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Investigating the reputation formation in dogs *(Canis lupus familiaris)* and wolves *(Canis lupus)*

Master Thesis

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Abstract

The ability to form reputations of others is considered a key component in the social interactions of group-living animals. Considering the great dependence of domesticated dogs *(Canis lupus familiaris)* on their human caretakers, it would be beneficial for them to form reputations of humans to choose the most appropriate partner with whom to interact. Previous studies on direct reputation formation in dogs have resulted in mixed outcomes. The current study investigated whether equally socialized dogs and wolves *(Canis lupus)* can form reputations of unfamiliar human partners in a food-involving context, where a generous partner fed the animal and a selfish partner kept the food to herself. We also tested whether this socio-cognitive ability is an effect of domestication or inherited from their ancestor, the wolves. We found no support for our hypothesis that dogs and wolves can form reputations of humans through direct experience, but we hesitate to conclude that dogs and wolves lack the ability to form reputations based on the small sample of tested individuals. Further, we did not find conclusive evidence for the question of how and if the domestication process changed the cognitive and social skills of dogs. Possible explanations for these results are discussed and the importance of future research is stressed, as this study provides the first data of reputation formation in dogs and wolves that experience the same socialisation with humans.

Keywords: direct reputation formation, cooperation, domestication, dogs, wolves, Canine Cooperation Hypothesis, Social Ecology Hypothesis

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1. Introduction

1.1. Reputation formation

Cooperation is the process of working together for a common purpose or benefit. Cooperation between conspecifics can be found throughout the animal kingdom, especially in animals that live in social groups, like bonobos (*Pan paniscus) (*Hare, Brown, Williamson & Tomasello, 2002), meerkats *(Suricata suricatta*) and lions *(Panthera leo)* (Thornton & Clutton-Brock, 2011). For a successful cooperation, it is important to select a cooperative partner. Reputation formation is the skill to gain knowledge about an individual's general behavior through observing or experiencing the individual's past behavior to form beliefs or opinions about them (Melis & Semmann, 2010). The skill of forming reputation can contribute to an animal's survival, as it can learn to avoid harmful individuals and choose an appropriate partner with whom to successfully cooperate (Abdai & Miklósi, 2016).

Reputations can be formed through direct (first-hand) or indirect (third-hand) interactions. The ability to gather information through indirect experience by observing interactions between other individuals is called eavesdropping (Melis & Semmann, 2010). While eavesdropping might be less costly in terms of having bad experiences and potentially losing resources, first-hand interactions provides the most accurate prediction of an individual's future behavior because the assumptions about the behavior of the individual have been confirmed through direct experience (Subiaul, Vonk, Okamoto-Barth & Barth, 2008).

1.2. Studies of non-human apes

Forming reputations of others and interacting cooperatively is common in the daily life of humans. Thus, it is important to study whether animals are capable of this socio-cognitive ability to understand human cooperation. Non-human apes are closely related to us and many studies have been conducted to reveal more about the evolutionary origin of cooperative behavior and reputation formation in humans (Subiaul et al., 2008; Hermann, Keupp, Hare, Vaish & Tomasello, 2013). Melis, Hare & Tomasello (2005) showed that chimpanzees *(Pan troglodytes)* can form reputations of conspecifics. They used a cooperative string-pulling task, where the chimpanzees had to choose between a collaborative and an unhelpful conspecific to solve the problem and get access to a food reward. They hypothesized that the ability to form reputations might have evolved in chimpanzees due to their hunting strategy with conspecifics (Melis et al., 2005). For example, they hunt other monkey species in groups more often when the prey is in dense forests with many escape possibilities. Moreover, during group hunts, chimpanzees seem to coordinate their positions between trees so that the prey gets surrounded and trapped (Watts & Mitani, 2002).

In another study, Hermann et al. (2013) tested if orangutans *(Pongo pygmaeus),* chimpanzees and bonobos could distinguish between a nice and a selfish human partner in a food-receiving context

through direct interactions. The nice experimenter gave food to the subject and the selfish experimenter interrupted the process of giving food to the animal. Afterwards, the subject could approach one of the two experimenters. They found that while orangutans chose the nice human more often than the selfish human and thus formed reputations of humans, chimpanzees and bonobos failed to choose the nice experimenter over the selfish one. Subiaul et al. (2008) also found that chimpanzees did not select the nice experimenter over the selfish one and thus did not form direct reputations of human partners in a food-sharing experiment, which is surprising as they hunt cooperatively. To form reputations of conspecifics could be very beneficial in this context. Most studies investigating reputation formation in animals involve interactions with humans because it is a challenge to control an animal's behavior in an experiment. Thus, it would be logical to test species that are capable of acquiring information from humans and for which this information about humans is relevant, such as dogs (*Canis lupus familiaris*) (Pongrácz et al., 2001).

1.3. Studies of domesticated animals

Since non-human apes do not typically rely on humans for social information, domesticated animals might be a better model for such experimental setups, since the social information about humans might be more relevant to them. This could be due to domestication *per se* because certain skills and traits, such as communication, cooperation and peaceful co-living were intensely selected for by humans (Botigué et al., 2017). Additionally, because of their extensive experience with humans during their development, domesticated animals might be more sensitive to human social cues (Agnetta, Hare & Tomasello, 2000). A recent study investigated whether cats (*Felis silvestris catus*) could form reputations of humans (Leete, Vonk, Oriani, Eaton & Lieb, 2020), but the scientists did not find evidence to support this. This may be because domesticated cats descend from solitary-living animals and social skills might be more advanced in group-living species that hunt with conspecifics, rear offspring together and form complex hierarchies (Dunbar, 1998).

Dogs descend from a more social ancestor, the wolf *(Canis lupus)*, than cats. Wolves typically live in social groups and depend on the behavior of conspecifics, making it possible that this ability in dogs generalizes to humans (Range & Virányi, 2015). Moreover, dogs have been selected for close cooperation with humans (Botigué, Song, Scheu, Gopalan & Pendleton, 2017). In line with this, dogs have been found to demonstrate more flexible cognitive skills than non-human apes in regard to interactions with humans (Hare et al., 2002; Udell & Wynne, 2008; Duranton, Rodel, Bedossa & Belkir 2015). For example, dogs outperform apes in using human pointing gestures to find hidden food (Bräuer, Kaminski, Riedel, Call & Tomasello, 2006). Since dogs live in the vicinity of humans, being able to form a reputation of the individuals they are interacting with would be advantageous, as they depend on humans for food and other needed resources and could make the cooperation of dogs

and humans more efficient (Hare et al., 2002). A study showed that dogs preferred to stay next to a nice person rather than to a person that ignored them in a first-hand experience test (Nitzschner, Melis, Kaminski & Tomasello, 2012). However, in another study, it was shown that dogs chose the generous over the selfish human partner only when the partners were of different gender. In Carballo, Freidin, Putrino, Shimabukuro, Casanave and Bentosela (2015), the generous partner pointed at the bowl with the food and let the subject eat the food. The selfish partner also pointed at the bowl with the food but when the dogs approached this bowl, the partner quickly took the food out of the bowl and ate it. In study 1, both partners were female and wore similar clothes and they found that the dogs needed more trials to discriminate between the generous and selfish partner, namely 12 trials in total. In study 2, one of the partners was female and the other was male, and the dogs chose the generous person within fewer trials, namely 6 trials. The results showed that dogs used gender to discriminate between the generous and selfish partner and therefore their ability to form reputations seems to be limited.

In a similar study with the same experimental setup as Carballo et al. (2015), adult shelter and family dogs and puppies were tested (Carballo, Freidin, Casanave & Bentosela, 2017). The adult shelter dogs and family dogs outperformed the puppies by selecting the generous person more times than the puppies did. Therefore, the authors suggest that the amount of experience over time with humans but not the quality of interactions with humans matters when discriminating between selfish and generous human partners. However, Piotti, Spooner, Jim and Kaminski (2017) concluded in their study that dogs did not form a reputation on humans that behaved skillfully or unskillfully when obtaining food for the animals or in a puzzle task.

