

Master thesis

**Are wolves (*Canis lupus*) and dogs (*Canis familiaris*)
prosocial in a location choice paradigm?**

Marie-Noémie Despraz

Supervisors

Prof. Klaus Zuberbühler (University of Neuchâtel, Switzerland)

Priv. Doz. Dr. Friederike Range (Messerli Research Institute, University of
Veterinary Medicine Vienna; Wolf Science Centre, Austria)

Dr. Sarah Marshall-Pescini, Senior postdoc researcher (University of Veterinary
Medicine Vienna; Wolf Science Centre, Austria)

Rachel Dale, PhD Student (University of Veterinary Medicine Vienna; Wolf
Science Centre, Austria)

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Contents

Abstract	3
Introduction.....	4
Materials and Methods	8
Subjects	8
Overview.....	8
Experimental set-up	10
Experimental design	11
Exposure sessions.....	11
Experimental Sessions	11
Schedule	12
Comprehension sessions	13
Behaviour coding.....	13
Analyses.....	14
Results	15
Wolves.....	15
Shima	15
Chitto.....	17
Yukon.....	18
Dogs.....	19
Nia.....	19
Maisha	20
Pepeo.....	21
Meru	22
Discussion	24
Acknowledgments.....	27
References.....	28
Tables	31

Abstract

The goal of this study was to investigate whether or not dogs (*Canis familiaris*) and wolves (*Canis lupus*) show prosociality in a simple T-maze experiment based on a previous study by Hernandez-Lallement *et al.* (2015). Prosociality, i.e. “voluntary behaviour that benefits others”, was initially thought to be uniquely humans and, to trace its origin, has mainly been investigated in non-human primates. More recently however, some non-primate species showed considerable amounts of prosociality, suggesting convergent evolutionary paths. This has led to the hypothesis that prosociality evolved in response to high levels of cooperation, allo-maternal care, or collective foraging, and is not a consequence of complex cognition. In this study, we have tested if wolves and dogs are prosocial and, second, whether prosociality in dogs is a by-product of domestication or an ancestral trait shared with wolves. We found no obvious difference between the level of prosociality in wolves and dogs. Although the data were limited we did not find strong overall evidence for prosociality but there was great individual variation. Although inconclusive, our results suggest prosociality in two individuals, a female wolf and a male dog, suggesting that prosociality is an ancestral trait in this group of mammals, in line with the Canine Cooperation Hypothesis (Range & Virányi, 2015), and unrelated to domestication.

Introduction

Prosociality can be defined as “*a voluntary behaviour that benefits others*” (Jensen *et al.*, 2014). These types of behaviours seem to appear very early in human ontogeny (Jensen *et al.*, 2014) with very young children helping people, even strangers, in situations without any benefit to themselves (Warneken & Tomasello, 2006). In 2007, Warneken & Tomasello showed that children of only 14 months old could already understand another person’s goal and help this person to reach it (Warneken & Tomasello, 2007). By 12-months infants cannot only use pointing gestures to show the adults what they want or what they are looking at, but they are also capable of using pointing gestures to inform an adult of the location of an object that that adult is looking for (Liszkowski *et al.*, 2006). In humans, these cases of aiding behaviours are thought to be motivated by empathy and sympathy (Batson & Shaw, 1991; de Waal & Suchak, 2010; Marshall-Pescini *et al.*, 2016).

Instead of concentrating on the motivations underlying prosocial behaviours in animals, researchers have focused on its evolutionary origins. And although research into the mechanistic perspective of prosociality is in its infancy, studies into the evolutionary routes of this behaviour have received growing attention over the last decade. To determine the evolutionary origins of prosociality, scientists have mainly focused on our closest living relative, chimpanzees (*Pan troglodytes*) to determine whether they are also a prosocial species. Indeed, as they live in groups, share territories, hunt collectively, and even comfort victims of aggression, which suggests they might feel empathy, chimpanzees are likely candidates to show prosocial behaviours (Silk *et al.*, 2005). At first, scientists found that, contrary to humans, the prosociality of chimpanzees is limited to kin and reciprocating individuals (Silk *et al.*, 2005). However, recent studies with varied methodologies suggest that chimpanzees are also a prosocial species (Horner *et al.* 2011) but the behaviour of the receiver, when begging and/or trying to reach the food, seems to be a key factor affecting the chimpanzee’s prosociality (Melis *et al.*, 2010). Despite these positive results, it is clear that humans show more prosociality and in a wider variety of contexts than chimpanzees (Melis *et al.*, 2010).

Besides chimpanzees, numerous other non-human primate species have been tested. To cite only a few, prosociality can be found in tufted capuchin monkeys (*Cebus paella*; Lakshminarayanan & Santos, 2008), brown capuchin monkeys (*Cebus apella*; de Wall *et al.*, 2008), cottontop tamarins (*Saguinus oedipus*; Cronin *et al.*, 2010), long-tailed macaques (*Macaca fascicularis*; Massen *et al.*, 2011), and common marmoset monkeys (*Callithrix jacchus*; Burkart *et al.*, 2007). As some of these species have demonstrated more consistent prosociality across tasks than chimpanzees, which are our closest living relative, prosociality could be the result of convergent evolution rather than phylogenetic relatedness (Burkart *et al.*, 2014; Marshall-Pescini *et al.*, 2016). In 2014, Burkart *et al.* identified one potential force driving this convergent evolution. They compared numerous experimental studies of 15 primate species including humans, and concluded that the amount of allomaternal care provided among primate species gave the most suitable explanation for the presence of proactive prosociality within this great number of species. In addition, collective foraging, cooperative breeding, high levels of social tolerance and cooperation may also be important factors in the appearance of these aiding behaviours (Marshall-Pescini *et al.*, 2016).

As allomaternal care and cooperative breeding is limited to only a few species of primates and widespread in other taxa, broadening the experimental studies to species other than primates may be a way to better understand why, where and when prosociality has evolved (Marshall-Pescini *et al.*, 2016). In fact, these past years, prosociality has been found in grey parrots (*Psittacus erithacus*; Péron *et al.*, 2013), jackdaws (*Corvus monedula*; Schwab *et al.*, 2012),

rats (*Rattus norvegicus*; Ben-Ami Bartal *et al.*, 2011; Ben-Ami Bartal *et al.*, 2014; Hernandez-Lallement *et al.*, 2015; Márquez *et al.*, 2015), and even in ants (*Cataglyphis cursor*; Nowbahari *et al.*, 2009).

Since it is already complicated to compare the studies within primates (e.g. the different levels of prosociality may be due to methodological disparity in the respective studies rather than real cross-species differences, Burkart *et al.*, 2014; Marshall-Pescini *et al.*, 2016), there is a need for a standardized social paradigm, which would allow us to establish the evolutionary forces behind prosocial behaviours (Burkart *et al.*, 2009; Burkart *et al.*, 2014; Hernandez-Lallement *et al.*, 2015; Marshall-Pescini *et al.*, 2016). Recently, Hernandez-Lallement *et al.* (2015) designed a double T-maze experiment with rats to study their prosocial behaviours. They decided to use a Prosocial Choice Test (PCT), which was first used by Colman, Liebold and Boren in 1969 with monkeys (Colman *et al.*, 1969). In PCTs the subject typically has the choice between a “selfish” option, termed OR by Hernandez-Lallement *et al.* (2015) for “own reward”, in which only the actor is rewarded with food (1/0), and a “prosocial” option, named BR for “both reward”, in which both the actor and a partner get rewarded (1/1). In fact, Hernandez-Lallement *et al.* found that the rats they used, all males, made on average 55% of prosocial choices in this test condition. As a control, they designed a toy condition, in which an inanimate toy rat replaced the living partner, and the actors chose the BR compartment significantly more in the partner than in the toy condition, indicating that the actors understood the difference between these two conditions. The choice preferences of the actors were stable over time and they re-acquired them faster after repetition.

However, the authors additionally noticed that the preference for either the OR or BR compartment greatly varied across individuals. This high amount of individual variation might be found in other species, and could add to the difficulty of comparing prosociality across diverse species. To determine the extent of the differences in BR-preferences between each rat, Hernandez-Lallement *et al.* calculated a social bias score (SB score) for each of the actors. These SB scores represent the percentage difference in BR choices in the partner condition in contrast to the toy condition and enabled the researchers to measure how much each rat preferred to be prosocial in the partner condition rather than in the toy condition. Rats with SB scores significantly higher than the upper interval bound were categorized as prosocial (N=29 of a total of 48 rats). The remaining rats (N=19) were categorized as non-prosocial. The range of the SB scores was wide, from -14.8 (14.8% less BR choices in the partner than in the toy condition) to 45.6 (45.6% more BR choices in the partner in comparison to the toy condition). Moreover, as socially dominant rats are usually heavier than subordinates and as weight possibly reflects position in the group hierarchy (Smith *et al.*, 1994), the difference in body mass between actors and partners was also measured as it could be biasing rats' helping behaviour toward lighter individuals. Indeed, they found that the actors of this study had a higher tendency to choose the BR compartment when paired with lighter partners. However, no significant correlation was found between weight difference and SB scores. Overall these results support those obtained in other experiments with rats (Ben-Ami Bartal *et al.*, 2011; Ben-Ami Bartal *et al.*, 2014; Márquez *et al.*, 2015) confirming that rats are prosocial animals (Hernandez-Lallement *et al.*, 2015).

The fact that species like rats are showing prosocial behaviours is exciting and leads the way to the study of prosociality in other species. As Burkart *et al.* already hypothesized in 2007, results indicate that prosocial behaviours might have evolved in cooperative species, and particularly species with cooperative breeding systems or collaborative foraging (Marshall-Pescini *et al.* 2016) rather than in species showing high cognitive abilities. In order to explore this hypothesis, the current study aimed to further broaden the spectrum of species tested for

prosociality by adapting the paradigm created by Hernandez-Lallement *et al.* for use with Canids. Dogs (*Canis familiaris*), for example, are a highly social species (Cafazzo *et al.*, 2010, Virányi *et al.*, 2015). In 2015, Quervel-Chaumette *et al.* used a simplified version of a prosocial bar-pulling paradigm. In this new version of the paradigm, the donor dogs could choose between a 0/0 and 0/1 food distribution, which is cognitively easier than the usual 1/0 and 1/1 food distribution, as the donors only had to focus on the location of a single piece of food. As with the primate bar-pull studies (e.g. Lakshminarayanan & Santos, 2008), the donor dog had the choice to pull one of two trays. One of these trays was not baited with a food reward, while the other had one piece of food delivered to the receiver dog. The results showed that dogs would work longer, and therefore provide more food, for a familiar receiver than for a stranger (Quervel-Chaumette *et al.*, 2015).

As dogs have been selected to cooperate with humans, it has been claimed that they have evolved specialized skills during their domestication process to read humans' social and communicative behaviour (Hare & Tomasello, 2005; Miklósi & Topál, 2013). And as dogs can help humans without getting any reward or being trained to do so (Bräuer *et al.*, 2013), a potential explanation for Quervel-Chaumette *et al.* results is that dogs are prosocial due to these specialized skills. They would therefore be predicted to be more prosocial than wolves. However, in regard to new insights into the evolution of prosociality, which, as previously explained, would be more likely in cooperatively breeding and foraging species, we would expect wolves to be at least as prosocial as dogs. Indeed, wolf packs typically consist of one breeding pair and non-breeding pack members, usually the offspring from previous years, which help to raise the young (Cordoni & Palagi, 2007; Range & Virányi, 2014; Quervel-Chaumette *et al.*, 2015). As with the prosocial primates, they also cooperate to complete multiple tasks such as defending their territory and hunting large prey (Mech, 1999; Mech *et al.*, 1999; Cordoni & Palagi, 2007; Cooper *et al.*, 2003; Range & Virányi, 2014; Quervel-Chaumette *et al.*, 2015). Therefore, another potential explanation for the difference in the actor's choice according to the partner's identity could be the dog's ancestry as well as their natural ecology (Quervel-Chaumette *et al.*, 2015).

Dogs obviously differ from wolves by, to cite only a few, their closeness to humans, along with their breeding system and reliance on scavenging over cooperative hunting (Range & Virányi, 2014). But despite these differences, free-ranging dogs show some allomaternal care (but to a lesser scale and rarely; see Paul *et al.* 2014), have social bonds, live in packs and coordinate to defend their territory (Pal *et al.*, 1998; Paul *et al.*, 2014). As a matter of fact, although dogs' bonds with their conspecifics may be looser than between wolves, it could still explain why the donor dogs gave more food to the receivers that lived in the same household (Quervel-Chaumette *et al.*, 2015).

