans compared to wolves (Deferential Behaviour Hypothesis, Range et al. 2019). Thus, dogs would have a greater acceptance of contact with humans compared to wolves, as well as being more prone to approach the human, considered to be a leader. Indeed this interpretation is in line with observational studies showing that greeting behaviour is most often observed between conspecifics from the subordinate to the most dominant individuals in both wolf and dog packs (Cafazzo et al., 2010; Cafazzo et al., 2016). Finally, the more explorative attitude of wolves compared to dogs might have additionally played a role in diverting wolves' attention to other aspects of their environment.

We found that despite the majority of both pet dogs and free-ranging dogs accepted the experimenter's cuddle session in the Pre-test social phase, free-ranging dogs spent a greater amount of the available time being cuddled than pet dogs tested in dog areas (free-ranging dogs: mean=24.43; pet dogs: mean=15.28). This finding contrasts with our predictions.

One possible reason for these unexpected results is a bias in our selection of animals. While we tested all pet dogs whose owners agreed to do the tests, we were potentially more biased when selecting free-ranging dogs. This might have affected the difference observed between the two groups. However, when selecting free-ranging dogs, we only excluded subjects that showed aggressive or extreme avoidance behaviours when initially approached by the handler (N=7). Potentially dog owners, who did not participate in the test when asked by the experimenters, made a similar selection, refusing to participate in the study if they knew their dogs to be aggressive or fearful towards strangers (although this cannot be confirmed). The overall longer acceptance of social contact by free-ranging dogs compared to pet dogs tested in the dog areas might be due to the former's greater desire for contact potentially driven by the free ranging-dogs' lack of human social contact, as has been already suggested for shelter dogs. For example, in a comparative concurrent choice study, shelter dogs stood out as a unique group for their high level of preference for petting (Feuerbacher and Wynne, 2014); they also rapidly formed attachment bonds with a human after only a few social interactions with them (Gácsi et al., 2001) and were shown to remain in proximity with an unknown human for longer than pet dogs (Barrera et al., 2010). It is moreover possible that free-ranging dogs might have a more generalized social response than pet dogs towards humans. Thus, while pet dogs are very friendly with the owners and generally friendly with familiar people, free-ranging dogs may show social behaviours towards a wider range of people, if they have come to view people as a potential source of food and comfort. However, another possibility should be considered, which is that the subjects' behaviour was affected by the test setting. In fact, while free-ranging dogs were tested in their (outdoor) home environment, pet dogs were not. Instead, they were tested in a dog area where dogs might go only for limited periods; thus, they might have been more interested in exploring the environment than staying in proximity to a human. To explore this potential interpretation, we tested an additional group of dogs in a quiet and familiar outdoor environment. The comparison including the two pet dog groups and free-ranging dogs showed that pet dogs tested in the familiar, undisturbed location spent more time being cuddled than pet dogs tested in dog areas, but did not differ from free-ranging dogs. Additionally, they showed a higher likelihood to approach an experimenter in the Test phase than the other two groups. This lends tentative support to the fact that pet dogs tested in dog areas may have been more distracted by their environment. However, it should also be noted that pet dogs tested in dog areas belong to owners that were recruited randomly while walking around with their dogs. Thus, they might be a more representative sample than pet dogs tested in a dog day care facility that might have owners that are more sensitive to dogs' behaviour and thus dogs with a greater 'socialization' experiences. Moreover, the environment of the free-ranging dogs also contains more distractor compared to the day care facility despite the fact that it is a familiar environment for the free-ranging dogs. However, these results show that the life experience and context have a huge impact on subjects' behaviour, highly affecting the interpretation of the results. In comparative studies, it should be of primary importance to keep these possible confounding factors into account.