As the results of the previous studies are mixed, the question if dogs can form direct reputations is still open for discussion and, if they can, whether this ability is an effect of domestication or if it is inherited from their ancestor, the wolf. It has been suggested that the domestication process of dogs, which started approximately 20,000-40,000 years ago, equipped this species with the social tolerance and social attentiveness that allows them to engage in cooperation (Botigué et al., 2017). However, it is still under discussion how the process of domestication has changed dogs compared to wolves. In the past decades, several hypotheses tackling the phenomena of the domestication process of dogs have been postulated.

1.4. Domestication hypotheses

Hare and Tomasello (2005) stated the “Emotional Reactivity Hypothesis” (Domestication Hypothesis), in which the cooperative behavior of dogs might have evolved as a by-product during the selection for tame behavior. They argue that dogs are the only non-human animal that displays such cooperative cognitive skills regarding human activities due to domestication since their closest relative, the wolf, does not show the same attentiveness to human social cues; dogs are more skillful than wolves at

using human social cues, like indicating to humans a container in which food was hidden (Hare, Brown, Williamson & Tomasello, 2002).

Range and Virányi (2015) proposed the "Canine Cooperation Hypothesis", which suggests that wolves are highly cooperative and show high social attentiveness and tolerance. Thus, they postulate that wolf-wolf cooperation is the basis for dog-human cooperation and that during the domestication of dogs, no further selection for tolerance and social attentiveness was needed to allow for dog-human cooperation to develop. Domestication rather helped the dogs to lose their fear of humans and allowed them to become more comfortable around non-conspecific partners and work closely with them. Therefore, this hypothesis predicts that wolves and dogs are equipped with similar cognitive and social skills (Range & Virányi, 2013; Heberlein, Turner, Range & Virányi, 2016).

Marshall-Pescini, Cafazzo, Virányi and Range (2017) proposed the "Social Ecology Hypothesis", which suggests that wolves show more cooperative behavior than dogs because their feeding niche and social organization differ and changed their social and cognitive skills. Since dogs do not rely as much on cooperative interactions with conspecifics in their daily life as wolves, their abilities to cooperate with conspecifics diminished during the domestication process. If their social skills for their conspecifics decreased, then their social awareness towards humans may also not be as well-developed either. Studies showed that wolves can follow human gaze into distant space (Range & Virányi, 2011), whereas dogs cannot (Werhan, Virányi, Barrera, Sommese & Range, 2016).

The Wolf Science Center provides a unique opportunity to test these domestication hypotheses. Here, the wolves and dogs are reared and kept under the same condition and some studies have shown that when wolves and dogs are intensively socialized with humans, both species perform similarly. Range and Virányi (2011) showed that young wolves can follow the gaze of humans and conspecifics and dogs also have this ability (Wallis, Range, Müller, Serisier, Huber, & Virányi, 2015). Moreover, it was shown that dogs, as well as wolves, chose human partners to cooperative with in a cooperative loose string-pulling task (Range, Kassis, Taborsky, Boada & Marshall-Pescini, 2019). Further, wolves and dogs can use information from conspecifics and human demonstrators in a local enhancement task to find hidden food (Range & Virányi, 2013).

Heberlein et al. (2016) tested whether dogs and wolves can communicate about an out-of-reach food location. In this study, the subjects could choose to indicate a location, where food was hidden by looking at the baited box, to two human partners. During a training session, the animals experienced a cooperative partner who handed the food to the subject when the subject indicated the correct box and a competitive partner who ate the food herself when the subject indicated the box with the food. The results showed that wolves and dogs preformed equally well and that they discriminated between the cooperative and competitive partner. The authors concluded that, when kept under the

same conditions and intensively socialized with humans, dogs and wolves can use humans as partners and take their cooperativeness into account. This study suggests that dogs and wolves might form an opinion on humans, but further research is needed to provide evidence for this assumption. Thus, the current thesis is based on Heberlein et al. (2017) and tests whether these two canine species can acquire reputations of humans.

1.5. Study hypothesis and expectations

The aim of the present study is to test the hypothesis that dogs and wolves can form reputations of humans in a begging situation, where a generous human partner feeds the animal and a selfish human partner does not feed the animal. Further, this study will test the above described domestication hypotheses. The prediction is that dogs and wolves will prefer the generous person over the selfish person. If both are equally able to show reputation formation, this would provide support for the "Canine Cooperation Hypothesis". In the case that the dogs outperform the wolves, this result would provide support for the "Emotional Reactivity Hypothesis". If, however, the wolves outperform the dogs, this would provide support for the "Social Ecology Hypothesis".

2. Material and Methods

2.1. Ethical statement

Ethical approval was obtained from the 'Ethik und Tierschutzkommission' of the University of Veterinary Medicine Vienna (Protocol number ETK-084/05/2020). All study animals were housed at the Wolf Science Center (WSC), which is situated within Wildpark Ernstbrunn in Lower Austria (License No.: AT00012014). The subjects' participation in the study was voluntary. If the animal was not motivated to leave their home enclosure, the session was cancelled and repeated on a different day. The individual persons who participated in this study have given approval to publish photographs and videos containing their images.

2.2. Study subjects

Six mixed breed dogs (2 males, 4 females) and eleven pure bred wolves (7 males, 4 females) from the WSC were tested. The age of the dogs ranged from six to eight years and the wolves were between four to twelve years old; these dogs and wolves were born in captive facilities and they all experienced the same upbringing (Table 1). At the age of ten days, the puppies were separated from their mothers and hand-raised by humans. All puppies had contact with conspecifics and pet dogs from the trainers (Range & Virányi, 2014). First, the puppies were bottle-fed and later hand-fed by humans for the first five months of their lives. After being raised inside a building until two months old, the animals then had access to a 1000m^2 outdoor enclosure all the time. The dogs and wolves were moved to 2000-8000m^2 large outdoor enclosures when they were five months old. From this point on, they did not receive continuous access to humans anymore, but all animals had social contact with humans at least once a day during training sessions and/or behavioral and cognitive experiments. This rearing assures that both species are socialized with conspecifics and humans on a similar level and are attentive and cooperative towards humans.

All the enclosures are equipped with bushes, trees, logs and wooden shelters and drinking water is always available. During this study period, every wolf received meat in the form of carcasses every three days and smaller snacks like pieces of sausages, meat and dry dog food as enrichment or as a reward during training sessions and experiments. The dogs were fed with commercial dog food every day and they also received meat as enrichment and during the study and training sessions.

All animals were habituated to participating in experiments and to being separated from their pack members, as they had taken part in different studies from a young age.

Table 1. List of the animals that participated in the experiment indicating the species, name, sex, year of birth and origin.

Species	Name	Sex	Born	Breeding facility
Wolf	Nanuk*	M	2009	Tripple D Farm, USA
Wolf	Geronimo	M	2009	Tripple D Farm, USA
Wolf	Yukon	F	2009	Tripple D Farm, USA
Wolf	Kenai	M	2010	Parc Safari, Canada
Wolf	Amarok	M	2012	Minnesota Wildlife Connection, USA
Wolf	Tala	F	2012	Minnesota Wildlife Connection, USA
Wolf	Chitto	M	2012	Minnesota Wildlife Connection, USA
Wolf	Una*	F	2012	Minnesota Wildlife Connection, USA
Wolf	Wamblee	M	2012	Haliburton Forest, Canada
Wolf	Maikan	M	2016	Zoo close to St. Petersburg, Russia
Wolf	Taima*	F	2016	Zoo close to St. Petersburg, Russia
Dog	Layla	F	2011	Győr, Hungary
Dog	Zuri	F	2011	Paks, Hungary
Dog	Panya	F	2014	Wolf Science Center, Austria
Dog	Enzi	M	2014	Wolf Science Center, Austria
Dog	Imara	F	2014	Wolf Science Center, Austria
Dog	Hiari	M	2014	Wolf Science Center, Austria

* Excluded from the experiment

2.3. Experimental set-up

The experiment took place throughout the day from June until November 2020. All subjects, except Wamblee (see chapter 2.5.), were tested inside the Old Test Enclosure of the WSC (Figure 1), which has a size of 702 m^2. This enclosure is outdoor and water was available ad libitum.