Quervel-Chaumette *et al.*'s recent findings have raised the following questions: is the prosociality of dogs due to their domestication or, as suggested above, does it come from their shared ancestry with wolves? And if both wolves and dogs show prosociality will their levels of prosociality differ?

As very little has been done on prosociality in canids to date, these questions remain unanswered. Indeed, the Canine Cooperation Hypothesis recently challenged many domestication hypotheses by postulating that dogs did not need to be selected for their tolerance and social attentiveness, but that dog-human cooperation arose from wolf-wolf cooperation (Range & Virányi, 2015). Yet, so far, most studies on dogs have been focusing on investigating their cognitive abilities, their cooperation with humans, and the skills they

developed for reading human social and communicative behaviours (Cooper *et al.*, 2003; Hare & Tomasello, 2005).

The Wolf Science Centre (WSC) in Austria, formed in 2008 with the aim of exploring the cognitive abilities of wolves and dogs with similar life experiences, provided the possibility to answer these questions. The centre's general approach of keeping all animals in similar conditions allows a comparison between wolf-wolf and dog-dog behaviours, as well as interspecific comparisons. The WSC can provide the relevant set up to address some key questions on the impact of domestication on dogs (Range & Virányi, 2015).

The current study was conducted at the WSC. The experimental design was similar as in the study of Hernandez-Lallement *et al.*, consisting of an actor having the choice to enter one of two compartments, the "Own Reward" (OR) compartment, or the "Both Reward" (BR) compartment, with a third compartment in between, where a partner awaited the actor's decision (see Figure 1). If the actor chose the OR compartment, it was the only one to get a reward (1/0), and if it chose the BR compartment, the partner and the actor were both rewarded (1/1). Apart from the test condition, a control condition was also conducted. The only difference between the two conditions was that in the control condition the partner was never rewarded, even when the actor entered the BR compartment.

Based on the performance of the rats and the studies conducted with dogs discussed above, we made two predictions, each one excluding the other:

1. Dogs are prosocial, but wolves are not. In this case, our results would support the argument that prosociality appeared in dogs during their domestication process and is due to their social closeness to humans.
2. Both wolves and dogs show prosociality by choosing the BR compartment more often in the test than in the control condition. If the results confirm this prediction, we also predicted that wolves would show more prosociality than dogs as they live in packs with strong social bonds, and, in contrary to most dogs, have a wider range of intraspecific cooperative behaviours including cooperative breeding (Paul *et al.*, 2014; Range & Virányi, 2014).

Materials and Methods

Subjects

All testing was carried out at the Wolf Science Centre (WSC), Ernstbrunn, Austria. All wolves (actors N=3, partners N=3; see Table 1) used in this study were born in captivity in North America and Europe. The dogs (actors N=4, partners N=4; see Table 2) were mixed breeds and came from Hungarian shelters or were born at the WSC. Ten days after birth, all of the wolves and the dogs from the Hungarian shelters were taken from their mother to be hand-raised, which included bottle-feeding and hand-feeding, as well as a continuous human presence during the five first months of their life. The dogs born in 2014 at the WSC spent 4-5 hours per day with a human hand-raiser and spent the rest of their time in packs with their mothers and other adults. This, combined with daily training into adulthood, ensured that both wolves and dogs were socialized to work calmly and voluntarily with people. It also allowed us to work with animals that were less stressed and did not have to be sedated during veterinarian checks. After these first five months they were moved to 2000-8000 m² enclosures, where they were integrated into existing packs according to their temperament and bonds. At this time, humans were not continuously present in their enclosure anymore. Dogs and wolves participated in multiple behavioural tests every week. Their participation in each testing and training session was voluntary (Range & Virányi, 2014).

Table 1 Wolf dyads. The actor's dominance over the partner is indicated by 0 or 1 where 1 indicated dominant and 0 submissive. Finally, the sex composition of the dyads is indicated in the last column.

Actor	Partner	Actor dominance	Sex composition
Chitto	Kaspar	0	M-M
Shima	Aragorn	0	F-M
Yukon	Geronimo	0	F-M

Table 2 Dog dyads. The actor's dominance over the partner, if known, is indicated by 0 or 1 where 1 indicated dominant and 0 submissive. Finally, the sex composition of the dyads is in the last column.

Actor	Partner	Actor dominance	Sex composition
Maisha	Binti	?	M-F
Pepeo	Nuru	0	M-M
Nia	Sahibu	1	F-M
Meru	Hiari	1	M-M

Overview

The T-maze consisted of an enclosure with one large compartment facing three smaller compartments. The two smaller external compartments were empty and open, and the middle one was close with the partner inside (see Figure 1). A session consisted of either a test or a control condition (see below). For each of these conditions, the actors had exposure sessions beforehand. The actor moved into one of the two compartments and the rewards were delivered to the actor only (OR) or to both of the animals (BR). After the consumption of the rewards, the actor would go back to its start position and a new trial could start.

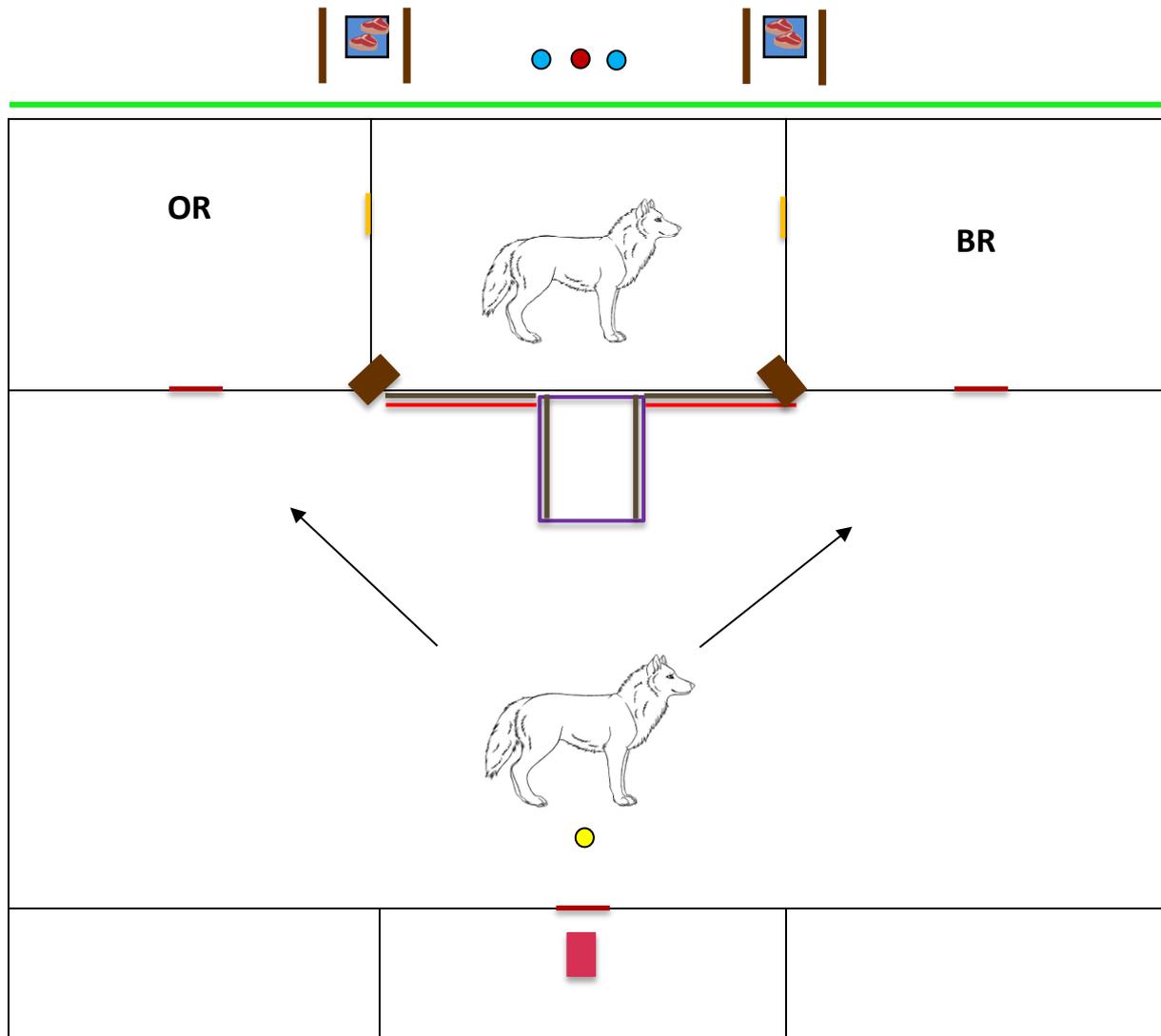


Figure 1 This figure represents the test enclosures of the Wolf Science Centre we used for this study. The starting point of the actor was in front of its partner, at the same distance from the OR (OR = own reward) and BR (BR = both reward) compartments, hold on its collar by a trainer (yellow dot). The actor had the choice to go to the OR or BR compartment. In OR, only the actor received a reward. In BR, both of the animals received a reward of the same quality. The non-occluded tunnel of fence (purple rectangle) was placed in between the actor and the partner, to avoid the influence of the location of the partner on the choice of the actor. The rest of the fence, as well as a part of the tunnel, was visually occluded (green lines) and protected by fence (red lines) to avoid the animals seeing each other in these areas and destroying the material. Four people were present during the experiment. The trainer (yellow dot) was standing at the starting point of the actor to call the animal back after each trial. A camera, standing on a tripod behind the fence (pink rectangle) was filming the front of the experiment and allowed to see the choice of the actor. An experimenter (red dot) was standing behind the partner's compartment, hidden behind a visual occluder (light green line), to give the reward(s). Two helpers (blue dot) were standing next to the experimenter to open and close the slides between each trial. The rewards were kept hidden in two bowls (blue squares), near to the 4 sticks (brown lines) which were used by the experimenter to deliver the reward(s). Two more cameras (brown rectangles) were hung at the corner of the middle slide to film the behaviour of the partner, as well as the consumption of the reward(s) by the animal(s). During the comprehension sessions, the actor could again choose to go either in the OR or BR compartment. If the actor had chosen the BR compartment, it got two rewards (its own and the absent partner's one), as the doors of the partner's compartment were opened.

Experimental set-up

The experiments took place in the “old test enclosure” for the wolves and one dyad of dogs, which was separated into seven parts by fences, and in the “new test enclosure” for the three other dyads of dogs, separated into five parts (see Figure 1). Each dyad was always tested in the same enclosure. The actor was able to choose between two compartments (OR or BR), to the left or to the right of their central position. The partner’s enclosure was between these compartments.

As the orientation of the body and the head, as well as the position of the partner and the visibility of its eyes are sufficient cues for an actor to know the focus of his/her partner’s attention (Virányi et al. 2004; Gácsi et al. 2004; Range & Virányi, 2011), it is crucial to ensure that the actor could see its partner right in front of him/her. However, if the partner was located closer to one of the two side compartments (OR or BR) than the other during the actor’s choice, this might influence the side the actor chooses due to the actor seeking, or indeed avoiding, proximity with the partner (e.g. Massen *et al.*, 2010; Amici *et al.*, 2014). Due to husbandry issues we were unable to restrict the partners to a small central compartment during the actor’s choice, as done by Hernandez-Lallement et al (2015). Instead, we placed visual occluders along the fence of the partner’s enclosure, except for the central part, where we installed an additional rectangular opaque fence (see Figure 1). With this set-up, the actor was only able to see its partner through a small tunnel when the partner was in the centre. Therefore the partner remained free in their ‘partner compartment’ but we obscured the actor’s view of all but the central part of the partner’s compartment, to ensure that they knew the partner was there but without their location influencing the actor’s choice.

For each session, four people were needed:

An **experimenter** and two **helpers**, hidden from both actor and partner by a visual occluder, were placed behind the partner compartment. The experimenter was responsible for delivering the reward to the actor and, when required, to the partner (see below). Pieces of raw meat were used as rewards. Between trials, the helpers closed the slides on both sides and opened them again to keep the animal focused on its task.¹

The **trainer** called the actor back to the starting point (24 meters from the compartments in the new test enclosure, 21 meters in the old test enclosure and centrally between them) after each trial and held it by its collar, a procedure these animals are accustomed to from an early age on. The trainer also took care of video recording the behaviour of the actor using a tripod placed behind the actor’s starting point on the other side of a fence (see Figure 1). A second and third camera were installed at the top of the compartments to record the behaviour of the partner and the consumption of the rewards (see Figure 1).

Three experimenters have worked for the experimental part of this study. Anna Griebler has tested the majority of the wolf dyads as well as one dyad of dogs with the occasional participation of Camille Basin, and I tested the three other dog dyads. Anna and Camille were both interns at the WSC.