Nevertheless, given that no significant difference between free-ranging dogs and pet dogs tested in dog areas emerged in the likelihood of approaching either one of the two experimenters at the beginning of the Test-phase (69% of free-ranging dogs and 71.7% of pet dogs approached), it would seem that pet dogs were interested in the task as well as free-ranging dogs. Interestingly, almost all pet dogs tested in the day care facility centre approached the experimenter (93.5%) and they did it significantly more than pet dogs tested in dog areas and free-ranging dogs. This result could be attributed to them being overall less distracted than pet dogs tested in dog areas as well as free-ranging dogs and/or more attracted to the humans than free-ranging dogs, or, more likely, to the fact that these dogs were used to interact with the trainers of the dog care centre. However, we did not find any difference in the frequency of choosing the 'social experimenter' over the 'food experimenter' (both groups chose 50-50 in the Test phase) for pet dogs tested in dog areas or for free-ranging dogs, as well as for pet dogs tested in dog areas and pet dogs tested in the day care facility. Perhaps the most surprising result is the lack of preference for the 'food experimenter' in free-ranging dogs considering the sporadic food availability in their environment. As we already discussed above, subjects might have forgotten which experimenter provided food or social contact and thus approached one or the other human randomly. However, their great interest in approaching and spending time in proximity to the experimenters remains an interesting finding. Free-ranging dogs' interest in social interactions with humans is in line with recent studies on Indian populations of free-ranging dogs that showed high friendliness towards humans and an understanding of humans' communicative social cues (Bhattacharjee et al., 2017a, 2017b, 2018, 2019).

In conclusion, our study supports the idea that domestication has affected dogs' interest in being in proximity to a human partner providing food or petting, and this seems to be the case also in dogs with a relatively sparse socialization experience (free-ranging dogs). However, at present it is not clear what the driving motivation to interact with the human may be, and future studies including group of dogs with different experiences and tested in different contexts as well as physiological measures and more detailed analyses of the types of behaviours exhibited may help answer such questions.

Author Contributions

ML, FR and SM-P designed the study. ML, JB, KP, KS prepared the study material, data acquisition, entered the data and prepared it for statistical analyses. ML analysed the data. All authors interpreted the data. ML wrote the first draft of the manuscript. All authors contributed to manuscript revision, read and approved the submitted version.

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Conflict of Interest Statement

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

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Supplementary material

Table 1. Sample sizes per model and number of negative and positive responses in the case of logistic models.

Data set	Response	Error distribution; link function	nr. obs.	nr. indiv.	nr. no	nr. yes
WSCd vs. WSCw	Proportion time in contact with CP in Pre-test	Beta; logit	58	29	NA	NA
	Approaches any human	Binomial; logit	58	29	19	39
	Approaches CP	Binomial; logit	39	25	21	18
	Proportion time in proximity of CP	Beta; logit	41	25	NA	NA
FRd vs. PdA	Proportion time in contact CP in the Pre-test	Beta; logit	98	98	NA	NA
	Approaches any human	Binomial; logit	98	98	29	69
	Approaches CP	Binomial; logit	69	69	40	29
	Proportion time in proximity of CP	Beta; logit	61	61	NA	NA
PdA vs. PdC vs. PdA	Proportion time in contact CP in the Pre-test	Beta; logit	129	129	NA	NA
	Approaches any human	Binomial; logit	129	129	31	98
	Approaches CP	Binomial; logit	98	98	54	44
	Proportion time in proximity of CP	Beta; logit	73	73	NA	NA

5. General discussion

The present PhD project aimed to investigate whether domestication has affected both aspects of dogs' socio-cognitive skills and their independent problem-solving and to what extent these skills are affected by dogs' social experience with humans. We designed three tasks to assess the relative roles of domestication and experience by comparing similarly raised wolves and dogs (WSC dogs and WSC wolves), and groups of dogs with different experiences (pet dogs, WSC dogs and free-ranging dogs).

The first study aimed to investigate whether differences in life experience might affect subjects' persistence when interacting with objects. In the second study, we focused on the seminal impossible task paradigm and we investigated whether the looking back at the human does indeed represent a help-seeking behaviour, comparing pet dogs that often rely on receiving help from their human partners and free-ranging dogs, which never experienced receiving help from humans. Finally, in the third study, we investigated the relative importance that wolves and dogs with different social experiences attributed to social contact with human over food.

5.1 New points of view on comparative studies of wolves and dogs: subjects' persistence is influenced by the feeding ecology and living conditions.

In the first study we investigated potential differences in "persistence" (i.e. task direct motivation) between equally raised wolves and dogs (WSC dogs and WSC wolves) (33) and dogs with different life experiences (i.e. WSC dogs, pet dogs and free-ranging dogs) (study 1). We directly compared WSC wolves with WSC dogs (33) and pet dogs with free-ranging dogs and with WSC dogs (107, study 1).