Four people who were unfamiliar to the subjects acted as the human partners in the experiment. The pair of human partners remained stable within the session. Thus, there were in total four partners in the whole experiment who were all females. One partner in condition 1 wore white clothes and the other partner wore black clothes to help the animals distinguish between the generous and selfish roles. In condition 2, one partner wore light-patterned clothes and the other wore dark-patterned clothes. The partner's role and the color of their clothes were randomized and fixed within-subjects and counterbalanced between sessions. To sum up, in both conditions, the subjects experienced the same procedure twice and only the human partners and the color of their clothes differed. (Figure 2a, 2b).

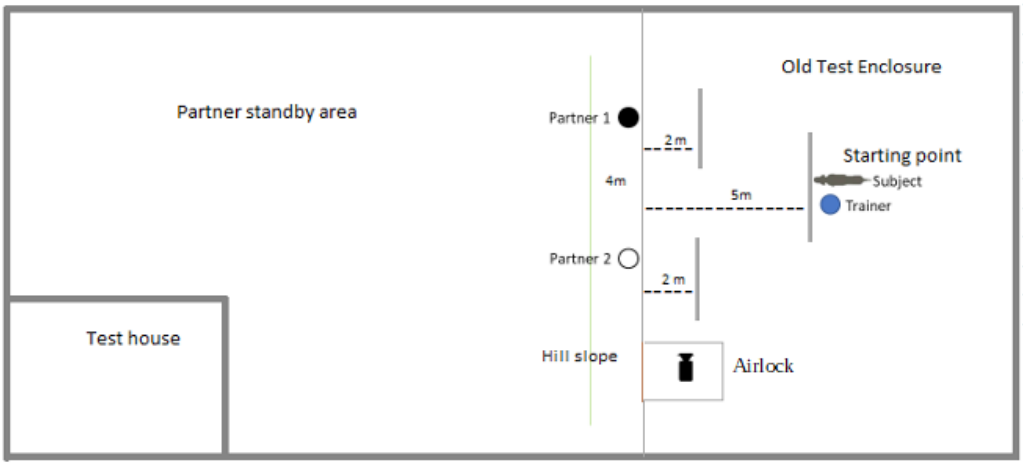

Figure 1. Schematic design of the experimental setup (not drawn to scale). The starting point was marked 5m away from the fence at which the two partners were positioned in the test phase. The partners stood 4m apart from each other. The grey line marks 2m away from the fence serves as the reference point at what point the subjects chose one of the partners. The camera was positioned in the airlock.

Figure 2a. Showing the test phase of Yukon (wolf) in condition 1. The partners wore black and white colored clothes.

Figure 2b. Showing the test phase of Amarok (wolf) in condition 2. The partners wore dark and light patterned clothes.

The animal trainers of the WSC either walked or shifted the subject into the Old Test Enclosure from their adjacent home enclosure and they handled the animals during the experiment. A

main experimenter was also present during the study to carry out the procedure of the experiment and to take notes.

The starting point where the trainers and the subjects stood at the beginning of the trials was measured 5m away from the fence of the Old Test Enclosure and in the center of where the two partners were positioned (Figure 1). For marking the 5m line and the 2m lines, which served as reference points for the animal's choice, a shovel was used to dig a small ditch into the ground. We did not use spray paint to draw the lines because the smell of the paint could have distracted the animals from participating in the study. However, the points outside the Old Test Enclosure, where the partners stood, were marked with white spray paint and renewed whenever the paint faded. During the test phase of the experiment, each partner wore a dark blue hip bag in which they stored six pieces of meat to control for olfactory cues.

We recorded the whole experiment with a GoPro Camera (Hero 4 Black) so that we could watch the experiment afterwards if needed. The camera was placed on a tripod in the airlock in the Old Test Enclosure (Figure 1). The videos were later uploaded to Loopy, a software to store, label and code experimental videos from the WSC. The subject's choices were coded and written down live.

2.4. Experimental procedure

The whole experiment consisted of one session per subject in two different conditions. The session was divided into three phases (Figure 4):

1. Habituation phase: Firstly, the subject could explore the Old Test Enclosure freely for five minutes. Then, the trainer put a collar on and leashed the animal and the trainer walked with the animal to the starting point (Figure 1).
2. Experience phase: The trainer and the subject stood at the starting point and the partners stayed in the partner's standby area at the bottom of the hill. Then, one partner walked from the standby area and stood in front of the fence with a piece of meat in her right hand (Figure 3). Next, the trainer and the subject walked 3m forward to the fence towards the partner. The partners took care that the animals noticed the raising movement of her hand in which they were holding the piece of meat to ensure the animal paid attention to the situation. If an animal did not look at the partner after a few seconds, the partner called the animal's name to get its attention. Then, the subject witnessed one of the following scenarios depending on the respective partner:

   a) Generous: The generous partner held the piece of meat up, making sure the animals had seen the food in her hand, and said: "Here you go!" in a friendly tone and threw the food into the enclosure so the animal could eat it. After the animal had eaten, the partner walked back to the standby area and the trainer and the subject returned to the starting point.

b) Selfish: The selfish partner held the piece of meat up and said: “You can’t have it!” in an unfriendly tone, folded her arms and turned around, keeping the food in her hand. After standing there for 3 seconds, the partner walked back to the standby area and the trainer returned to the starting point with the subject.

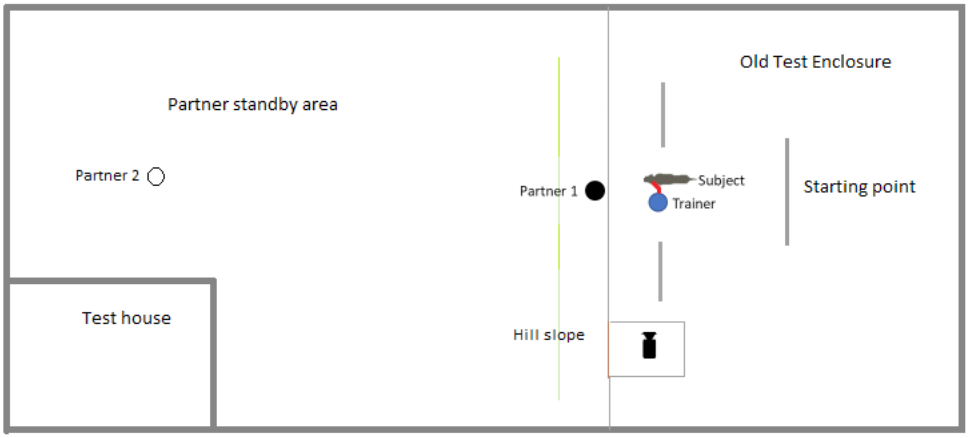

Figure 3. Schematic design of the experimental setup (not drawn to scale) in the experience phase. The partner stood in the center.

After this, the second partner interacted with the subject (i.e., if the first partner was generous, then the second partner was selfish). The interaction with the partners alternated each time and this procedure was repeated four times, so there were eight demonstrations in total (Figure 4). The order of the interactions was counterbalanced across subjects, i.e., the generous partner started for the one half of the subjects and the selfish partner started for the other half. After the experience phase, the trainer unleashed the animal and held it by the collar at the starting point.

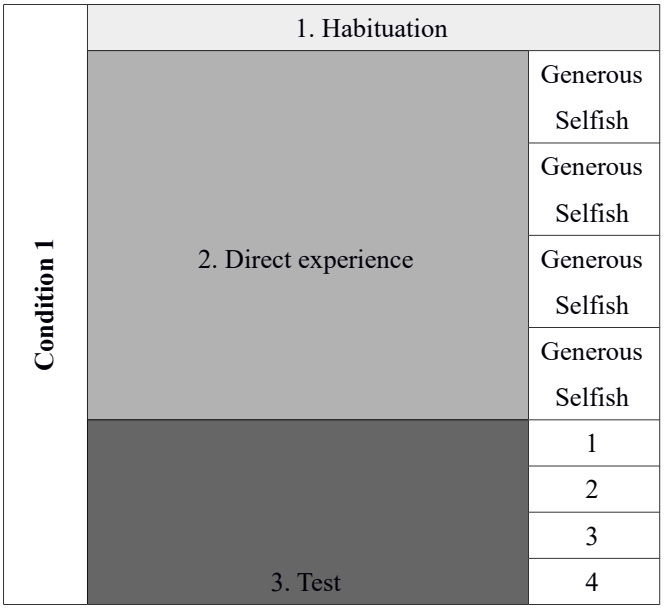

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Figure 4. Experimental procedure: The session was conducted twice in two different conditions. A session consisted of the habituation phase, the experience phase and the test phase.