¹ At the beginning of the experiment, I was also opening the slides in between the trials and two actors started to make their choices according to where I opened the slide last, so an adjustment had to take place after two months of testing. These two actors were excluded from the study and the experiment restarted with new actors, an experimenter and two helpers. When having this setup, the helpers were opening the slides in a pseudo-randomized order.

In order to prevent frustration on the part of the partner and to ensure that they moved to the food delivery location for every trial, the partner was rewarded on the OR side as well but only after the actor had returned to its start location and was unable to see or hear its partner getting rewarded.

The general procedure included exposure sessions (to allow the actor to become familiar with task contingencies, i.e. which side compartment delivered the prosocial reward distribution and which resulted in a selfish choice) and experimental sessions (the latter including a test session and a control session- see below). The experiment started with two exposure sessions prior to the first two experimental sessions (1x test condition, 1x control condition). Following this, 1 exposure session was delivered prior to every experimental session (regardless of whether it was a test or control condition), to ensure that animals have had experience of the task contingencies (see Table 3). For each dyad, the side of OR or BR was held constant within an experimental block (2x exposure, 1x test, 1x control) but switched from one block to the next. The order of test/control and the OR/BR sides was counterbalanced across dyads (see Table 3).

Experimental design

Exposure sessions

In exposure trials (24 trials per session) actors were exposed to a forced choice, in that animals were released into the testing area. Only one door, selected in a pseudo-randomized order (the same side presented no more than twice in a row), was opened forcing the animals to choose this option. This allowed the animals to be exposed to the outcome of choosing each side compartment (i.e. food delivered just to self or also to partner).

During these exposure sessions, both the actor and the partner were present. A trial started when the experimenter shouted “ok” and the trainer released the actor’s collar from the middle part of the test enclosure. During the first few trials, the experimenter called the actor to the open compartment when he failed to enter it within 30 seconds.

Experimental Sessions

An experimental session consisted of one of the two following conditions.

The procedure of the **test condition** was the same as that of the exposure sessions, except that both OR and BR compartments were simultaneously opened before each trial. The actor could then decide to go into either the BR or the OR compartment. When the actor had fully entered the chosen compartment, the experimenter gave a piece of raw meat to the actor (OR), or to both the partner and the actor (BR). To ensure the actor saw where the food was delivered, the experimenter slowly placed the rewards on a stick(s) and wiggled them around a bit before pushing them through the fence of the compartment(s). If the partner was to be rewarded as well (i.e. the actor made a BR choice), the food was delivered to the partner 2 seconds prior to the delivery of food to the actor to ensure that the actor saw this. After the rewards were consumed, the trainer called the actor back to its starting point, gave a small treat to the actor, and held it by its collar, and a new trial could start when the experimenter shouted “ok”.

In the **control condition**, as in the test condition, both the actor and the partner were present, but the partner was not rewarded even if the actor entered the ‘BR’ compartment. In other words, when the actor chose the prosocial compartment, the experimenter wiggled the two sticks with the pieces of meat but only gave the reward to the actor and clearly took back the other piece of meat (by pulling the stick backwards).

This control was conducted to insure whether the actor was making his choices based solely on their outcome, or whether he was influenced by the quantity and the availability of the rewards. Indeed he could have been less on the BR side because he could not consume the two rewards and it was frustrating him; or he could have been more on the BR side because there were two pieces of meat, which was visually attractive, regardless of whether his partner was getting one or not.

To avoid any negative consequences from the partner, the piece of meat was given to it after the actor had left the compartment and went back to the trainer.

Both test and control sessions were composed of four exposure trials (i.e. forced choice trials) to begin with and 12 test trials, in which both of the slides were open. During these 12 trials, the actor was completely free to choose either the OR- or the BR-compartment. A total of six test condition sessions and 6 control condition sessions were presented to each subject.

Schedule

Our study consisted of a total of 28 sessions per dyad. These 28 sessions included: two exposure sessions followed by either a control or test session, then another two exposure sessions followed by the test/control session. Then, the prosocial side (indicated as L+ for left or R+ for right) and the condition were reversed three times (see Table 3). However, this time only one exposure session was done before the testing.

Example of the schedule of one dyad:

- 2 exposure test sessions L+ 24 trials each
- 1 test session L+ 4 exposure + 12 trials
- 2 exposure control sessions L+ 24 trials each
- 1 control session L+ 4 exposure + 12 trials
- 1 exposure control session R+ 24 trials
- 1 control session R+ 4 exposure + 12 trials
- 1 exposure test session R+ 24 trials
- 1 test session R+ 4 exposure + 12 trials
- 1 exposure test session L+ 24 trials
- 1 test session L+ 4 exposure + 12 trials
- 1 exposure control session L+ 24 trials
- 1 control session L+ 4 exposure + 12 trials
- 1 exposure control session R+ 24 trials
- 1 control session R+ 4 exposure + 12 trials
- 1 exposure test session R+ 24 trials
- 1 test session R+ 4 exposure + 12 trials
- 1 exposure test session L+ 24 trials
- 1 test session L+ 4 exposure + 12 trials
- 1 exposure control session L+ 24 trials
- 1 control session L+ 4 exposure + 12 trials
- 1 exposure control session R+ 24 trials
- 1 control session R+ 4 exposure + 12 trials
- 1 exposure test session R+ 24 trials
- 1 test session R+ 4 exposure + 12 trials

Comprehension sessions

After the testing phase of each dyad, there were two comprehension sessions of 18 trials² each (see Table 3). During these comprehension sessions, the partner was absent. As in the test, the actor could choose to enter either the OR or BR compartment and receive the reward distribution of the compartment they entered, but this time the doors between the 3 compartments (OR, BR and partner compartments) were opened so that the subject had access to both pieces of food if it entered the BR compartment. Moreover, no exposure sessions were run prior to the comprehension sessions to avoid any learning effect. The prosocial side was on the same side as the one of the last testing session. This allowed the actor to move between the three compartments and get the rewards. If the actor understood the outcome of each compartment, he would choose to go to the BR compartment to get two rewards instead of one which they would receive if OR is chosen.

Behaviour coding

Diverse behaviours such as latency in choice making, begging, looking, barking, of three dyads (Nia and Sahibu; Pepeo and Nuru; Maisha and Binti) recorded during the trials were coded as additional data using the program Solomon Coder version beta 15.11.19. The behaviours coded are detailed in a coding sheet (see Table 4). Unfortunately, the videos of the other dyads used for this study were lost due to a technical failure. Therefore behavioural differences between wolves-dogs were not possible to analyse.

² The number of 18 trials was selected to maximize the statistical power of these two sessions.

Analyses

Each actor's choices were analysed separately, due to the small number of subjects and the high degree of variation between individuals.

First, a binomial test was done for the test condition and the control condition separately to check whether the actor was choosing the prosocial side above chance in each condition. For some actors who did not chose randomly the compartment in the control condition (Shima, Yukon, Nia and Maisha), these tests were redone using the percentage of time they chose the BR compartment in the control condition to determine the expected level of choice for the BR compartment in the test condition (i.e. Maisha went 40% of the time in the BR compartment in the control condition, therefore, the choice level of this binomial test was set to 0.4).

To test for a difference in the number of BR choices between the test and control conditions, a Wilcoxon signed rank test was done.

Next, a GLMM model was designed using the lme4 package in the software RStudio version 3.1.1 to determine if and which factors affected the choice of the animals, assessed using a Type III Anova. The number of BR choices was the response variable and session, condition, trial and the BR side were included as main effects. Furthermore, for the dyads for which we were able to code the behaviour, whether or not the partner was on the same side as the actor during their choice was also included as a factor. The identity of the human helpers was included as a random factor to control for potential biases towards certain individuals by the actors.

A second model was similarly designed for two actors, Nia and Pepeo, which had behaviour coding data to determine if and which factors affected their latency between the start of a trial and their choice. The latency was the response variable and session, condition, trial and the BR side as well as the position of the partner were included as main effects. The identity of the human helpers was once again included as a random factor.

The difference in latency between the test and control conditions of the third actor who had behaviour coding data, Maisha, was calculated using a Wilcoxon signed rank test. His difference in latency was tested differently as the result of the Shapiro test done beforehand the second model was significant, preventing us from using the same method as Nia and Pepeo.

Finally, the social bias score (SB) used by Hernandez-Lallement *et al.* was adapted to our data set. The SB of actor i represents the percent change in the total number of BR choices in the test condition $[BR(test)_i]$ relative to all the BR choices in the control condition $[BR(control)_i]$:

$$SB_i = \left[\frac{BR(test)_i - BR(control)_i}{BR(control)_i} \right] * 100$$

The resulting SB-value can be either positive or negative as it quantify the tendency to choose the BR compartment more or less often in the test condition relative to the control condition.

Results

As the data were analysed for each actor separately, this section will be presented actor by actor. The name of the actors and their partners can be found in the annex (Tables 1 and 2). For each of them results are presented for i) whether or not their choices were above chance, ii) whether or not they chose the prosocial side more often in the test than the control, and iii) whether prosocial choices were affected by session, condition, trial or side of the BR. Furthermore, in line with the analyses by Hernandez-Lallement *et al.* in 2015, the social bias score (SB) for each individual is shown. Finally, the comprehension of each subject is also presented. The three conditions allowed us to determine: for the test condition whether the actors were prosocial or not, for the control whether they made a distinction between the BR and OR compartment regardless of the outcome for the partner, and for the comprehension whether the actors understood the experiment. Moreover, all of these conditions were used to determine if the actors had a side bias.

On Figure 1, an overview of the actors' mean prosocial choices per condition is represented.

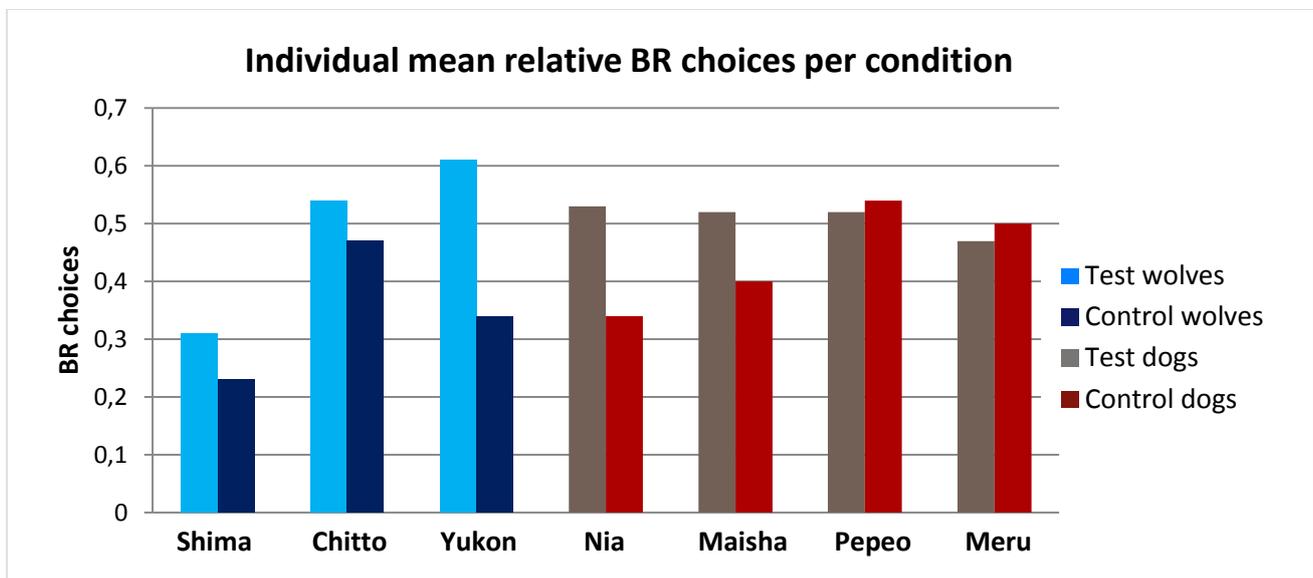


Figure 2 Proportion of BR choices made by each actor per condition. In light blue (wolves) and grey (dogs) are the average number of BR choices per test condition. In navy blue (wolves) and in red (dogs) are the average BR choices per control condition.