In line with other studies, where overall wolves have been shown to be more persistent - and often more successful - than dogs (string-pulling task, 34; puzzles boxes, 28, 76, 81), we found that WSC wolves were more persistent than WSC dogs when manipulating a novel object baited with food which was impossible to reach (33). Since we compared equally raised dogs and wolves and subjects were tested in the absence of humans, we excluded that differences in persistence between the two groups were a result of dogs' prior experience in receiving help from humans or of dogs being inhibited in interacting with objects, explanations that had been previously advanced by other authors (81). Rather we suggested that dogs' lower persistence than wolves was due to an effect of domestication that altered subjects' persistence to better adapt to their feeding niche.

In study 1 we aimed to investigate how different experiences might affect subjects' persistence comparing WSC dogs, pet dogs and free-ranging dogs. We found that WSC dogs and pet dogs were more persistent than free-ranging dogs (107) and our results were in line with the findings of another comparative study where pet dogs (tested indoors) were more persistent than free-ranging dogs (28, but see study 1 for further discussion). These findings are in contrast with the classic idea that living in close contact with humans might reduce dogs' independence in interacting with objects (81). On the contrary, it seems that humans may provide subjects with a socially guided experience in manipulating and interacting with objects, which could increase their motivation to engage in such tasks (even in their absence).

The finding that free-ranging dogs were poorly manipulative might be unexpected since it is a common idea, and it has been previously suggested, that a low persistence is maladaptive for free-ranging dogs in the context of scavenging efficiency (103). However, in third world countries, human refuses are easily reachable by dogs because they are spread out on the ground and there is no need for dogs to be highly persistent. Indeed, thanks to the low persistence of subjects, one of the easiest strategies to reduce free-ranging dogs' population is to make human refuse inaccessible to dogs with very simple precautions (see figure 2).

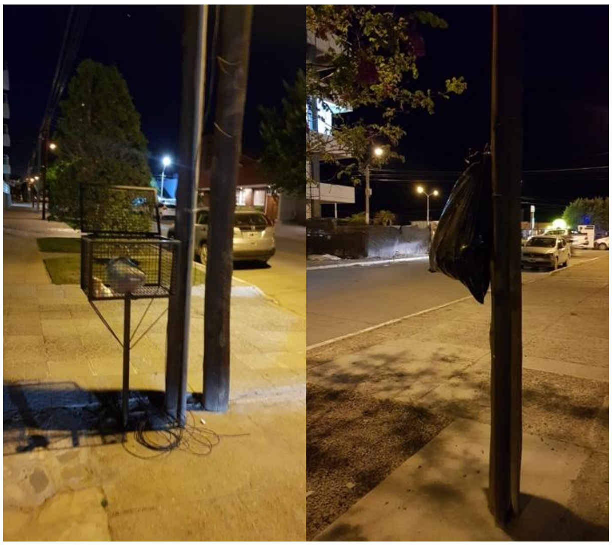

Figure 2. Puerto Madryn (Argentine): strategies to prevent dogs access to garbage (pictures made by Stefano Basso).

The level of persistence of the Indian population of free-ranging dogs tested around the streets of Kolkata reported in Brubaker et al. (28) is similar to the one found in our population, suggesting that free-ranging dogs might overall show very low levels of persistence. However, in a second study of the same authors, the mean value of subjects' persistence resulted higher than the previously observed value (103). In fact, in the first study subjects were tested with a rigid Tupperware (which is comparable with the rigid plastic bottle used in our study) while in the second study subjects were tested with a soft plastic box and a plastic bag (103). Moreover, in this second study, the authors found that free-ranging dogs were more persistent when interacting with the plastic bag than with the plastic box, and thus suggested that the difference in subjects' performance could be attributed to differences in familiarity with the objects or/and to differences in the difficulty of the tasks. In study 1, we also found that subjects (both pet dogs and free-ranging dogs) were more persistent when manipulating the bottle (familiar object) than the ball (unfamiliar object), however also in this case, the bottle was easier to manipulate than the ball. Thus, it is not possible to assess to what extent subjects' persistence is affected by the familiarity and the characteristics of the objects (i.e. more or less easy to manipulate).