3. Test Phase: When the trainer and the subject were standing at the starting point, the partners walked up the hill and stood side by side, 4m apart from each other, outside the Old Test Enclosure with their backs turned to the fence (Figure 5). The sides were counterbalanced across subjects. Both partners had a piece of meat in their hand.

Figure 5. Test phase of Chitto (wolf). The partners have their backs turned to the fence.

When everybody was ready, the trainer said: “OK“. Then, the partners turned around simultaneously. When facing the trainer and the subject, the partners moved their hand with the meat in it up in front

of them and made a waving movement for a few seconds to draw the animal's attention. All these movements were done synchronously by the partners and they turned in the same direction. When the partners stopped waving, the trainer let go of the animal's collar so the animal could choose whom of the two partners to approach (Figure 6).

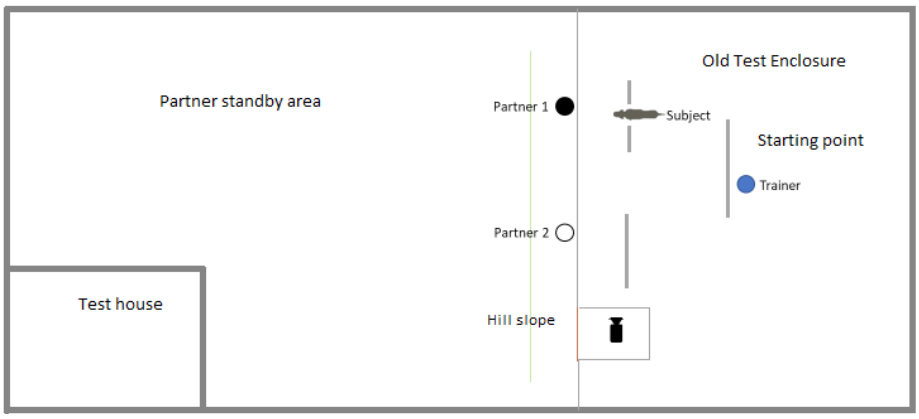

Figure 6. Schematic design of the test phase. In this diagram the subject chose Partner 1.

After the animal had made a choice, defined as when its front paws crossed the 2m line and its head was oriented towards the partner, the chosen partner acted the same way as she did in the experience phase (i.e., the generous partner said her words and fed the food to the animal and the selfish person said her words and turned around). Then, the non-chosen person turned around as well to signal to the subject that this person was not an option anymore. If the animal did not approach either partner within one minute, it was considered a "no-choice" response. The main experimenter used a stopwatch to exactly time one minute. After each test trial, the trainer called the subject back to the starting point and then the next test trial started; this procedure was repeated five more times. Thus, there were six trials in total (Figure 4). The positions of the generous and selfish partner were predetermined and semi-randomized, never remaining on the same side more than twice in a row. The main experimenter told the partners when to swap positions in the six trials. After these six trials, the animal was returned to its home enclosure by the trainer, the partners walked away from the fence and the session was over.

After approximately eight or nine weeks later, the same procedure was repeated with the subjects with two different human partners (Figure 4).

2.5. Experimental adjustments and exceptions

There were special arrangements for some subjects. While testing one of the dogs (Panya) in condition 1, we realized that she would not approach the partners because she feared the unknown people and the experimental setup. Therefore, we conducted habituation sessions, where the two partners sat on the ground in the Old Test Enclosure and Panya could run around freely and get pet by them when she wanted. We repeated the session three times until Panya felt confident enough to approach the partners

without fear. During the test phase, the partners kneeled on the ground instead of standing at their positions and instead of showing their backs first and then turning around, the partners faced the fence and looked down to the ground. When the trainer said "OK", the partners looked up and raised their hand and waved the meat (Figure 7). These adjustments made it possible to test Panya.

Figure 7. Test phase of Panya (dog). The partners kneeled during the interactions instead of standing on their feet.

For two wolves, we adapted the experimental setup as well. Maikan showed some signs of stress, so we minimized the partners' movements; they did not turn around and stood in their positions facing forward, looking down to the ground and only looking up after the trainer said "OK". Then, the partners performed the same actions as described in the experimental procedure. We tested Wamblee in his home enclosure, which had a size of 1,109 m^2, since he was scared of entering the Old Test Enclosure.

We had to exclude three wolves from our study. During the first round of the experience phase, Nanuk felt uncomfortable being held on a leash and instead of walking towards the partners, he moved further away from the unknown people. Since the trainers saw no possibility of improving this situation, we decided not to test him further. Una showed great signs of fear even after training sessions, in which she saw two unfamiliar people walk up to the fence. Since Taima showed neophobic reactions too, we excluded them both because of ethical reasons, as it would have caused the animals too much stress to remain in the experiment.

2.6. Statistical analyses

The statistical analyses were carried out using the program R (version 4.0.3; R Core Team 2020). The significance threshold was fixed at 0.05 and all tests were two-tailed. In total, the sample size included 138 observations made on 14 individuals (six dogs and eight wolves). Six data points were missing, as two dogs did not select a partner during some trials during the test phase (see Table 1 in Appendix).

The outcome variable was the subject's choice to approach the generous or selfish partner in the session. This was defined as when the animal's front paws crossed the 2m line and its head was

oriented towards the partner. Trials in which the subjects chose none of the human partners were excluded from analysis (4.3%).

To evaluate the animal's choice, we conducted Generalized Linear Mixed-Effects Models (GLMMs) with a binomial distribution and a logit link function, which was fitted using the function glmer of the R package "lme4". The GLMM integrates both random and fixed effects terms in a linear predictor expression from which the depending mean of the response can be assessed (Bates, Mächler, Bolker & Walker, 2015). Thus, the linear predictor contains random effects in addition to the usual fixed effects. Differences between certain groups can be seen and modelled as random effects.

To test whether the animals could form reputations of humans through direct experience, we analyzed their choice to approach the generous partner in all six trials in the session. For our model, the fixed effects were trial as a covariate (1-6), species as a factor (dog or wolf) and order as a covariate (condition 1 or condition 2). The random intercept was subject to include individual differences. The covariates trial and order were *z*-transformed (to a mean of zero and a standard deviation of one) to make model estimates easier to interpret and because it greatly increases the chance for the model to converge (Schielzeth, 2010). To keep the type I error rates at the nominal level of 5%, the random slopes of trial and order were included. We changed the optimizer, used by the function glmer, to "bobyqa" to ease convergence (Johnson, n.d.). We included the correlation between random intercept and slope as it was estimated to be essentially 0, which indicates it to be identifiable (Matuschek et al., 2017).

By visually examining a box plot, we checked if the Best Linear Unbiased Predictors (BLUPs) were normally distributed, which is an assumption of the GLMMs. The shapes of the distributions showed no violations. We checked for model stability by excluding subjects one at the time from the data and then comparing the model estimates acquired for these subsets of the data with those derived for the full data set. As can be seen by the long range of the estimates, the model was very unstable. This might be due to the small sample size and consequently the model is not very trustworthy. To check for issues with collinearity, we looked at the Variance Inflation Factors (VIF, Field, 2005) by using the function VIF of the R-package "car" (Fox & Weisberg, 2018) adapted to a standard linear model which included only the fixed effects. Hence, the random effects and interactions were excluded. This revealed no problem with collinearity among the predictors (trial: VIF=1.000, species: VIF=1.083, and order: VIF=1.083).

To assess the overall effect of the predictors, we tested the significance of the full model compared to the null model by means of a likelihood ratio test (R function anova with argument test set to "Chisq"; Dobson & Barnett, 2018). The full model included an interaction between z-transformed trial × species × z-transformed order. Z-transformed trial was added as a random intercept

and slope for subject. The null model lacked the interaction of trial, species and order compared to the full model.