Wolves

Shima

i) Using a binomial test, we found that Shima went significantly less than chance to the BR side in both the test condition ($p = 0.0029$, sample estimates, probability of success: 0.31) and the control condition ($p < 0.0001$, sample estimates, probability of success: 0.23). Still using a binomial test but this time to test if Shima was going to the non-prosocial side above chance level, we found that she went significantly less on the prosocial side in both conditions (test: $p = 0.0029$, sample estimates, probability of success: 0.68; control: $p < 0.0001$, sample estimates, probability of success: 0.76). Using a binomial test with a different choice level than 50% (here 0.23), the results of Shima indicated that she still went not significantly less than chance to the BR side in the test condition ($p = 0.0912$, sample estimates, probability of success: 0.31).

ii) A Wilcoxon signed rank test revealed that the number of prosocial choices was similar in test and control condition ($Z = -0.707$, $p = 0.75$) (see Figure 3).

iii) Her choices were strongly affected by the session ($\chi^2 = 54787(1)$, $p = <0.0001$) and the side of the prosocial choice ($\chi^2 = 2044216(1)$, $p = <0.0001$), as well as the interaction of these two factors ($\chi^2 = 121726(1)$, $p = <0.0001$). As there was an interaction, the data of the left side and the right side were analysed separately. When the BR side was on the left, there was a significant effect of session ($\chi^2 = 12.359(1)$, $p = 0.0004$). When the BR side was on the right, the effect of session was only a tendency ($\chi^2 = 3.6176(1)$, $p = 0.0571$). Therefore, Shima was acting extremely differently from one session to another without being affected by the condition ($\chi^2 = 1.6717(1)$, $p = >0.05$) or trial ($\chi^2 = 1.0026(1)$, $p = >0.05$). When only the test condition was taken into account, no factors (session, BR side and trial) were influencing Shima (session: $\chi^2 = 0.0037(1)$, $p = >0.05$; BR side: $\chi^2 = 1.2341(1)$, $p = >0.05$; trial: $\chi^2 = 0.2505(1)$, $p = >0.05$).

iv) Social bias score

Shima had a tendency to choose the BR compartment more often in the test condition than in the control condition with a SB score of 35.29 (35.29% more prosocial choices in the test than in the control condition). This tendency changed with time as her SB score decreased to -33.33 for her last round of sessions (i.e. only her last test and last control session were taken into account). Her first SB score for her first round of sessions was of 0, as she always went on the non-prosocial side.

v) Comprehension

During the two comprehension sessions of Shima, the prosocial side was on the right. Shima went one time on the prosocial side during the first comprehension session and zero during the second, for a total of 1 BR choice on 36 trials ($p = < 0.0001$, sample estimates, probability of success: 0.0277) (see Figure 12), suggesting that either she did not understand the experiment, her side bias was too strong, or she had learned to avoid the BR side due to the frustration to see two pieces of meat and only get one.

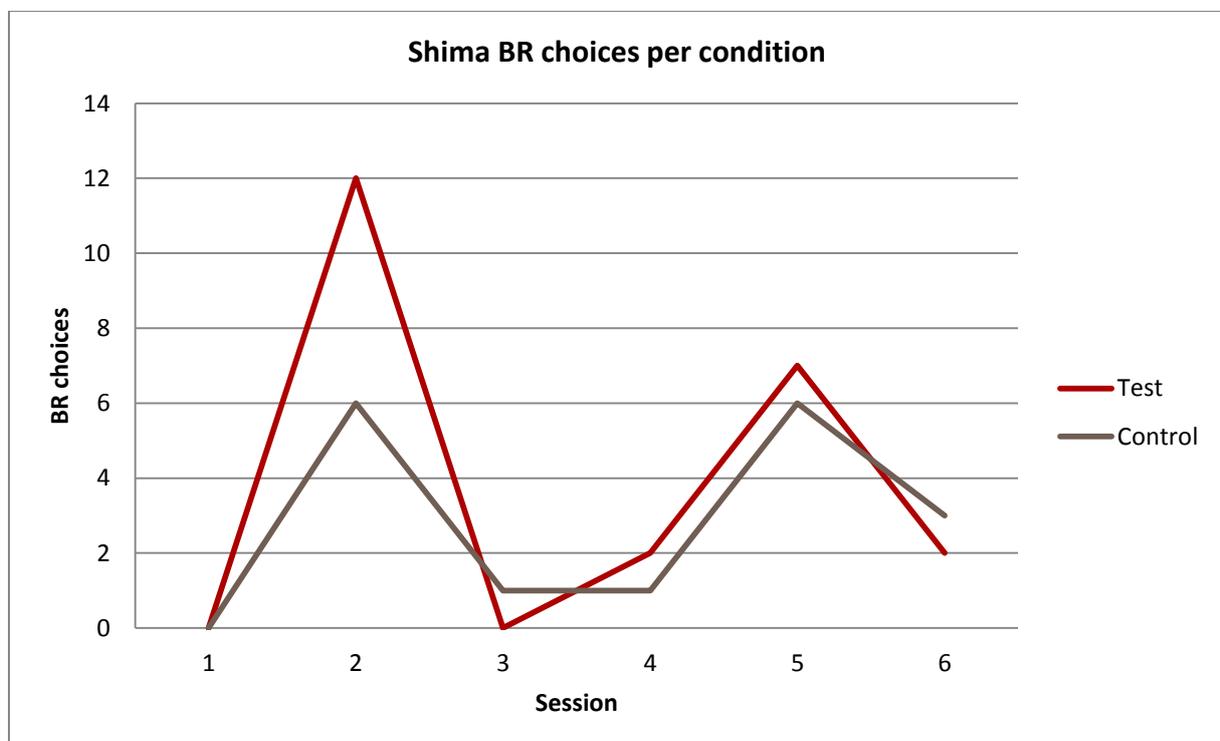


Figure 3 Number of BR choices made by Shima (wolf) during the test condition (red line) and the control condition (grey line).

Chitto

i) Chitto went randomly to each side in both test ($p = 0.63$, sample estimates, probability of success: 0.53) and control ($p = 0.72$, sample estimates, probability of success: 0.47) conditions.

ii) He was indifferent to the condition, with no difference in BR choices between test and control ($Z = -0.948$, $p = 0.37$) (see Figure 4).

iii) Chitto was very random as neither session, condition, trial, or side of the BR seemed to have affected his choices (session: $\chi^2 = 0.4437(1)$, $p = >0.05$; condition: $\chi^2 = 0.0591(1)$, $p = >0.05$; trial: $\chi^2 = 0.0000(1)$, $p = 1$; BR side: $\chi^2 = 0.0102(1)$, $p = >0.05$).

iv) Social bias score

Moreover, Chitto's social bias score (13) is low with only 13% more BR choices in the test than in the control condition. As for Shima, Chitto's number of BR choices in the test condition decreased with time and the BR score of his last round of sessions was -22.67 (22.67% less BR choices in the test condition than in the control condition). In comparison, his first SB score was of 19.4.

v) Comprehension

In both comprehension sessions, Chitto chose the BR side on 10/18 trials (see Figure 12). This result is not above chance ($p = 0.6177$, sample estimates, probability of success: 0.55).

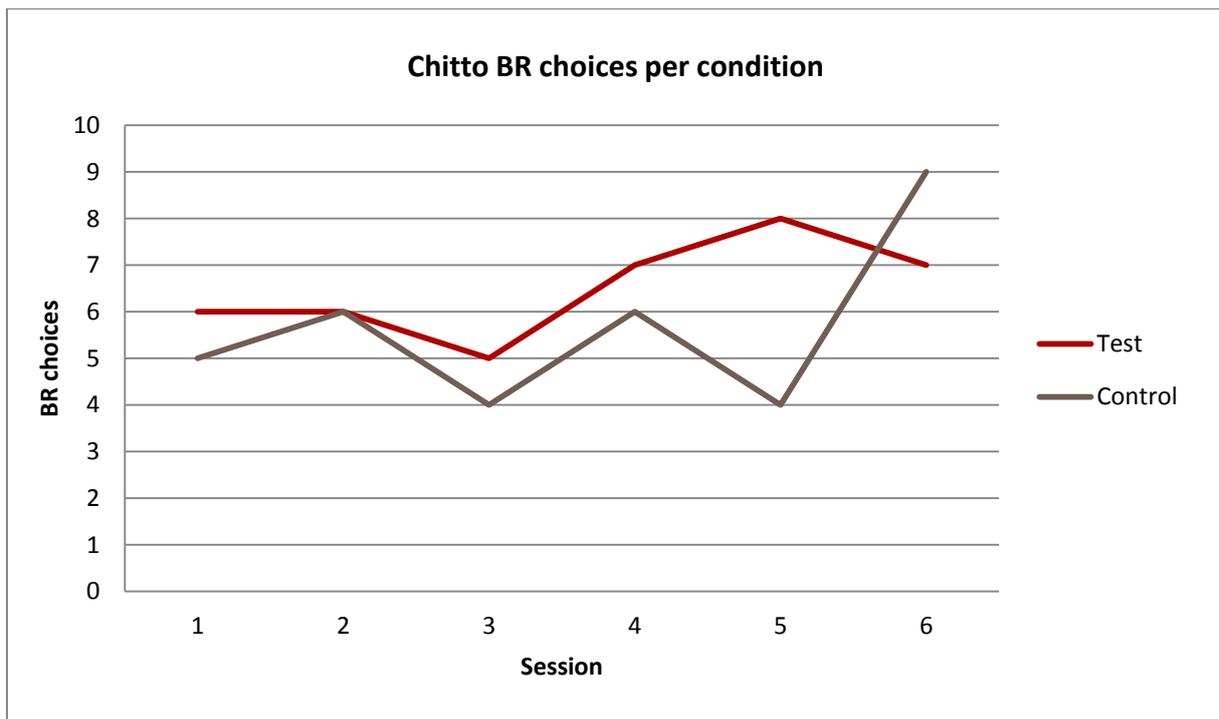


Figure 4 Number of BR choices made by Chitto (wolf) during the test condition (red line) and the control condition (grey line).

Yukon

i) Yukon tended to go more on the prosocial side during the test condition than expected by chance ($p = 0.076$, sample estimates, probability of success: 0.61). On the contrary, she went significantly less on the prosocial side during the control condition ($p = 0.012$, sample estimates, probability of success: 0.34). When taking her probability of going to the BR side in the control condition to set the expected prosocial choice level of the binomial test (0.34), her results became significant ($p = > 0.005$, sample estimates, probability of success: 0.61), meaning that she chose the BR side more than expected by chance in the test condition.

ii) Yukon had a small tendency to choose the prosocial side more in the test than in the control conditions (One sample Wilcoxon signed rank test; $Z = -1.897$, $p = 0.094$) (see Figure 5).

iii) As with Shima, Yukon's choices were affected by the session ($\chi^2 = 66440(1)$, $p = <0.0001$) and the side of the prosocial choice ($\chi^2 = 3295026(1)$, $p = <0.0001$), as well as the interaction of these two factors ($\chi^2 = 200762(1)$, $p = <0.0001$). When the sides were analysed individually, the session had a similar effect when the BR side was on the left ($\chi^2 = 4.3574(1)$, $p = 0.0368$) and on the right ($\chi^2 = 4.3634(1)$, $p = 0.0367$).

iv) Social bias score

Yukon has by far the highest SB score of all the actors of this study with her overall score being 76 (76% more BR choice in the test than in the control condition). Her SB score decreased from her first (57.14) to her last round of sessions (-16.67).

v) Comprehension

Yukon went only 5/18 times on the prosocial side during the first comprehension session and 8 times during the second ($p = 0.1325$, sample estimates, probability of success: 0.3611) (see Figure 12).