Indeed familiarity (i.e. the experience that some food could be obtained manipulating that object) might play an important role in affecting subjects' persistence. In study 2, we presented subjects with four overturned soft plastic bowls baited with food, placed on a wooden board. One of them (impossible) was locked on the board but three (possible) were very easy to move in order to reach the food below. The first dogs that we tried to test approached and sniffed the bowls but did not obtain the food because they were not manipulative at all. Thus, to 'teach' them that some food could be obtained by moving the bowls, we put a piece of sausage under the border of the overturned possible bowls in a way that subjects could touch it with their nose and thereby move the bowl. Thanks to this trick, all the following tested subjects obtained all the food hidden under the possible bowls and finally manipulated the impossible bowl for quite a long time, showing a higher persistence in this test than in study 1 and emerging as equally persistent to pet dogs.

This would additionally support our interpretation of study 1 where we suggested that pet dogs and WSC dogs higher persistence compared to free-ranging dogs might have been determined by their overall higher experience in manipulating objects guided by humans which might teach and encourage dogs to interact with objects in general. Indeed, these results are in line with observations in other species where captive subjects have often been observed to be more persistent than wild subjects (113-115). However, since free-ranging dogs are overall seen as abandoned pet dogs, previous studies have never considered them as the wild representatives of the dog species.

Concluding, the innovative aspect of study 1 was to include a new point of view in the wolf-dog comparison taking into account the different feeding ecologies of the two species. Moreover, we considered free-ranging dogs as the main representatives of dogs' species (43) and pet dogs' differences as reflecting their more intensive human socialization experience. The paradigm shift is potentially important in informing future studies on similar topics.

5.2 The misinterpretation of the seminal 'impossible task'.

In study 2 we investigated whether the 'looking back' behaviour in an impossible task is indeed a help-seeking strategy as has been widely suggested (116-124), testing two populations of dogs differing in their experience in receiving help from the humans (i.e. pet dogs and free-ranging dogs). Subjects were tested with a modified version of the classic impossible task, where subjects simultaneously faced three possible and one impossible trials and were tested in different conditions: social condition (with an unknown experimenter); asocial condition (subject alone); 'dummy' human condition (with a fake 'dummy' human); object condition (with a big sheet of cardboard).

Studies investigating dogs' cognition and behaviour are overall quite recent because for a long time dogs were considered 'artificial animals' that did not live in a natural environment. A shift in thinking occurred when it was suggested that, rather than an artificial process, the process of domestication might have selected for traits which allowed dogs to adapt to their new environment, where the new environment was specifically considered to be human families and dogs were specifically considered to be ‘pet’ dogs (42). Following this new approach studies on pet dogs exploded (see figure 3).

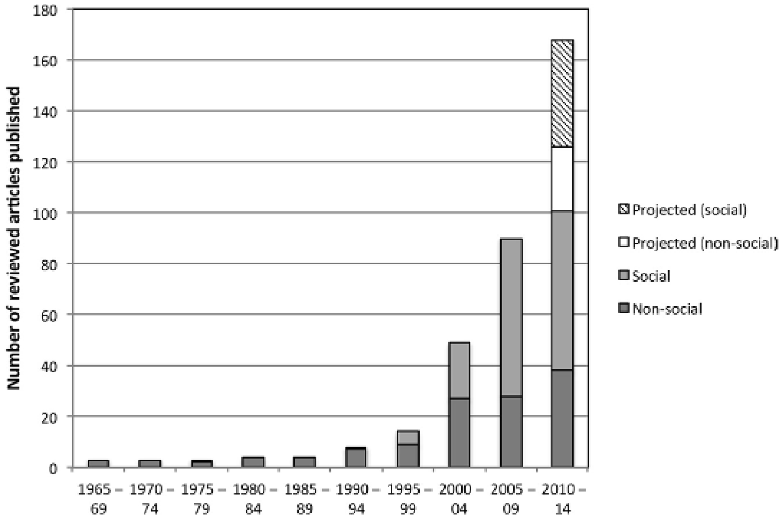

Figure 5.1 Articles on dog cognition published every five years since 1965. Publications are divided into nonsocial and social publications based on classifications given in Table 5.1. Projections through 2014 are based on the average number of articles published each year between January 2010 and December 2012.

Figure 3. From Bensky et al, 2013.