As the results of the GLMM was non-significant, we conducted binomial tests (one-sided) to check whether dogs and/or wolves had a bias for our control variables, which were the color of the clothes (white or black in condition 1; light or dark in condition 2), the partners' ID (partner 1 or 2 in condition 1; Partner 3 or 4 in condition 2) and the side on which the partner was standing in the test (left or right grouped together in condition 1 and 2).

3. Results

Only preliminary results are presented in this paper, as the data of five wolves in condition 2 had not been collected due to the Covid-19 situation, when this thesis was written (see Table 2 in Appendix).

3.1. General Results

The likelihood ratio test comparing the full and null model showed that the interaction between trial × species × order did not have a significant effect on the subjects for choosing the generous partner over the selfish partner (χ^2 = 2.924, *df* = 7, *p* = .892) (Table 2). Therefore, dogs and wolves did not show a significant preference for the generous over the selfish human partner and they did not learn to form reputations of the humans with more experience within or between test sessions (Figure 8). Overall, dogs chose the generous partner on average 63,33% of all trials and wolves 59,10% (Figure 9).

Table 2. Results of the full model [estimates, standard errors, and confidence intervals (CIs)], *z*-value, *p*-value, and the estimates obtained for model stability (minimum and maximum).

Term	**Estimate**	***SE***	**95% CI**		***z***	***p***	**Min**	**Max**
			Upper	**Lower**				
Intercept	0.673	0.325	-0.943	2.455	2.069	0.039	0.416	0.780
Z-transformed trial	0.387	0.319	-0.703	2.765	1.215	0.225	0.308	0.461
Z-transformed order	-0.097	0.403	-1.164	0.890	-0.241	0.810	-0.528	0.162
Species[a]	-0.145	0.471	-3.893	1.013	-0.307	0.759	-0.529	0.526
Z-transformed trial× Species	-0.358	0.444	-3.574	1.402	-0.805	0.421	-0.562	0.207
Z-transformed trial × *Z*-transformed order	-0.263	0.327	-1.549	0.540	-0.804	0.421	-0.479	-0.105
Species × *Z*-transformed order	0.405	0.584	-0.652	2.632	0.694	0.488	0.166	1.068
Z-transformed trial ×Species × *Z*- transformed order	0.455	0.469	-0.983	2.250	0.971	0.332	0.203	1.044

Species[a]: dog serves as reference model

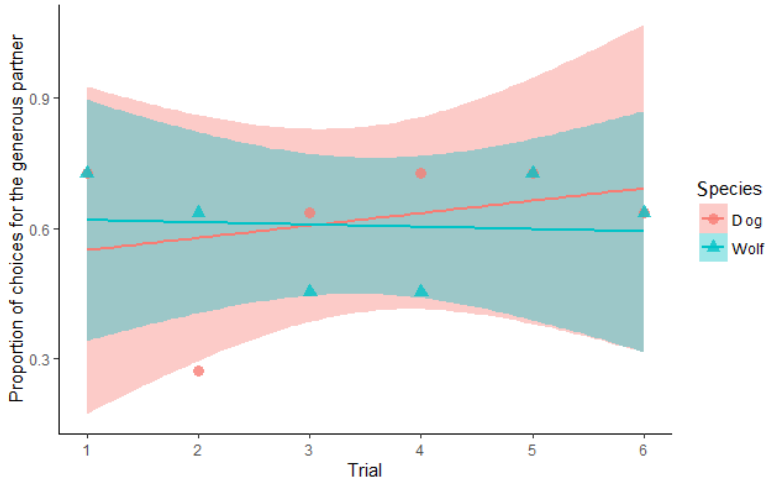

Figure 8. ggplot: Showing the proportions of the subjects' choices for the generous person in both conditions in all six trials.

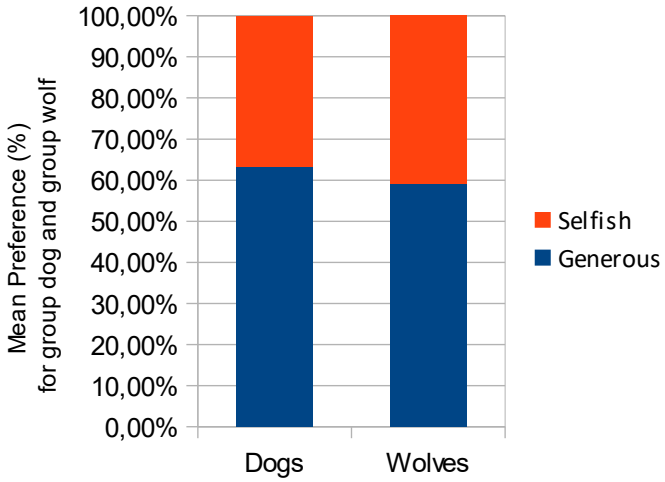

Figure 9. Mean preference for choosing the generous and selfish partner for dogs and wolves in both conditions.

As the likelihood ratio test was non-significant, we conducted binomial tests to check whether the animals showed a bias for the variables we controlled for but did not include in the model to reduce model complexity: partner ID (partner 1, 2, 3 and 4) and the color of the clothes (white, black, light and dark) for each condition separately and the position of the partners in the test phase (left and right) in both conditions.

3.2. Performance of dogs and wolves in condition 1

Each subject was tested in six trials, thus there were 48 trials for the wolves and 36 trials in total for the dogs. However, there were six trials where a dog did not approach either partner: Hiari was

responsible for five of these trials and Zuri for one (see Table 1 and Figure 1 in Appendix). Therefore, the binomial tests only included 30 trials for the dogs.

Independent of the role of the partners, the dogs chose Partner 1 11 times and Partner 2 19 times and there was no significant bias for one of the partners (p = .201) (Figure 10). In contrast, the wolves selected Partner 1 16 times and Partner 2 32 times and the binomial test revealed a bias for Partner 2 (p= .029) (Figure 10).

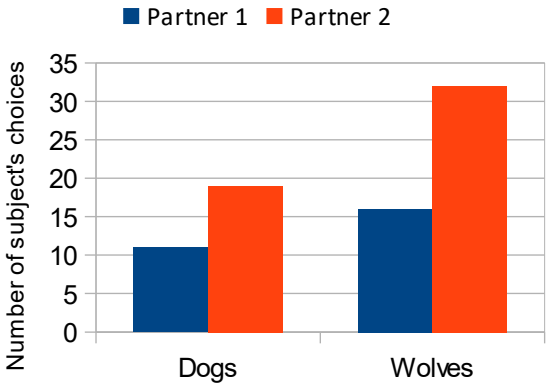

Figure 10. Bar graph indicating which partner the dogs and wolves selected during the test trials in condition 1.

Independent of the role of the partners, the dogs chose 23 times the person wearing white and 8 times the person wearing black. The dogs showed a significant bias for the white color (p = .005) (Figure 11). The wolves also chose the white color more often, with respectively 30 times and 18 times black, but the binomial test revealed no significant bias for one of the two colors (N = 48, p = .111) (Figure 11).

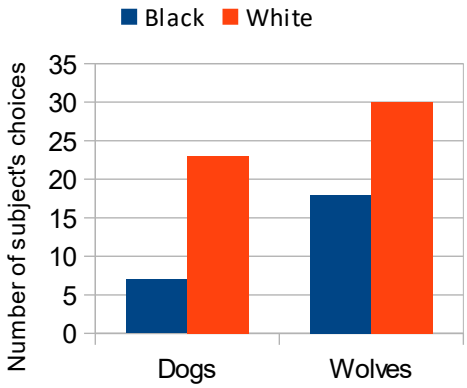

Figure 11. Bar chart showing which color the subjects selected during the test trial in condition 1.

To sum up, the binomial tests showed that wolves had a bias for Partner 2 and dogs had a bias for white clothes.

3.3. Performance of dogs and wolves in condition 2

Data collection is ongoing and so far, only three wolves have completed testing, thus there are currently 18 trials for the wolves and 36 trials for the dogs. Independent of the role of the partners, the dogs chose Partner 3 16 times and 20 times Partner 4 and there was no significant bias for one of the partners (p = .618). The wolves selected Partner 3 9 times and Partner 4 9 times. Hence, they selected both partners equally often and they did not show a bias for one of them (p = 1).