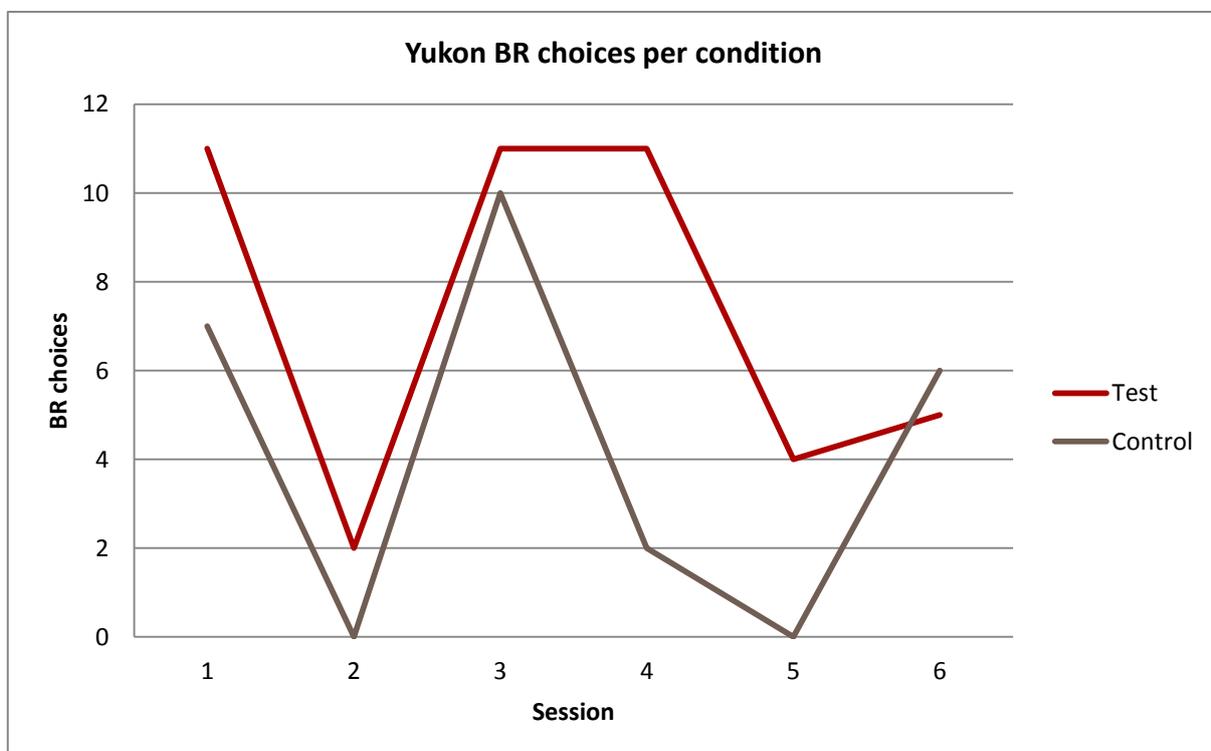


Figure 5 Number of BR choices made by Yukon (wolf) during the test condition (red line) and the control condition (grey line).

Dogs

Nia

i) Nia did not choose the prosocial side above chance in any of the conditions (test condition: $p = 0.81$, sample estimates, probability of success: 0.52; control condition: $p = 0.12$, sample estimates, probability of success: 0.40). When using a 40% choice level in the binomial test for the test condition, her results are still not significant but a tendency to go more on the BR side appeared ($p = 0.03$, sample estimates, probability of success: 0.52).

ii) She made her choices indifferently to the condition (Wilcoxon signed rank test; $Z = -0.674$, $p = 0.62$) (see Figure 6).

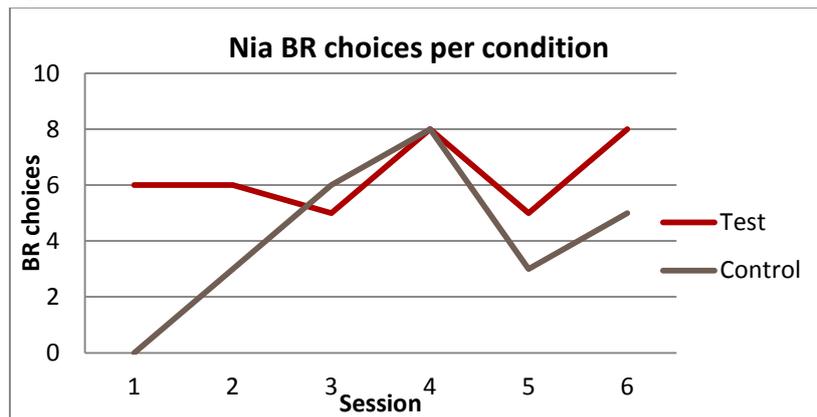


Figure 6 Number of BR choices made by Nia (dog) during the test condition (red line) and the control condition (grey line).

iii) She had a slight tendency to make her choices according to the location of her partner, Sahibu, by going more in the compartment close to his position in the middle compartment than to the other ($\chi^2 = 2.80(1)$, $p = 0.093$), the session, trial and condition didn't had any effect on her choices (session: $\chi^2 = 0.9764(1)$, $p = >0.05$; trial: $\chi^2 = 0.0123(1)$, $p = >0.05$; condition: $\chi^2 = 0.1122(1)$, $p = >0.05$).

Her latency significantly increased across each trial of a session regardless of the condition ($F(1) = 11.86$, $p = <0.0001$) (see Figure 7).

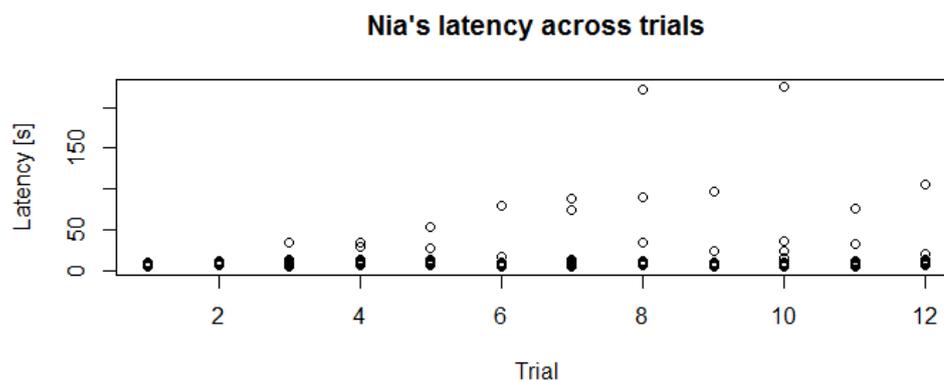


Figure 7 Nia's increase of latency across the 12 trials of a session. All of the circles are open; the darkest ones are the result of numerous superposed open circles.

iv) Social bias score

The SB of her first (test and control) session (50) is consistent with her last (59.52). However her total SB score is only 13.42.

v) Comprehension

Nia went 12/18 times on the prosocial for the first comprehension session and 11 times the second time ($p = 0.1325$, sample estimates, probability of success: 0.6388) (see Figure 12).

Maisha

i) Maisha did not make prosocial choices above chance in the test condition ($p = 0.72$, sample estimates, probability of success: 0.52) nor in the control condition ($p = 0.12$, sample estimates, probability of success: 0.40). As for Nia, when using a 40% choice level in the binomial test for the test condition, Maisha's results are still not significant but a tendency to go more on the BR side also appeared ($p = 0.03$, sample estimates, probability of success: 0.52).

ii) Maisha had a tendency to make more prosocial choices in the test condition than in the control (Wilcoxon signed rank test; $Z = -2.042$, $p = 0.063$) (see Figure 8).

iii) The side of the prosocial choice significantly affected the choice of Maisha ($\chi^2 = 4.66(1)$, $p = 0.03$), suggesting he had a side bias. He also tended to have a higher latency for his choice during his control session than during his test sessions (Once sample Wilcoxon signed rank test; $Z = -1.807$, $p = 0.071$).

iv) Social bias score

Maisha has a total SB score of 13.42. During his first round his SB score was of 60 and 100 for his last. However this score of 100 (100% more prosocial choices during the last test session compared to the last control session) needs to be considered with caution, as Maisha chose only four times the prosocial side in the test condition and two in the control condition.

v) Comprehension

Maisha had a tendency to go more to the non-prosocial side during the comprehension sessions than to the prosocial one ($p = 0.0652$, sample estimates, probability of success: 0.3333). He went only 5 times to the BR side during the first comprehension and 7 during the second so a total of 12 times out of 36 (see Figure 12).

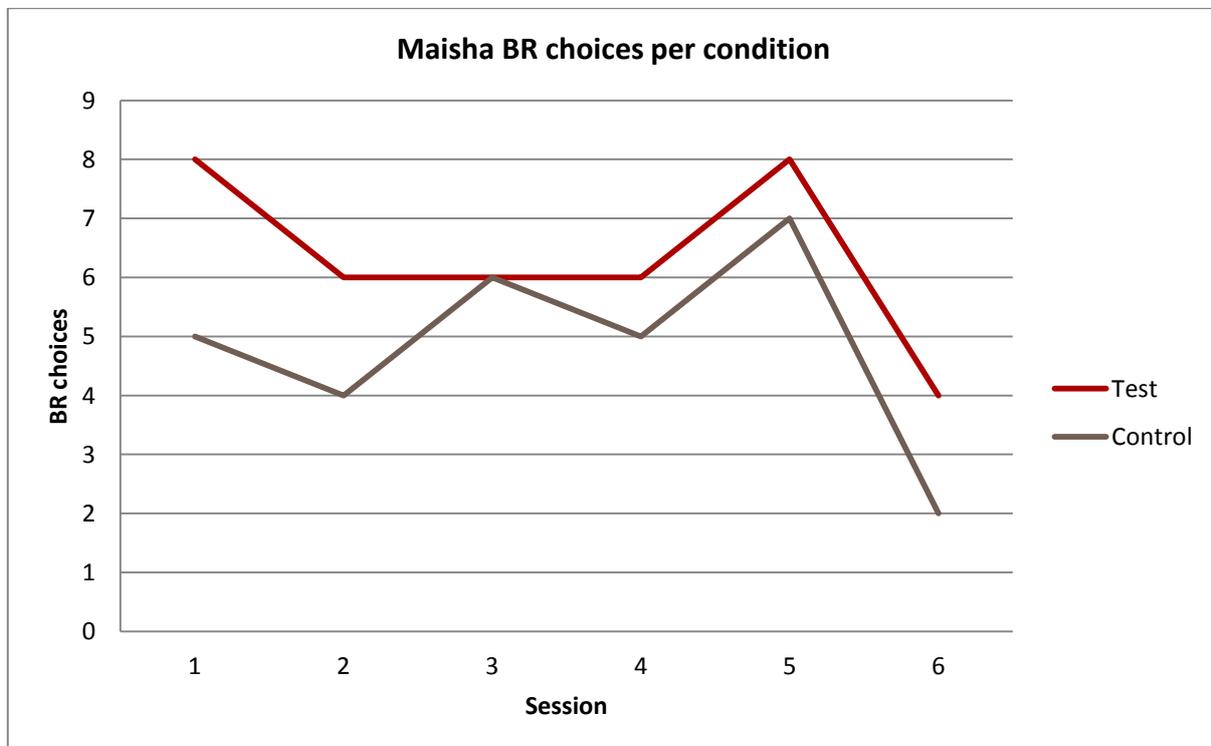


Figure 8 Number of BR choices made by Maisha (dog) during the test condition (red line) and the control condition (grey line).

Pepeo

i) Pepeo was not prosocial above chance (test condition: $p = 0.72$, sample estimates, probability of success: 0.52; control condition: $p = 0.55$, sample estimates, probability of success: 0.54).

ii) Pepeo's choices were almost identical in the test and control conditions ($Z = -0,184$, $p = 1$) (see Figure 9).

iii) His choices were influenced by the session ($\chi^2 = 11.80(1)$, $p = 0.0005$), the side of the prosocial choice ($\chi^2 = 21.04(1)$, $p = < 0.0001$), and the interaction between them ($\chi^2 = 15.63(1)$, $p = < 0.0001$). When the BR side was on the left there was a strong significant effect of session ($\chi^2 = 11.808(1)$, $p = 0.0005$). When the BR side was on the right, the effect of session was also significant, but at a lesser extent than on the left side ($\chi^2 = 4.1476(1)$, $p = 0.0416$). There was no effect of the condition or the trial (condition: $\chi^2 = 0.2484(1)$, $p = >0.05$; trial: $\chi^2 = 0.0471(1)$, $p = >0.05$).

iv) Social bias score

Pepeo had a negative total SB score of -5.56. In comparison, his first was of -16,67 and his last of 0 (7 prosocial choices in his last test condition and 7 in his last control condition).

v) Comprehension

During his first comprehension sessions, Pepeo went 9 times out of 18 to the prosocial side and 11 times out of 18 during the second one (see Figure 12), which is not above chance ($p = 0.6177$, sample estimates, probability of success: 0.5555).