Perhaps one of the most well-known studies used the so-called “impossible task”. This paradigm has been widely used to test pet dogs in many different contexts, from domestication to comprehension of other’s attentional states (10, 76, 116-123, 125-128). In all of these studies, it was never doubted that the looking back after attempting an impossible task was caused by dogs being more attracted to humans than food or dogs asking for the human’s help (for a review see 124). In fact, all dogs tested in these studies were pet dogs (but see 76) shown to be quite skilful in the social domain. For example, studies suggested that dogs could use the ‘showing’ behaviour to indicate a food location to humans (129, 130) adjusting their communication to the cooperativeness of the experimenter (98) and to recruit a partner in a cooperative string-pulling task (88).

However, after a study by Marshall-Pescini et al. (76), we started to question that the looking back was indeed a help-seeking request. In fact, the authors found that subjects’ persistence in manipulating the object emerged as the best explanatory variable to account for differences between wolves and dogs in their latency to look back. Moreover, they did not find differences between pet dogs and Indian free-ranging dogs, the latter population representing animals that have no experience of receiving help from the humans (and should thus take a lot longer to use this communicative cue). Thus, in the study included here we decided to dig deeper to better understand the ‘meaning’ of the looking back behaviour by comparing pet dogs with free-ranging dogs and crucially adding a number of different test conditions. In particular, we added a condition in which dogs were tested with no person present, and conditions in which salient, but non-social stimuli were present (a big box) and a human-shaped cardboard cut out was present. We expected that, if looking back is help-seeking request, it should be used more frequently by pet dogs than by free-ranging dogs and more frequently when the human was present than when the subjects were alone (or in presence of non-social stimuli). We found clear evidence that the looking back was not used as help-seeking strategy but was solely driven by the salience of the stimuli presented. Our results were surprising and highlight how testing free-ranging dogs might be crucial for a better understanding of dogs' behaviour and cognition as well as a better comprehension of dog-wolf differences.

5.3 The effect of domestication and experience on dog-wolf differences on social behaviour towards humans.

The results of the most recent studies on dog-wolf comparison suggest that, rather than acting on specific social skills ('Domestication Hypothesis'; 9, 37) or making dogs more tolerant and attentive (10, 40), domestication might have affected a broader aspect of dogs' behaviour. For example, dogs might have become less afraid of humans (38, 39), have increased their sociability ('Hypersociability Hypothesis'; 90) or their deferential attitude towards humans ('Deferential Behaviour Hypothesis'; 87).

The two last hypotheses are supported by behavioural studies, which found that dogs display less aggression and avoidance towards humans than human socialized wolves (12) and have a higher tendency to seek human social contact (131). Moreover, when cooperating with a human in a string-pulling task, wolves are more likely to initiate movement, but less likely to follow the human partners' initiative than dogs, while dogs tend to wait for the human to take the lead (87). In line with the previous studies, in study 3 we found that WSC dogs spent more time in contact with the experimenter that provided them with social attention than WSC wolves and approached the experimenters more than WSC wolves, which instead preferred to move around exploring the test enclosure.

Additionally, as suggested by vonHoldt et al. (90) it is unlikely that dogs' behavioural characteristics have been selected specifically in relation to humans. Rather dogs should show an increase in sociability and deferential attitude towards other dogs and all other species in general. Indeed, dogs' have shown to easily socialize with other species (132-134). When living as free-ranging dogs they easily tend to aggregate in packs formed by unrelated individuals and they can form a multitude of packs living in small areas very close to each other (66, 135, 136). Despite that, the occurrence of severe aggressions between different packs' members are rare and rather subjects are quite free to move in other packs' territories (67). It is common to observe external males intruding in a pack to mate with the females present in that territory (personal observation). On the contrary, this rarely occur in wolves (see 137), where normally the intrusion of a stranger wolf in a pack's territory, as well as the meeting between two packs, often results with the death of some individuals (138, 139). Finally, dogs have shown to be highly deferential towards other dominant pack members (140).

Other than domestication, it has been suggested that also life experience and socialization with humans might widely affect dogs' behaviour ('Two Stage Hypothesis'; 91, 101). In fact, comparative studies on groups of dogs with different life experiences found that experience does matter in some cases. The majority of these studies found differences in the duration of looking at the humans between groups of dogs that differed for extant and quality of their social interaction with humans (i.e. pet dogs vs shelter dogs 123, 127; old vs young dogs 118, 119; pet dogs vs free-ranging dogs study 2; trained vs untrained dogs 126, 127, 141). These studies showed that subjects that spent long time with humans, or interacted more with them, such as old dogs or trained dogs, looked longer at the human than subjects with less experience of humans, thus highlighting that overall dogs' looking duration might be determined by subjects' past reinforcement history to look at the human (see study 2).