The dogs chose the light-colored clothes 20 times and the dark-colored clothes 16 times. The binomial test revealed no significant bias for one colour (N = 36, p = .618). The wolves selected the light and the dark color 9 times, hence they chose both colours equally often (p = 1).

3.4. Choices of the sides

Finally, we tested whether dogs and wolves had a side bias. Independent of the role of the partners, the dogs chose the right side 41 times and the left side 25 times, and the wolves chose the right side 40 times and the left side 26 times (Figure 12). The binomial test revealed that neither dogs nor wolves had a preferred side when both conditions were considered (dogs: N = 66, p = .064; wolves: N = 66, p = .109).

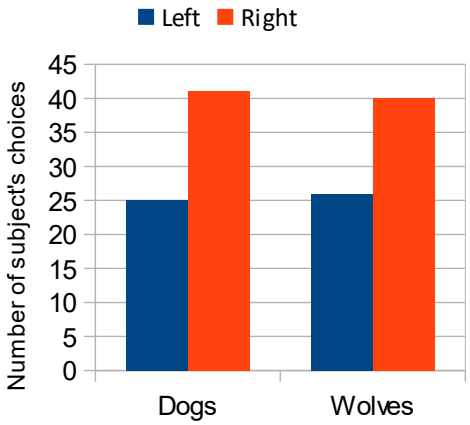

Figure 12. Bar chart indicating the total number of how often the subjects chose the left or right side.

4. Discussion

4.1. General discussion

The aim of the study was to assess whether equally socialized dogs and wolves can form reputations through direct experience with a generous human, who fed the animal, and a selfish person, who withheld food from the animal. We found that dogs and wolves did not choose the generous partner significantly more often than the selfish one. Therefore, our results do not provide evidence to support our hypothesis that dogs and wolves can form reputations about unfamiliar humans in a food-involving context. However, we argue that this conclusion is highly unlikely; since dogs that live close to or with humans should be able to form reputation-like interferences, as this could be advantageous for them, because they depend on humans for food and other resources.

It is surprising that we did not find evidence of direct reputation formation in these two species because previous studies at the WSC have shown that dogs and wolves successfully recruited a human in a cooperative string-pulling task (Range et al., 2019) and they looked more at and indicated more often the hidden food location to the cooperative human, who gave them the food, than to the competitive human, who ate the food herself (Heberlein, Turner, Range & Virányi, 2016). These results suggest that the dogs and wolves differentiated between the humans. However, the humans who participated with the animals in these studies were hand-raisers and trainers and therefore familiar to the subjects, which might explain the discrepancy in our results. Studies have demonstrated that dogs can discriminate between familiar humans using social cues and scent (Racca, Amadei, Ligout, Guo, Meints & Mills, 2010) and that dogs pay more attention to their owners than to unfamiliar experimenters (Mongillo et al., 2010). However, little is known about wolves' and dogs' ability to discriminate strangers or how much training is required to develop such determinations. Nevertheless, human voices are a salient cue for dogs (Marshall-Pescini, Passalacqua, Ferrario, Valsecchi & Prato-Previde, 2011) and the dogs and wolves in our study had access to acoustic, olfactory and visual cues. In addition, apart from the individuals' smell, the partners wore contrasting clothes and said different sentences with a different pitch and tone when they interacted with the subjects. The partners also displayed a different body language during the experience and test phase depending on their role. Thus, we provided several cues for the animals to distinguish the two partners in this study**.**

An increased number of experience phases, where the animals experienced which partner was generous and who was selfish, could have changed the outcome of this study. In Experiment 2 of Subiaul et al. (2008), five out of seven chimpanzees only learned to discriminate between the selfish and generous partner after 15-75 experiences and further one of those did not maintain a preference for the generous partner. Kundey, De Los Reyes, Molina and Monnier (2010) investigated indirect reputation formation in dogs and found that they needed ten interactions with each partner to be able to choose the nice partner on a significant level. The dogs and wolves in our study only had four

experiences with each partner. Therefore, we may have found evidence for direct reputation formation if the subjects had had more experience phases, as eight experience trials were probably not enough for the dogs and wolves to learn to discriminate between the two unfamiliar partners. Individual recognition seems to be based on basic conditioning processes (Huber, Racca, Scaf, Virányi & Range, 2013), thus the role of experience in the development of this ability might be important. We chose to have the animals only experience eight interactions in total per session because our aim was to reflect a situation in daily life. Animals should form reputations about others quickly, since unknown individuals are not encountered several times sequentially, and we were not interested if the subjects learn the discrimination of unfamiliar persons over growing trial numbers. Further, it is known that the motivational state of dogs and wolves decreases over time in scientific studies (Marshall-Pescini, Virányi, Kubinyi & Range, 2017).

A possible reason why the animals did not significantly choose the generous person could be that the animals may have paid attention only to the partner's arm and hand that had the food in it, neglecting other more discriminating features of the partners. Nitzschner et al. (2012) argued that the dogs that were tested in a pilot study did not develop a favour for the generous person even after several direct experiences because they focused too much on the food, which distracted them from the actual situation. Therefore, Nitzschner et al. (2012) conducted the study with physical interactions rather than food rewards and found that dogs stayed significantly longer with the nice experimenter than the ignoring one. However, other studies have shown that dogs and wolves show high attentiveness when a human indicated a hidden food reward (Range & Virányi, 2015). It is still unknown how much food is needed for it to be a distraction for the animals in such studies. In our study, the dogs and wolves seemed to pay attention to all interactions and whenever the subject did not look at the partner, she called its name to get the subject to interact with her. Since the subjects had direct experience trials first, where they had to walk up to the partners and experienced getting fed with a piece of meat every time the generous partner appeared, they experienced that they could expect a treat from at least one of the two unknown persons standing there. This observation is consistent with the fact that the wolves always chose one of the experimenters in the test phase and an experimenter was not chosen in only six trials by two dogs. However, if the animals had only focused on the experimenters' hands, they were probably an insufficient cue to distinguish the partners in the test phase (Carballo et al., 2015). As both of the partners posed in the same way in the test phase as they did during the experience phase before they interacted differentially with the animal, the subjects might have only looked at the arm and hand of the partner and not at the whole person. Future studies should address this problem and put effort in assessing how dogs and wolves pay attention to specific parts of the human body and the salience of the action.

We found that the wolves preferred Partner 2 in condition 1. This is interesting as the roles of being generous or selfish were counterbalanced between the partners. A possible explanation for this result could be that the wolves liked the personality or scent of Partner 2 more and thus were more likely to approach this person, or the wolves may have found Partner 1 more dominant or not appealing. Another explanation could be that Partner 2 wore the white clothes when playing the generous partner three times, whereas Partner 1 only wore white once and wore black three times when playing the role of the generous partner. Since the dogs showed a significant bias for the white color and the wolves showed a greater, but not significant, preference for white than for black (30 times white and 18 times black), the color white might have been more attractive for the wolves and therefore the bias for Partner 2 occurred. It is surprising that the dogs chose the person in the white-colored clothes more often, as we supposed that the animals would prefer black clothing because the WSC trainers wear black clothing. The trainers are the humans who interact the most with the animals and provide them with food and shelter. The other way round it is possible that the subjects noticed that the person wearing black was not a trainer which freaked them out and thus they preferred to approach the novel person wearing white. However, because of the small sample size, these conclusions should be drawn with caution. A way to resolve this issue in future studies could be to use unfamiliar partners for every subject.

To sum up, in condition 1 the dogs seemed to make their choice of who to approach based on the color (preferring white), whereas the wolves preferred one of the partners (Partner 2). These findings suggest that the subjects were able to discriminate between the two unfamiliar persons, but they based their preferences on other factors than getting food, which may be why they did not choose the generous partner. As the data collection of condition 2 is ongoing, the results of condition 2 may provide more insight into the reasons why the animals made certain choices and if they really based their choice on different factors like preference of one person or color rather than on the roles the persons played.

Although we did not find evidence of reputation formation, we will discuss the domestication hypotheses and how or if the domestication process changed the cognitive and social skills of dogs may explain the current results. The “Emotional Reactivity Hypothesis” suggests that dogs were selected for tameness, thus dogs should be less fearful of humans than wolves (Hare & Tomasello, 2005). Overall, the dogs in the current study were less afraid of approaching and working with the unfamiliar people and all six dogs participated in the experiment. Conversely, two wolves were excluded from the test because of neophobic signs.