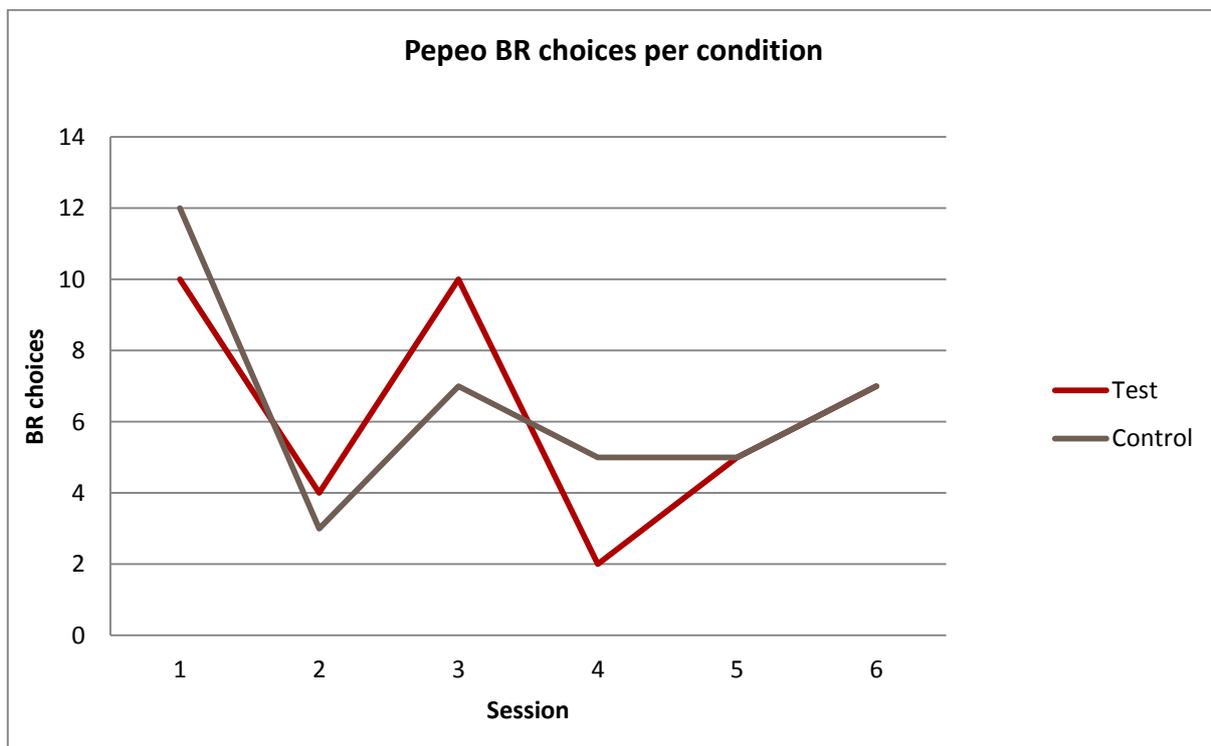


Figure 9 Number of BR choices made by Pepeo (dog) during the test condition (red line) and the control condition (grey line).

Meru

i) Meru was random in his prosocial choices in both conditions (test condition: $p = 0.72$, sample estimates, probability of success: 0.47; control condition: $p = 1$, sample estimates, probability of success: 0.5).

ii) Again there was no difference in prosocial choice in test and control ($Z = -0,743$, $p = 0.5$) (see Figure 10).

iii) It seems that the side of the prosocial choice slightly influenced the choices of Meru ($\chi^2 = 2.76(1)$, $p = 0.09$).

iv) Social bias score

Like Pepeo, Meru is the only other actor with a negative total SB score of -5.56, which is too small to classify them as non-prosocial individual, as he chooses almost the same amount of time the prosocial side in the test and the control condition. The SB score of his first round of condition was of -33.33 and his last, as Pepeo, was 0.

v) Comprehension

Meru went 9/18 times on the prosocial side during his first comprehension session and 15 during the second (see Figure 12). He is the actor who went the most on the prosocial side during the comprehension sessions. Even if his result is not significant, it shows that Meru had a tendency to go more to the prosocial side than to the other during these two sessions ($p = 0.0652$, sample estimates, probability of success: 0.6666).

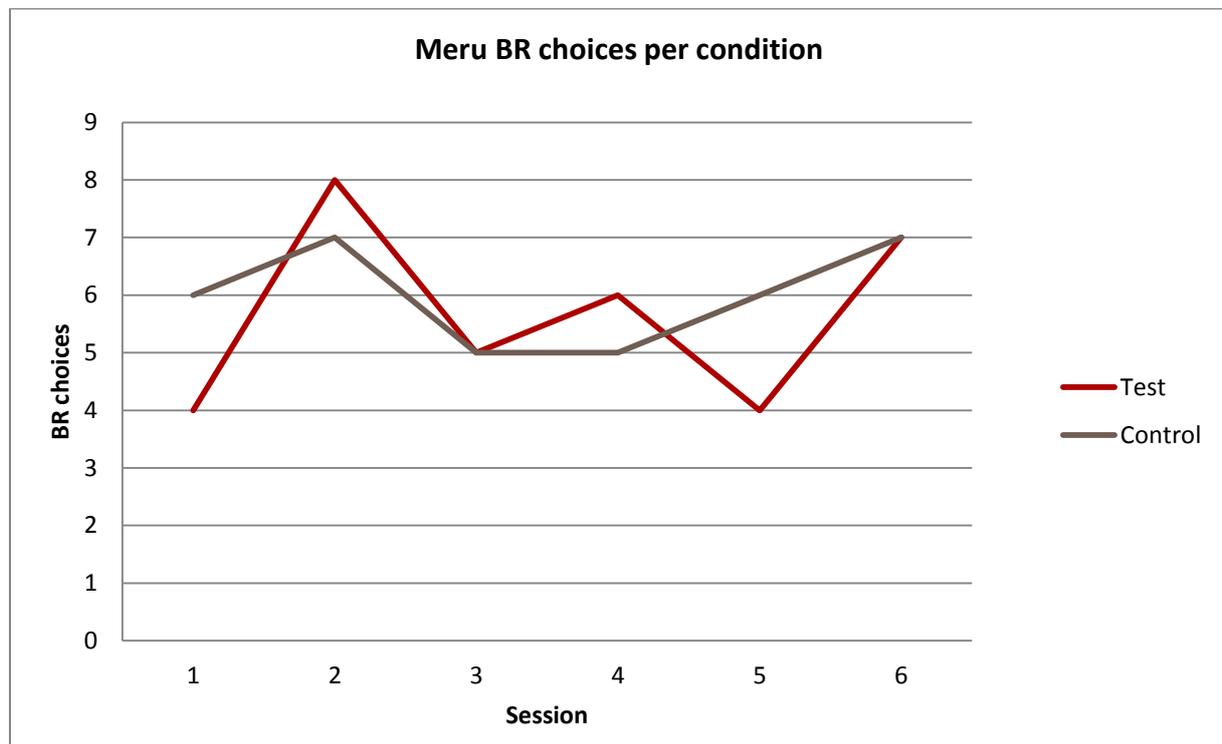


Figure 10 Number of BR choices made by Meru (dog) during the test condition (red line) and the control condition (grey line).

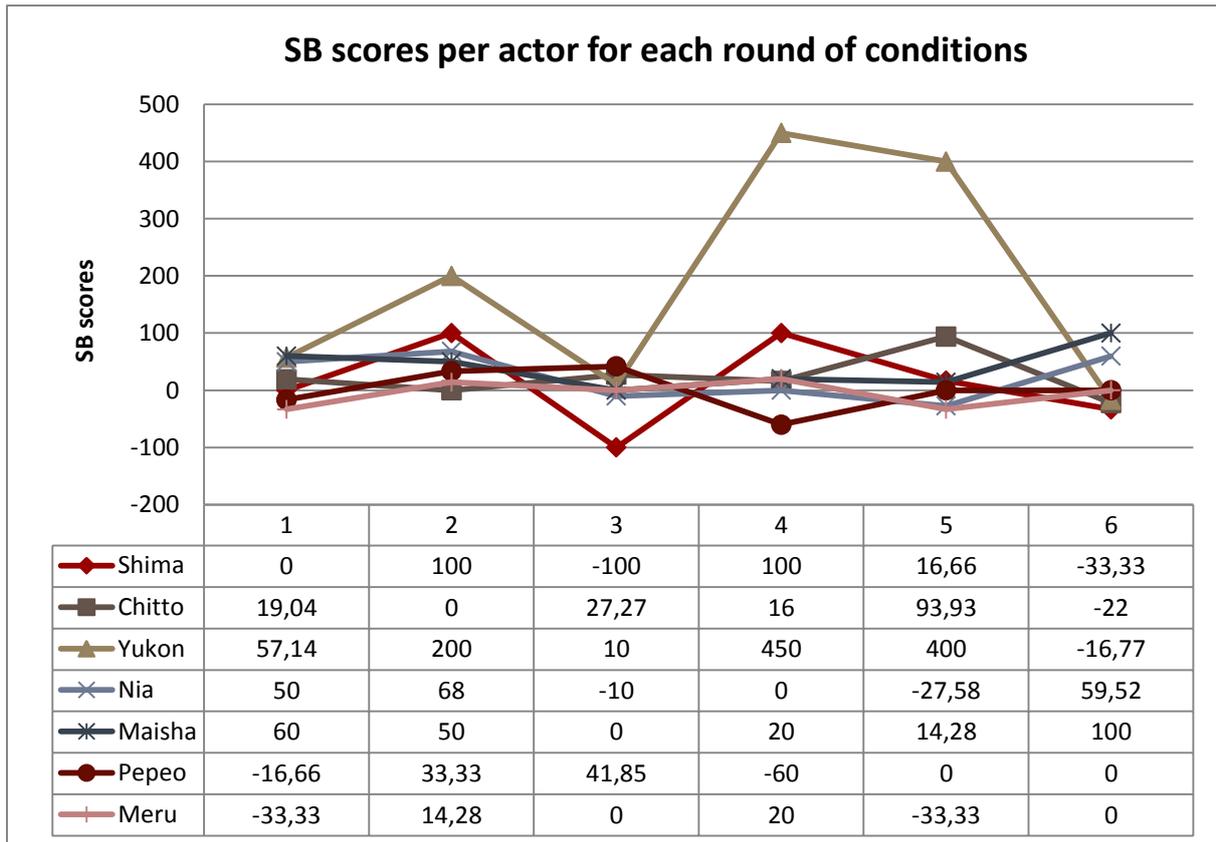


Figure 11 SB scores (positive and negative) of each actor for the 6 rounds of conditions (test and control). Shima, Chitto and Yukon are wolves and Nia, Maisha, Pepeo and Meru are dogs.

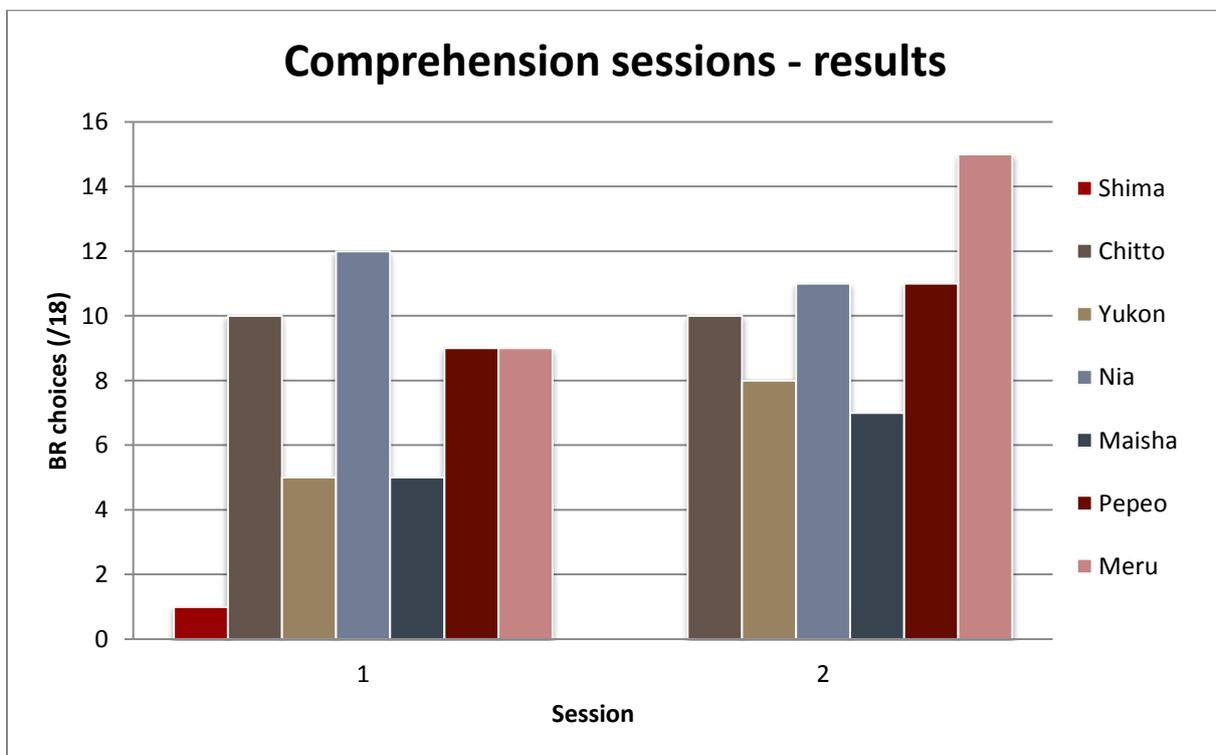


Figure 12 Results of the two comprehension sessions for each of the actors. Shima, Chitto and Yukon are the wolves. Nia, Maisha, Pepeo and Meru are the dogs.