A few other studies have compared groups of dogs with different life experiences. In a recent study, Brubaker et al. (2019) compared pet dogs, shelter dogs and Indian free-ranging dogs to assess subjects' responses to different human's attentional state (attentive – making eye contact, and inattentive – turned away). In both the attentive and the inattentive phase pet dogs and shelter dogs gazed longer and spent more time in proximity with the experimenter than free-ranging dogs and no differences were found between pet dogs and shelter dogs. However, only free-ranging dogs looked longer at the human in the attentive condition than in the inattentive one, resulting to be the most sensitive to human attentional state cues (105). Indeed, pet dogs have previously shown to understand human's attentional states too (96, 129, 142, 143), however, the finding that in this study free-ranging dogs outperformed pet dogs is interesting and in line with the most recent studies on free-ranging dogs.

In fact, free-ranging dogs seem to display high social skills when it comes to interacting socially with humans. For example, in study 3 we found that both pet dogs and free-ranging dogs did not show a clear preference for the experimenter providing food or providing social contact despite the motivation for food should be quite high for free-ranging dogs. Moreover, 86% of free-ranging dogs accepted to be cuddle and spent almost all the available time being cuddled by the experimenter. Additionally, the studies conducted in India by the 'Dog Lab' found that free-ranging dogs appeared to place a high value on social contact with humans (102), were attracted to humans and able to follow the human pointing gesture (106, 144) as well as understand human social cues (friendly and threatening), adjusting their behaviours accordingly (104).

The finding that free-ranging dogs might behave similarly to pet dogs or might show a better understanding of humans' cues might be unexpected, and indeed should be further investigated. Such social skills might be adaptive for village dogs, while are not necessary for pet dogs that are not under natural selective forces and do not face any consequence in acting incoherently or wrongly when interacting with humans. Moreover, differently from pet dogs, free-ranging dogs do not receive possible confounding messages from incoherent behaviours of their owners, and additionally are highly socialized with others dogs and domestic free-ranging animals, an experience that might increase their overall skills in socially interacting with other species, including humans.

Concluding, thanks to the domestication process, dogs easily socialize with humans also if having a scarce exposure to them (101) and are indeed predisposed to interact socially with humans and other species as well (90). Dogs have the social skills required to communicate, understand and cooperate with humans which likely derive from wolves (89). Additionally, the quality of experience with humans, rather than the intensity of socialization with humans (which is instead strongly important for wolves), seems to affect dogs' behaviours. Despite the occurrence of socialization with humans might still be necessary (90), overall the role of subjects' life experience is appearing to be of minor importance in comparison with the role of domestication in determining dogs' overall social behaviour toward humans.

5.4. How are dogs different from wolves?

The **aim** of the current research was to investigatigate whether domestication has affected both dogs' socio-cognitive skills and their independent problem-solving skills by comparing wolves and dogs raised in the same manner (WSC wolves and WSC dogs), and to investigate to what extent these skills are affected by dogs' social experience with humans by comparing dogs differing on this factor: free-ranging dogs (village dogs), WSC dogs and pet dogs.

Based on the relative importance of domestication and experience in affecting dogs' behaviours we formulated three general predictions:

- Prediction 1:

  If *experience* (i.e. the learned dependency on humans during their life) plays a major role in dogs enhanced socio-cognitive abilities towards humans and their poor performance in independent problem solving, we would expect pet dogs living in close contact with the owner to excel in the former and show the least capacities in the latter compared to less socially dependant dogs (i.e. village dogs). Furthermore, wolves and dogs raised in the same way (WSC dogs and wolves) should largely show similar patterns of results.
- Prediction 2:

  If *domestication* plays a major role in these differences, we would expect free-ranging dogs, WSC dogs and pet dogs to perform relatively similarly, and show large differences compared to wolves (e.g. all groups of dogs are better in social tasks and worse in independent problem solving tasks than wolves).
- Prediction 3:

  Finally if both aspects are important, in that *domestication predisposes dogs for social dependency* making them more sensitive to it, then we expect dogs with more experience of human contact to perform better in socio-cognitive tasks than dogs with less experience of human contact (Pet dogs> free-ranging dogs), and vice versa be less proficient in independent problem solving. Importantly, we also expect dogs that are raised with the same high level of human contact as wolves (WSC dogs), to show a better performance in social tasks and poorer performance in independent ones.