The “Canine Cooperation Hypothesis” (Range & Virányi, 2015) states that wolves are highly cooperative and that dogs lost their natural fear of humans during the domestication process. Wolves should be more scared to interact with humans and only wolves who have had intensive human

socialization can overcome their fear and use their species-specific abilities to interact with humans. Wolves can use information, given from humans as well as dogs can, when they have learned to accept humans as social partners, as dogs did over time during domestication (Range & Virányi, 2011; Heberlein et al., 2016). Although this current study did not involve cooperation, the observations and exclusions of some wolves in our study suggest that not all of the wolves at the WSC have lost their fear of humans; they might be socialized and comfortable with the trainers and caretakers after familiarization but not with unfamiliar humans. These differences could also derive from the personality of the individual wolves, as animals display various characteristics like boldness or shyness (Ogden, 2012). To conclude, it is difficult to convey certain characteristics like how fearful a species behaves in contact with humans on a species level, as individual characteristics can play a role in how much such traits are developed.

The "Social Ecology Hypothesis" proposes that wolves show more cooperative behaviour than dogs because their feeding niche and social organization differ, which changed their social and cognitive skills. Since dogs do not rely as much on cooperative interactions with conspecifics in their daily life as wolves, their abilities to communicate with conspecifics and cooperative skills diminished during the domestication process (Marshall-Pescini, Cafazzo, Virányi & Range, 2017). If their social skills for their conspecifics decreased, then their social awareness towards humans may not be as well-developed either. However, this current study does not require cooperation but rather interactions with unknown humans and as the dogs and wolves preformed similarly in this study (Figure 9), it does not provide support for this hypothesis.

4.2. Improvements of the methodology of prior studies

There are several differences between the earlier studies (Nitzschner et al., 2012; Carballo et al., 2015) and the present study that may explain some of the discrepancies in the results. We improved previous methodologies that were used to test direct reputation formation in animals in former studies; first, we controlled for local enhancement (a demonstrator attracts an observer's attention to a particular location), as the setup in the experience phase differed from the setup in the test phase. In the experience phase, one partner stood in front of the fence at the center point and interacted with the subject. In the test phase, both partners stood in front of the fence and swapped their positions, so the animals had to pay attention to which side the generous person was positioned prior to selecting one person. Although the wolves and dogs showed no significant side bias, there was a trend for dogs to choose the right side over the left side, irrespective of the where the generous partner was standing. An explanation why the dogs might have preferred the right side could be because when the partners walked up to the fence, the partner who was standing on the right side appeared in the view of the animals first and drew most of the attention from the subject to herself. Also, the bucket with drinking

water for the animals was positioned on the right side close to where the partner was standing. Even though the animals hardly went to drink water in-between the test trials, the right side might be already positively locally enhanced. As the positions of the partners were counterbalanced and randomized, this may explain why the results did not reach statistical significance. A closer look at the data set shows that certain individuals, like Imara, Layla, Yukon and Maikan, showed a side bias in one condition, but since they did not show the same bias again in the other condition, their choice for one side might have been an individual effect and situation dependent (see Table 1 & Table 2 in Appendix).

Carballo et al. (2015) also argued that in previous studies on reputation formation in dogs, the animals may have relied on cues other than the individual characteristics of the human experimenters, such as local enhancement. Therefore, Carballo et al. (2015) conducted two experiments on whether dogs could discriminate between two individuals in a food-sharing context. In study 1, the experimenters were two females and in study 2, the experimenters were of different gender. Thus, they concluded that dogs could use human gender as a cue to differentiate between cooperative and selfish experimenters and the amount of experience dogs have with the partners affects their ability to differentiate between them (Abdai & Miklósi, 2016). As the experimenters were all female in our study, they wore contrasting clothes to help the animals distinguish the individuals and form a reputation of them being generous or selfish. However, since the result of this study is non-significant, the different colored clothes the partners wore may not have been salient enough for the animals to discriminate between the partners. A future study with these subjects could be conducted with partners of different genders based on the study of Carballo et al. (2015).

Finally, the differences in our findings to previous studies on direct reputation formation in dogs may have been because this study was conducted outside in an enclosure, where the subjects were exposed to different weather conditions, which may have impacted the motivational level of certain animals and distracted them. Most of the data collection took place in the summer months (June until September) and we observed that the animals were sometimes difficult to motivate to take part in the experiment. Further, their motivation in food was lower during this hot weather period compared to when the animals were tested during the months of fall (September until November). Their metabolic rate and need for food are higher during the colder months, as they need more energy to maintain a constant core body temperature (Tudor, 2014). This is in line with the fact that the wolves that were tested later in the year seemed to perform better than their conspecifics that took part in the study in the hot summer months; for example, Kenai and Maikan in condition 1 and Amarok and Chitto in condition 2 chose in total the generous partner more often compared to the wolves tested before that (Table 1 & Table 2 in Appendix; Figure 3 & Figure 4 in Appendix; see them also to learn more about the choices the individuals made during the trials). However, this suggestion is only based

on observations, thus it should be considered carefully. Moreover, we considered only the data of Kenai and Maikan in condition 1. The yet non-included results of condition 2 can therefore reveal something different. In addition, for Amarok and Chitto, it was the second round of the study and therefore a learning effect might have occurred. Further analysis would be needed of the full data set to draw more reliable conclusions. To rule out distractions by the weather in future studies and to make the sessions with single-study subjects more standardised and thus the results more comparable, the whole experiment could be carried out in a room where all subjects experience the same environment without external influences.

4.3. Limitations

A limitation of this study is that the sample size is small, as only six dogs and eight wolves were tested and only 138 data points in total were analyzed. Therefore, a high level of performance would be needed across all individuals of dogs and wolves (e.g., at least 5 out of 6) for the result to be convincing. For this reason, we cannot make strong conclusions about direct reputation formation in dogs and in wolves from this result. If more subjects would have participated, the study might have yielded different results, since six dogs and eight wolves are not high numbers to represent the cognitive abilities of these two canine species. Small sample sizes raise problems of validity in deducting data to the entire species or using the data as arguments for comparing species. However, it can be argued that general abilities are shared by all individuals of the species and so justify individual-based experiments (Miklósi et al., 2004).

One potential confound to consider in such interspecific testing scenarios like this study is that these interactions are often highly artificial. Dogs are domesticated and rely on humans for food, thus a food-sharing situation is an appropriate way to study cognitive abilities in dogs when humans are involved in the study setup (Freidin et al., 2013). Although it is not ecologically valid for wild or non-domesticated animals like wolves, the wolves in this sample do rely on humans for food and are used to interacting with humans. Further, due to the dogs' and wolves' extensive experience and companionship with humans at the WSC, it is not necessarily disadvantageous to use human partners in experiments.

5.4. Outlook for the future and relevance

To our knowledge, these data provide the first comparison of reputation formation in equally raised and kept wolves and dogs. As there is a lack of knowledge of whether wolves are capable of reputation formation and studies on pet dogs had debatable outcomes, this study does not provide much clarity. One way to widen our knowledge of the animals' capacity to from reputations is the conduction of a pursuing study that investigates the capacity of dogs and wolves to form indirect reputation formation

about human partners, where they observe an interaction between a generous and selfish partner with a conspecific. Such a study is already in process. However, it is important to continue studying equally reared dogs and wolves to gain a better understanding of if and/or how the domestication process influenced dogs' cognition. Additionally, a study with the same setup as this recent study could be carried out using pet dogs that have much more contact with humans, to test if more experience with humans leads dogs to form reputations about them.