Discussion

By adapting the rodent version of a Prosocial Choice Task designed by Hernandez-Lallement *et al.* (2015) to canids, we were able to test whether dogs and wolves were prosocial in a single T-maze setup. To achieve this adaptation, the whole design needed to be rethought to fit the infrastructures of the Wolf Science Centre and match the needs of the actors and partners.

Overall our results did not show any individual that acted prosocially above chance. The results of the Wilcoxon test and the SB scores are sometimes quite contrasting and a high number of our actors might have been influenced by side preference (see below). All in all, the number of trials might have not been enough to mimic and compare the results of Hernandez-Lallement *et al.* (2015), as our wolves and dogs did 72 free choice trials per condition versus 105 to 150 free choice trials per condition for the rats. This difference between the number of trials of the rats and our actors is explained by the difficulty to work with larger animals, since the sessions took much longer with canids, our set-up was bigger, the distances between the choices larger, and only a few trials could be run by the animals before a decrease in their motivation, as Nia's and Maisha's results in latency showed it (see below).

The SB scores of the actors, which represent the relative difference in prosocial behaviour between test and control conditions, ranged from -5.56 (5.56% less prosocial choices in the test condition than in the control condition) to 76 (76% more prosocial choices in the test condition than in the control condition). In detail, two dogs scored at -5.56, two dogs and one wolf ~13, one wolf at 35.29 and the last wolf at 76. In comparison, the SB scores of the rats used in the study of Hernandez-Lallement *et al.* (2015) ranged from -14.8 to 45.6 (from 14.8% less prosocial choice in the partner condition than in the toy condition to 45.6% more prosocial choices in the test condition than in the toy condition). As with the rats, our results present a high degree of heterogeneity. However, contrary to the rats, none of the dogs or the wolves' prosociality level was above chance in the test, even for Yukon who had a very high SB score. In addition, if we only take into account the way they made their choices we can see that the SB score does not necessarily match up with the other measures of prosociality. Indeed, it is important to note that despite a positive SB score it is still possible to have an animal is not prosocial, as the SB scores depend only on the number of BR choices in the test relative to the number of BR choices in the control condition. Therefore, an animal making, for example, four prosocial choices in a test and three prosocial choices in a control will have for these two sessions a SB score of 33.33 (i.e. 33.33% more prosocial choices in the test condition than in the control condition). However, by looking at the total number of trials, there are only 4/12 prosocial choices in the test session and 3/12 in the control condition, which cannot qualify as a prosocial behaviour and explains why we can have such diverse results with the same data but different ways of analysing them. Taking Shima as an example, even with a SB score of 35.29, she still went significantly less to the prosocial side than chance during both conditions when the results of the binomial tests are taken into account. As for the difference in the two conditions, the result of the Wilcoxon test was also not significant. Moreover, Shima had a strong side bias, which likely precluded the possibility to assess the presence or absence of prosociality. In fact, she had a strong preference for the right side at the beginning of the testing period and for the left side at the end. As the side of the conditions also changed, there were some test sessions in which Shima made more prosocial choices than in the control ones, and only a few more trials in the test condition compared to the control condition is sufficient to completely change the SB score.

Thus, the side bias of some animals need to be taken into account and the results interpreted with caution, as Shima would be labelled as prosocial when only her SB score is considered but non-prosocial when the binomial test results are included. By looking at her binomial test results, Shima also went only 23% of the time on the prosocial side during the control sessions and 31% of the time during the test session, which definitely does not qualify her as a prosocial individual. Shima, Maisha, Pepeo were all influenced by the side of the prosocial choice. Meru and Yukon were also influenced but at a lesser scale, for example, the side of the prosocial side as well as the session both had an effect on Yukon's choices, but there was still no difference in her amount of choices between the left and the right side. To counterbalance these side biases, a larger sample size and especially a higher number of trials would be needed.

These side biases might also have impeded on the results of the comprehension sessions (see Figure 12). If we take the example of Shima again, she went only once on the prosocial side, which was on the right, during her two comprehension sessions. At this time, she had a strong preference for the left side. Indeed, as it was comprehension sessions, we cannot disregard that this result might simply reflect the fact the Shima, along with the other actors, did not understand the task. However, given the side bias results, conclusions cannot be made regarding comprehension at this stage.

The pack composed of Chitto, Kaspar, Aragorn, Shima and a fifth wolf not involved in this study had a number of separations and reunions that happened in April 2016, at the same time as the end of Shima and Chitto's testing period. In the end, Chitto was no longer in the same pack as his partner, Kaspar. These events might also partly explain the non-prosocial results of these two actors.

In contrast to Hernandez-Lallement *et al.*'s study (2015), the prosocial choices of our animals did not increase over time (see Figure 11). Changes in the amount of prosocial choices across time could be due to disruptions to the pack structure (e.g. females in heat, pack composition changes). Or the actors might have learned the differences between the two conditions and made their choices according to this knowledge. For example, Maisha had a tendency to go more on the prosocial side during the test conditions than during the control conditions. It would be interesting to continue this experiment with him and see if, with more trials, this difference in the two conditions would become significant. Alternatively, avoidance of the prosocial side might have been due to the frustration of seeing two rewards but only receiving one of them, as he went less on the prosocial side in both of the conditions during the last round of sessions.

Yukon also seemed to make a difference between the two conditions as she went significantly less than expected by chance on the prosocial choice in the control condition but not in the test condition, in which she had a tendency to go more on the prosocial side than to the non-prosocial side. This difference might be due, as for Maisha, to the frustration of seeing two sticks carrying meat but being able to access only one and see the other one taken away by the experimenter and not given to her partner.

As previously mentioned (see section Behaviour coding), most videos of the experiment were lost. Redoing this whole experiment and filming it would be interesting to determine if, for example, begging behaviours had an impact on prosociality, as it has been found for chimpanzees (Melis *et al.*, 2011; Horner *et al.*, 2011). For those dyads where the behaviour could be coded, the latency and the location of the partner at the time of the choice of the actor were taken into account. The results of Pepeo showed that he was not influenced by these two factors. Nia and Maisha both showed an increased latency between the beginning

and the end of a session (see Figure 7 for Nia's latency representation). This could be due to the decrease of appetite or interest over time, as a session could be quite long for the animals. Interestingly, Maisha had a higher latency for his choice during his control sessions than his test sessions, which indicates that he made a distinction between the two conditions. Finally, Nia was influenced by the position of her partner, Sahibu. Indeed, when she was making her choices, she had a tendency to choose the side that was closer to the location of her partner, regardless of the condition. Nia might have been seeking proximity to her partner as in fact, social contact seeking, not empathy, has found to be a driver of prosocial behaviour in other studies (Silberger *et al.*, 2014).

These results suggest that there was an issue in the experimental design as the actors should have been random in their BR and OR choices in the control condition and not have an aversion for the BR side regardless of the outcome. Indeed, if there was such an aversion and some individuals still went to the BR side in the test condition, it would suggest that they were willing to make their partner benefit of the situation. Therefore, the binomial tests of the four actors which were not choosing randomly the compartments in the control condition (Shima, Yukon, Nia and Maisha) were redone. The percentage of time they chose the BR compartment in the control condition was used to set the expected level of choice for the BR compartment in the test condition (i.e. Maisha went 40% of the time in the BR compartment in the control condition, therefore, the choice level of the binomial test was set to 0.4). With this modified chance level, the results of Yukon became significant ($p = <0.005$) indicating that, when using this new choice level, she had chosen the BR compartment significantly more in the test condition than in the control condition and could be considered as fully prosocial. The design of the experiment should therefore be modified to correct this issue in future researches.

Yukon, as previously mentioned, got a high SB score (76) and also had a tendency to go more on the BR side than chance during the test condition (61% of the time) and less during the control conditions (only 34% of the time). Maisha, who had a lower SB core than Yukon (13.42 versus 76), had also a tendency to be more prosocial in the test condition than in the control condition. Although not conclusive, perhaps due to power issues in the statistical analyses, these results still suggest some prosociality in these two individuals. The prosocial choices they made during this experiment might have been motivated by diverse reasons or mechanisms, such as a spontaneous impulse to help other individuals (spontaneous/proactive prosociality), the calculation of what future benefit could result from the situation (calculated reciprocity), or even by resignation after being harassed or intimidated by the receiver for help/food (Burkart *et al.*, 2009). The rats of Hernandez-Lallement *et al.* (2015), which were all strangers to each other, showed spontaneous prosociality as their behaviour did not required any kind of solicitation or expectation of reciprocation, but was only the result of a motivational predisposition (Burkart *et al.*, 2009). However, as the actors and partners used at the Wolf Science Centre live together, we cannot know the type of prosociality we observed using the same PCT without monitoring the changes or absence of change in their behaviour after this test. For example, it might be that Yukon made more prosocial choices than the other actors in order to get food from her partner, Geronimo, when they were back together in their enclosure after a test session (i.e. in this case, she would have shown calculated reciprocity). Therefore to check for calculated reciprocity, it would be necessary to reverse the role of the actor and the partner, here Geronimo, and see if he would be more prosocial than the other actors.

With the exception of maybe one wolf female (Yukon) and a male dog (Maisha) we found no indication of prosociality in this set-up, as well as no obvious difference between the level of prosociality in wolves and dogs, were found. In addition, a great individual variation was found. This variation does not allow us to make conclusions regarding species differences. For example, Yukon can be considered as the most prosocial actor of the study and Shima the least, despite both being wolves and being paired with their brothers. Therefore, to assess any general species differences, a larger sample size would be needed. Also, this design might have been cognitively too demanding as no actor went above chance in the comprehension sessions.

In conclusion, despite no massive difference between the wolves and the dogs, the finding of tentative prosociality in one wolf and one dog is consistent with our second prediction as this slightly leans in the direction of supporting the Canine Cooperation Hypothesis (Range & Virányi, 2015), rather than the domestication hypothesis (Hare & Tomasello, 2005; Miklósi & Topál, 2013). Prosociality might therefore be present in species with high levels of cooperation, social breeding and foraging. However, this conclusion needs to be treated with caution as this study would require more trials with the same dyads to mimic the number of trials in the rat study of Hernandez-Lallement *et al.* and see if our results would meet theirs at some point.

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Tables

Table 3 Order of the sessions per dyads, side of the pro-social compartment and number of trials.

Species	Actor	Partner	Session	Pro-social side	Nbr of trials
Wolf	Chitto	Kaspar	Exposure test	Right	24
Wolf	Chitto	Kaspar	Exposure test	Right	24
Wolf	Chitto	Kaspar	Test condition	Right	4+12
Wolf	Chitto	Kaspar	Exposure control	Right	24
Wolf	Chitto	Kaspar	Exposure control	Right	24
Wolf	Chitto	Kaspar	Control condition	Right	4+12
Wolf	Chitto	Kaspar	Exposure control	Left	24
Wolf	Chitto	Kaspar	Control condition	Left	4+12
Wolf	Chitto	Kaspar	Exposure test	Left	24
Wolf	Chitto	Kaspar	Test condition	Left	4+12
Wolf	Chitto	Kaspar	Exposure test	Right	24
Wolf	Chitto	Kaspar	Test condition	Right	4+12
Wolf	Chitto	Kaspar	Exposure control	Right	24
Wolf	Chitto	Kaspar	Control condition	Right	4+12
Wolf	Chitto	Kaspar	Exposure control	Right	24
Wolf	Chitto	Kaspar	Control condition	Right	4+12
Wolf	Chitto	Kaspar	Exposure test	Right	24
Wolf	Chitto	Kaspar	Test condition	Right	4+12
Wolf	Chitto	Kaspar	Exposure test	Left	24
Wolf	Chitto	Kaspar	Test condition	Left	4+12
Wolf	Chitto	Kaspar	Exposure control	Left	24
Wolf	Chitto	Kaspar	Control condition	Left	4+12
Wolf	Chitto	Kaspar	Exposure control	Right	24
Wolf	Chitto	Kaspar	Control condition	Right	4+12
Wolf	Chitto	Kaspar	Exposure test	Right	24
Wolf	Chitto	Kaspar	Test condition	Right	4+12
Wolf	Chitto	-	Comprehension	Right	18
Wolf	Chitto	-	Comprehension	Right	18
Wolf	Shima	Aragorn	Exposure control	Left	24
Wolf	Shima	Aragorn	Exposure control	Left	24
Wolf	Shima	Aragorn	Control condition	Left	4+12
Wolf	Shima	Aragorn	Exposure test	Left	24
Wolf	Shima	Aragorn	Exposure test	Left	24
Wolf	Shima	Aragorn	Test condition	Left	4+12
Wolf	Shima	Aragorn	Exposure test	Right	24
Wolf	Shima	Aragorn	Test condition	Right	4+12
Wolf	Shima	Aragorn	Exposure control	Right	24
Wolf	Shima	Aragorn	Control condition	Right	4+12
Wolf	Shima	Aragorn	Exposure control	Left	24
Wolf	Shima	Aragorn	Control condition	Left	4+12
Wolf	Shima	Aragorn	Exposure control	Left	24
Wolf	Shima	Aragorn	Control condition	Left	4+12
Wolf	Shima	Aragorn	Exposure test	Left	24
Wolf	Shima	Aragorn	Test condition	Left	4+12
Wolf	Shima	Aragorn	Exposure test	Right	24
Wolf	Shima	Aragorn	Test condition	Right	4+12
Wolf	Shima	Aragorn	Exposure control	Right	24
Wolf	Shima	Aragorn	Control condition	Right	4+12
Wolf	Shima	Aragorn	Exposure control	Left	24
Wolf	Shima	Aragorn	Control condition	Left	4+12
Wolf	Shima	Aragorn	Exposure test	Left	24
Wolf	Shima	Aragorn	Test condition	Left	4+12
Wolf	Shima	Aragorn	Exposure test	Right	24
Wolf	Shima	Aragorn	Test condition	Right	4+12
Wolf	Shima	Aragorn	Exposure control	Right	24
Wolf	Shima	Aragorn	Control condition	Right	4+12
Wolf	Shima	-	Comprehension	Left	18