From the current results of behavioural studies comparing wolves and groups of dogs differing in their life experience, it is possible to draw some conclusions regarding the above predictions, despite the current research project is still ongoing and further studies would be necessary to make a more solid discussion.

Our first prediction was based on the hypothesis that life experience would have played a major role in determining differences among groups. It seems unlikely that experience plays such important role since it is evident that equally raised wolves and dogs behave somehow differently both in the physical and in the social domain and that different groups of dogs behave quite similarly.

In the physical domain, differences between equally raised dogs and wolves are evident both regarding subjects' overall behaviour, such for example persistence in interacting with objects (33) or exploration (74, 75), and subjects' specific skills, such for example understanding of causal relationships (32). Despite it seems evident that some of these characteristics are adaptive for both species, such for example high persistence for hunters and low persistence for scavengers, it remains unclear if some scarce dogs' physical skills are also the result of the adaptation to a specific ecological niche (52) or are instead due to a relaxing effect of selecting forces (30).

Despite raised in the same manner, also in the social domain WSC wolves and WSC dogs behaved differently, especially regarding their overall social behaviour towards humans (for example searching for human proximity; study 3, 131). However, relevant differences in specific social skills (for example use of 'showing' behaviour to indicate food location to a human, 98) were not observed: wolves resulted as skilled as dogs in understanding humans.

Interestingly, wolves' skilfulness has only emerged when testing WSC wolves that were intensively socialized with humans, thus suggesting that intense socialization with humans is necessary for the emergence of such social skills in wolves, highlighting that socialization with humans is indeed important. However, contrary to what has been previously suggested (9, 10, 37) the ability to comprehend humans was already present in both dogs and wolves and has not been selected during the domestication process, which has probably just modified dogs' fearfulness (38, 39), sociability (90) or deferential attitude (87) towards humans, favouring dogs' interaction with them.

In the physical domain, differences between groups of dogs having different experiences are poorly studied and, basing on the current knowledge, they seem to be almost only determined by differences in subjects' persistence (28, 107). From these studies, it seems that the effect of social experience with humans is not very relevant and that overall the experience of living with humans might just change subjects' motivation rather than modifying subjects' skills (107). However, such motivation might be similarly affected also by other factors such for example the presence of other dogs (which increased subjects' persistence, 107) or of environmental distractions (that decreased subjects' persistence, 28), suggesting that the effect of the interaction with humans is not of extreme relevance.

Surprisingly, also in the social domain differences between groups of dogs are not strongly evident and studies are showing that overall differently socialized dogs behave similarly (study 3, 108). The few differences observed between groups are just determined by subjects' past reinforcement history (for example looking duration (108)) and do not regard subjects' social skills, which we wrongly hypothesized should have been more expressed in highly socialized dogs due to their higher experience with humans.

The second prediction was based on the hypothesis that domestication would have played a major role in determining differences among groups. Domestication seems to be of greater importance than life experience in shaping differences among subjects. In fact, we found that overall, whenever relevant differences could be observed between groups, both in the physical or in the social domain, these differences were more expressed between equally raised dogs and wolves than between groups of dogs having different life experiences. It seems that life experience has just a minor effect in shaping differences among groups of dogs, but it could be instead of primary importance for wolves. Thus, as previously suggested (101), due to the effect of domestication, dogs and wolves might differ in their phenotypic plasticity and dogs may display human-like behaviours in the anthropogenic environment following a lower intensity of social stimulation than wolves.

The previous dicussion is based on results of studies that compared pet dogs and WSC dogs with village dogs that, despite being free-ranging dogs, are quite well socialized with humans. Thus, to properly comprehend the overall strength of domestication over experience in affecting dogs' cognition, expecially when it comes to interact with humans, it would be of great importance to include in comparative studies groups of free-ranging dogs not socialized with humans (for example feral dogs) but habituated to their presence. However, the results are still quite informative because the behaviour of village dogs, that are less socialized with humans than WSC wolves, confirm that dogs require a less intense socialization with humans than wolves to show complex social skills other than a strong social response towards humans (101). Additionally, these results suggest that interacting socially with humans might be adaptive for free-ranging dogs that live near humans. Thus, dogs' overall sociability towards human might have been selected during the self-domestication process because increasing individuals' fitness and dogs' social skills in communicate with humans, likely inherited from wolves, might have favoured this process.