Although we did not find evidence to support our hypothesis that dogs and wolves that share the same experience of humans can form reputations of humans after direct experience, our study investigated a new avenue of research in socio-cognitive behavior in canines and aimed to further our understanding of human-dog and human-wolf interactions. Our research highlights the importance of considering individual differences in animals, even if they are cared for in a similar way. Therefore, further research on reputation formation, involving also studies on indirect reputation formation in dogs and wolves, is needed because it could help explain how knowledge about humans is passed on in dogs and their ancestors. In addition, since this study is the first one to compare whether dogs and wolves can form reputations in the same scenario, this study provides a fundamental basis for future studies on wolf cognition. Finally, a greater understanding of wolf cognition and behavior, as well as the possible flexibility of their decision-making process, could have important implications for improving the management of wild and captive wolves and could be relevant for tempering the increasing conflict between farmers, hunters and wild wolves immigrating into countries where the wolf used to be extinct, particularly as it pertains to their decisions regarding whether to interact with specific humans. Studies investigating the intelligence of such a "problem" species could diminish their negative public image as the "big bad wolf" and instead demonstrate that wolves are smart, intelligent, caring and only living beings like us humans.

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7. Appendix

Table 1. Showing the decisions the individual subjects made during the six test trials in condition 1, indicating the species, the name of the subjects, the partner who was the generous partner, the color of the clothes the generous partner wore during the trials and the animals' choices in the test phase broken down to all six trials. Yellow background indicates that the person who the subject chose was standing on the left side. S = selfish person, G = generous person, nc = no choice

Species	Name	Generous person	Color	Trial 1	Trial 2	Trial 3	Trial 4	Trial 5	Trial 6
Wolf	Geronimo	Partner 2	black	S	G	G	S	G	G
Wolf	Yukon	Partner 2	white	S	S	G	S	G	G
Wolf	Kenai	Partner 2	white	G	S	G	G	G	G
Wolf	Amarok	Partner 1	black	G	S	S	S	G	S
Wolf	Tala	Partner 2	white	G	G	G	G	G	S
Wolf	Chitto	Partner 1	black	G	S	S	S	G	S
Wolf	Wamblee	Partner 1	black	G	G	S	S	S	S
Wolf	Maikan	Partner 1	white	G	G	S	G	S	S
Dog	Layla	Partner 2	white	G	S	S	G	G	G
Dog	Zuri	Partner 1	white	G	S	G	G	G	nc
Dog	Panya	Partner 1	black	S	S	S	S	S	G
Dog	Enzi	Partner 2	white	G	G	G	G	G	G
Dog	Imara	Partner 2	black	G	S	S	G	G	S
Dog	Hiari	Partner 1	white	nc	nc	nc	nc	nc	G

Table 2. Showing the decisions the individual subjects made during the six test trials in condition 2, indicating the species, the name of the subjects, the partner who was the generous partner, the color of the clothes the generous partner wore during the trials and the animals' choices in the test phase broke down to all six trials. Yellow background indicates that the person who the subject chose was standing on the left side. S = selfish person, G = generous person [when finishing this paper not all wolves were tested yet, thus this table shows only preliminary results; the data collection will continue (see complete results in future paper)]

Species	Name	Generous person	Color	Trial 1	Trial 2	Trial 3	Trial 4	Trial 5	Trial 6
Wolf	Amarok	Partner 4	dark	S	G	G	G	G	G
Wolf	Tala	Partner 3	light	G	G	S	G	G	G
Wolf	Chitto	Partner 4	light	G	G	S	S	S	G
Dog	Layla	Partner 3	dark	G	S	G	S	G	S
Dog	Zuri	Partner 4	light	S	S	G	S	S	G
Dog	Panya	Partner 4	light	G	G	G	G	G	G
Dog	Enzi	Partner 3	dark	S	G	G	G	G	S
Dog	Imara	Partner 3	light	G	S	G	G	G	G
Dog	Hiari	Partner 4	light	G	S	S	G	S	S

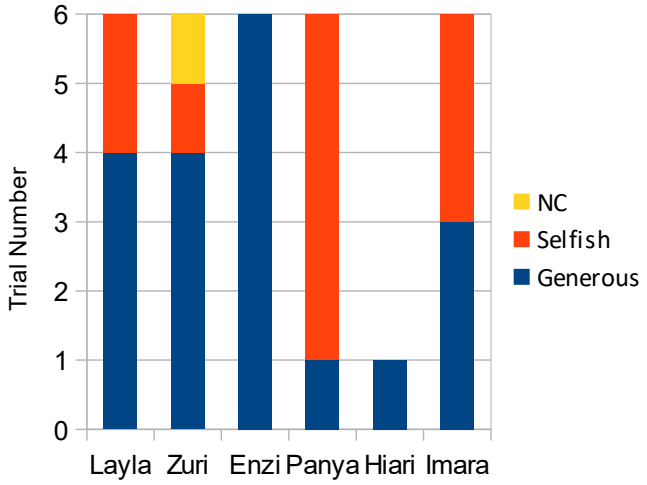

Figure 1. Showing the choices of the individual dogs for the generous and selfish partner in all six trials in condition 1. (NC = no choice response)

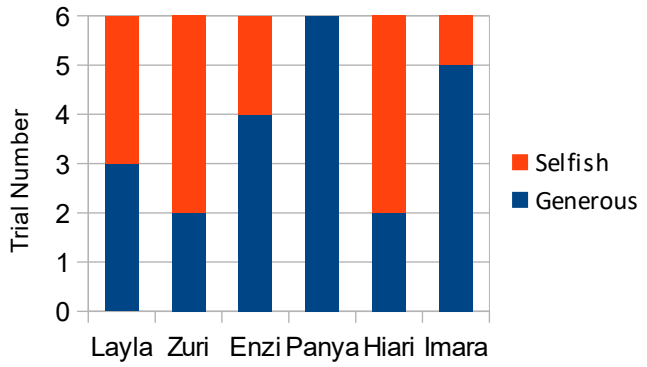

Figure 2. Showing the choices of the individual dogs for the generous and selfish partner in all six trials in condition 2.

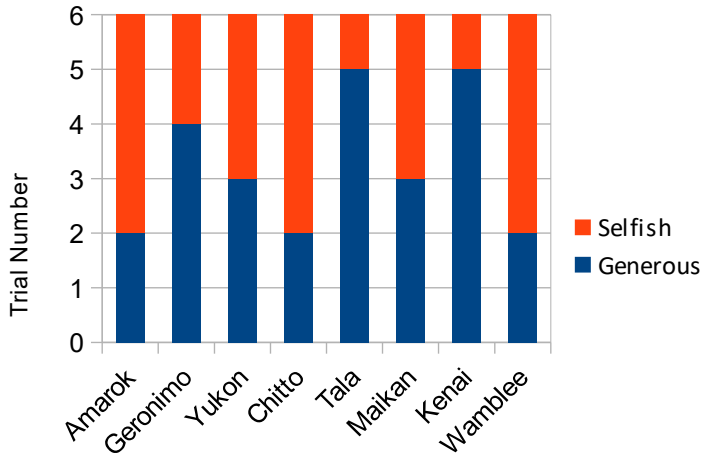

Figure 3. Showing the choices of the individual wolves for the generous and selfish partner in all six trials in condition 1.

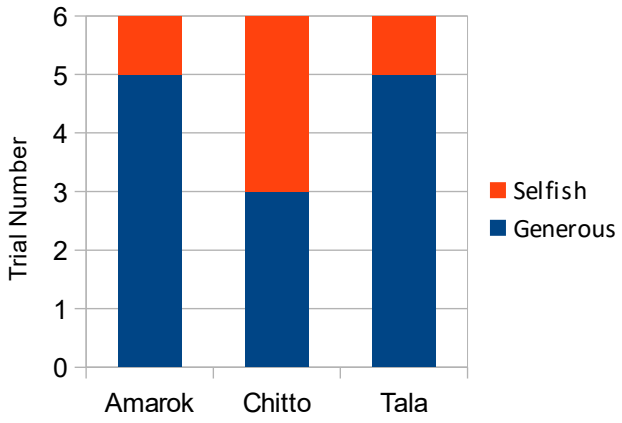

Figure 4. Showing the choices of the individual wolves for the generous and selfish partner in all six trials in condition 2.

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8. Declaration in lieu of oath

I herewith declare in lieu of oath that this thesis has been composed by myself without any inadmissible help and without the use of sources other than those given due reference in the text and listed in the list of references. I further declare that all persons and institutions that have directly or indirectly helped me with the preparation of the thesis have been acknowledged and that this thesis has not been submitted, wholly or substantially, as an examination document at any other institution.

12.02.2021 Signature