Wolf	Shima	-	Comprehension	Left	18
Wolf	Yukon	Geronimo	Exposure test	Right	24
Wolf	Yukon	Geronimo	Exposure test	Right	24
Wolf	Yukon	Geronimo	Test condition	Right	4+12
Wolf	Yukon	Geronimo	Exposure control	Right	24
Wolf	Yukon	Geronimo	Exposure control	Right	24
Wolf	Yukon	Geronimo	Control condition	Right	4+12
Wolf	Yukon	Geronimo	Exposure test	Left	24
Wolf	Yukon	Geronimo	Test condition	Left	4+12
Wolf	Yukon	Geronimo	Exposure control	Left	24
Wolf	Yukon	Geronimo	Control condition	Left	4+12
Wolf	Yukon	Geronimo	Exposure test	Right	24
Wolf	Yukon	Geronimo	Test condition	Right	4+12
Wolf	Yukon	Geronimo	Exposure control	Right	24
Wolf	Yukon	Geronimo	Control condition	Right	4+12
Wolf	Yukon	Geronimo	Exposure test	Left	24
Wolf	Yukon	Geronimo	Test condition	Left	4+12
Wolf	Yukon	Geronimo	Exposure control	Left	24
Wolf	Yukon	Geronimo	Control condition	Left	4+12
Wolf	Yukon	Geronimo	Exposure test	Right	24
Wolf	Yukon	Geronimo	Test condition	Right	4+12
Wolf	Yukon	Geronimo	Exposure control	Right	24
Wolf	Yukon	Geronimo	Control condition	Right	4+12
Wolf	Yukon	Geronimo	Exposure test	Left	24
Wolf	Yukon	Geronimo	Test condition	Left	4+12
Wolf	Yukon	Geronimo	Exposure control	Left	24
Wolf	Yukon	Geronimo	Control condition	Left	4+12
Wolf	Yukon	-	Comprehension	Right	18
Wolf	Yukon	-	Comprehension	Right	18
Dog	Pepeo	Nuru	Exposure test	Left	24
Dog	Pepeo	Nuru	Exposure test	Left	24
Dog	Pepeo	Nuru	Test condition	Left	4+12
Dog	Pepeo	Nuru	Exposure control	Left	24
Dog	Pepeo	Nuru	Exposure control	Left	24
Dog	Pepeo	Nuru	Control condition	Left	4+12
Dog	Pepeo	Nuru	Exposure control	Right	24
Dog	Pepeo	Nuru	Control condition	Right	4+12
Dog	Pepeo	Nuru	Exposure test	Right	24
Dog	Pepeo	Nuru	Test condition	Right	4+12
Dog	Pepeo	Nuru	Exposure test	Left	24
Dog	Pepeo	Nuru	Test condition	Left	4+12
Dog	Pepeo	Nuru	Exposure control	Left	24
Dog	Pepeo	Nuru	Control condition	Left	4+12
Dog	Pepeo	Nuru	Exposure control	Right	24
Dog	Pepeo	Nuru	Control condition	Right	4+12
Dog	Pepeo	Nuru	Exposure test	Right	24
Dog	Pepeo	Nuru	Test condition	Right	4+12
Dog	Pepeo	-	Comprehension	Left	18
Dog	Pepeo	-	Comprehension	Left	18
Dog	Maisha	Binti	Exposure test	Right	24
Dog	Maisha	Binti	Exposure test	Right	24
Dog	Maisha	Binti	Test condition	Right	4+12

Dog	Maisha	Binti	Exposure control	Right	24
Dog	Maisha	Binti	Exposure control	Right	24
Dog	Maisha	Binti	Control condition	Right	4+12
Dog	Maisha	Binti	Exposure control	Left	24
Dog	Maisha	Binti	Control condition	Left	4+12
Dog	Maisha	Binti	Exposure test	Left	24
Dog	Maisha	Binti	Test condition	Left	4+12
Dog	Maisha	Binti	Exposure test	Right	24
Dog	Maisha	Binti	Test condition	Right	4+12
Dog	Maisha	Binti	Exposure control	Right	24
Dog	Maisha	Binti	Control condition	Right	4+12
Dog	Maisha	Binti	Exposure control	Left	24
Dog	Maisha	Binti	Control condition	Left	4+12
Dog	Maisha	Binti	Exposure test	Left	24
Dog	Maisha	Binti	Test condition	Left	4+12
Dog	Maisha	Binti	Exposure test	Right	24
Dog	Maisha	Binti	Test condition	Right	4+12
Dog	Maisha	Binti	Exposure control	Right	24
Dog	Maisha	Binti	Control condition	Right	4+12
Dog	Maisha	Binti	Exposure control	Left	24
Dog	Maisha	Binti	Control condition	Left	4+12
Dog	Maisha	Binti	Exposure test	Left	24
Dog	Maisha	Binti	Test condition	Left	4+12
Dog	Maisha	-	Comprehension	Right	18
Dog	Maisha	-	Comprehension	Right	18
Dog	Nia	Sahibu	Exposure control	Right	24
Dog	Nia	Sahibu	Exposure control	Right	24
Dog	Nia	Sahibu	Control condition	Right	4+12
Dog	Nia	Sahibu	Exposure test	Right	24
Dog	Nia	Sahibu	Exposure test	Right	24
Dog	Nia	Sahibu	Test condition	Right	4+12
Dog	Nia	Sahibu	Exposure test	Left	24
Dog	Nia	Sahibu	Test condition	Left	4+12
Dog	Nia	Sahibu	Exposure control	Left	24
Dog	Nia	Sahibu	Control condition	Left	4+12
Dog	Nia	Sahibu	Exposure control	Right	24
Dog	Nia	Sahibu	Control condition	Right	4+12
Dog	Nia	Sahibu	Exposure test	Right	24
Dog	Nia	Sahibu	Test condition	Right	4+12
Dog	Nia	Sahibu	Exposure test	Left	24
Dog	Nia	Sahibu	Test condition	Left	4+12
Dog	Nia	Sahibu	Exposure control	Left	24
Dog	Nia	Sahibu	Control condition	Left	4+12
Dog	Nia	-	Comprehension	Right	18
Dog	Nia	-	Comprehension	Right	18
Dog	Meru	Hiari	Exposure control	Left	24
Dog	Meru	Hiari	Exposure control	Left	24
Dog	Meru	Hiari	Control condition	Left	4+12
Dog	Meru	Hiari	Exposure test	Left	24
Dog	Meru	Hiari	Exposure test	Left	24
Dog	Meru	Hiari	Test condition	Left	4+12
Dog	Meru	Hiari	Exposure test	Right	24

Dog	Meru	Hiari	Test condition	Right	4+12
Dog	Meru	Hiari	Exposure control	Right	24
Dog	Meru	Hiari	Control condition	Right	4+12
Dog	Meru	Hiari	Exposure control	Left	24
Dog	Meru	Hiari	Control condition	Left	4+12
Dog	Meru	Hiari	Exposure test	Left	24
Dog	Meru	Hiari	Test condition	Left	4+12
Dog	Meru	Hiari	Exposure test	Right	24
Dog	Meru	Hiari	Test condition	Right	4+12
Dog	Meru	Hiari	Exposure control	Right	24
Dog	Meru	Hiari	Control condition	Right	4+12
Dog	Meru	Hiari	Exposure control	Left	24
Dog	Meru	Hiari	Control condition	Left	4+12
Dog	Meru	Hiari	Exposure test	Left	24
Dog	Meru	Hiari	Test condition	Left	4+12
Dog	Meru	Hiari	Exposure test	Right	24
Dog	Meru	Hiari	Test condition	Right	4+12
Dog	Meru	Hiari	Exposure control	Right	24
Dog	Meru	Hiari	Control condition	Right	4+12
Dog	Meru	-	Comprehension	Right	18
Dog	Meru	-	Comprehension	Right	18

Table 4: Video coding sheet

<u>Variable / Behaviours</u>	<u>Variable / Behaviour type</u>	<u>Description</u>
# Trial variables		
Start	Point event	A trial starts when the experimenter shouts ok
Stop	Point event	A trial stops when the experimenter shouts ok again, after the reward(s) have been consumed.
Trial	State event	The period between start and stop. This state can be used as a marker to extract the behaviours that occur within each trial.
Enter enclosure (Ent)	Point event	The moment the actor takes to reach a compartment after the trainer released it. The actor is considered to have entered the enclosure when all four feet are across the threshold. Coded in the coding sheets of both animals (in order to use it as a marker for the partner's location) but only the actor's behaviour is of interest.
# Frustration/stress behaviours		
Yawning (Yaw)	Point event	To open the jaws wide without vocalizing
Laying down (La)	State event	The actor and/or the partner lie on the ground in the test enclosure or in one of the three compartments.
Sitting (Sit)	State event	The actor and/or the partner sit on the ground during a trial. Sitting next to the trainer in between the trials is not taken into consideration.
Scratching (Scr)	Point event	To scratch any part of the body.
Licking (Li)	Point event	To lick any part of the body, including lips licking.
Escape (Esc)	State event	The body of the animal is orientated toward one of the two lateral slides. The animal is either scratching the slide with their paws or pushing it with their nose.
Reach Food (ReFo)	Point event	Attempting to put nose and/or paws through the fence in the direction of the food or digging at the location where the food is delivered. Only coded when the actor is present on the other side of the fence (during a reward event).
# Social interaction (actor and partner)		
Inspection (Ins)	Point event	To interact in a friendly way through the separation fence; stand next to each other, rubbing against each other side by side, smelling each other, putting heads together and licking, sniffing and so on.
Stand friendly (sf)	Point event	The subject stands with tail perpendicular to or below the plane of the back, wagging it, ears pointed forward, while another is approaching it or orienting/looking towards it.
Social sniff (Ss)	Point event	To sniff in direction of the receiver through the lateral fences.
Greeting (Gre)	Point event	To interact in a friendly and relaxed manner holding the ears back, showing much tail wagging and licking of the other's mouth/muzzle. The subject however does not show crouching/lowered hindquarters nor is the tail tucked between the legs.
Look (Lk)	State event	Head oriented toward the actor/partner dog.
Stand tall (st)	Point event	Animal straightens up to full height, with a rigid posture and tail, may include raised hackles, ears erect and tail perpendicular or above the back.
Threat (th)	State event	Animal orients towards another performing one or more of the following: staring at, curling of the lips, baring of the canines, raising the hackles, snarling, growling, and barking, sometimes with the tail perpendicular or above the back.
Snapping (sp)	Point event	To snap teeth into the air, noisily.
# Vocalizations (actor and partner)		
Barking (ba)	State event	A short explosive outburst and coarse voice, sounds like wuf.
Howling (Ho)	State event	The partner or the actor emits a long plaintive sound.
Growling (Gro)	State event	A very low frequency, noisy vocalization of widely varying length.
Whine (Wh)	State event	High, elongated and tonal sounds.

# Partner's position		
Left (Le)	State event	The partner is sitting, stopping or laying in the left part of the compartment for at least two seconds.
Middle (Mid)	State event	The partner is sitting, stopping or laying in the middle part of the compartment for at least two seconds.
Right (Ri)	State event	The partner is sitting, stopping or laying in the right part of the compartment for at least two seconds.
Pacing (Pac)	State event	The partner is walking back and forth in its compartment.