In line with this last suggestion it might be wrong to predict that, thanks to their experience, pet dogs and WSC dogs might be more skillfull than free-ranging dogs when it comes to socially interact with humans (see prediction 3 and 1), since high social skills might be adaptive for free-ranging dogs. Additionally, in line with the results that we found in study 1, it might be wrong to predict that the experience of living with humans might result in an overall reduction of dogs' problem-solving skills and that domestication might have had a detrimental effect on dogs’ physical cognition. Rather, domestication might have changed dogs’ cognition to better adapt dogs to their living environment and feeding niche. Thus, future comparative studies should take subjects’ ecology into account, and predictions should be drawn considering the possible ecological function that the specific tested behaviour might have.

Based on the current results, we can conclude that domestication has strongly modified dogs’ physical and social cognition, favouring behaviours that allowed dogs to best adapt to their ecological niche and that the effect of domestication seems to be of more relevance than the effect of subjects’ life experience in affecting dogs’ differences. However, future studies on a wide variety of differently experienced dogs are needed to better comprehend the relative roles of domestication and experience in shaping dog’ behaviour.

6. Conclusions

Since the beginning of the 21st century, when the explosion of studies on dogs' behaviour started, the majority of research has focused on pet dogs. However, pet dogs, which are 20% of the total dog world population, only partly represent dogs, which are instead mainly represented by free-ranging dogs. Despite that, many of the hypotheses on the effect of domestication in dogs were based on the results of comparative studies on captive wolves and pet dogs, or studies conducted on solely pet dogs.

In the far majority of these studies, it was not taken into account the important role that subjects' life experience and socialization with humans could have had in affecting the dogs-wolves behavioural differences observed. Indeed, studies conducted on equally raised wolves and dogs have shown that differences between the two species have often been overestimated and wrongly attributed to an effect of domestication rather than to the intensity of subjects' socialization with humans, leading to wrong hypotheses regarding the effect of domestication on dogs' behaviour.

Additionally, focusing the majority of the research on pet dogs has only provided a partial knowledge of dogs and likely led to misinterpreting some results, providing a distorted version of what a dog is. Some behaviours have likely been wrongly interpreted since dogs' ecological traits were not taken into account (see for example study 1) and some social competences have been overestimated (see for example study 2).

Taking into account the possible effects of both species ecology and subjects' life experiences reveals to be of major importance for correctly interpreting the results of behavioural studies on wolves and dogs, providing a better understanding of what dogs are and how domestication has changed them.

7. Future directions

Despite the evidence that the studies on free-ranging dogs are of relevant importance to better comprehend the effect of domestication in dogs as well to understand dogs' cognition and behaviours in general, only few studies have been conducted on them until now. Indeed, more cognitive studies on free-ranging dogs should be conducted, but it is of great importance that these studies also include pet dogs, since the comparison between the two groups is indispensable to better comprehend both populations. Unfortunately, comparing these populations is extremely difficult since the testing conditions are very different and might strongly affect the differences observed. Thus, it would be necessary to conduct comparative studies that include groups of pet dogs tested in different contexts (i.e. outdoor areas, indoor areas, private homes, etc…) to find the testing context in which pet dogs are better comparable with free-ranging dogs.

It has been observed that free-ranging dogs might be very different in their friendliness and confidence towards humans. In the studies that we are conducting in Morocco, as well as the studies conducted in India, we include only village dogs, which are quite well socialized with humans, but indeed represent only one kind of free-ranging dog, and we do not even know how common these dogs are in relation to the whole population of free-ranging dogs. Indeed, including less 'urbanized' dogs or even feral dogs in comparative studies might be of extreme importance. In fact, these dogs have a different experience of humans and live in different conditions than village dogs, such as stable packs of numerous individuals that likely rely on group cooperation.

Finally, the data of the few studies that directly compared free-ranging dogs and pet dogs show that variability in behaviours among pet dogs seems larger than variability among free-ranging dogs. It would be interesting to investigate the reason for this difference, which might be due to an overall more homogenous experience of free-ranging dogs compared to pet dogs or/and to the effect of natural selection that is still acting on free-ranging dogs but not on pet dogs.

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