Piloting a new prosociality paradigm in dogs and wolves: The location choice task

Rachel Dale[a,b,*,1], Marie-Noémie Despraz[c,1], Sarah Marshall-Pescini[a,b], Friederike Range[a,b]

[a] Wolf Science Center, Konrad-Lorenz Institute of Ethology, University of Veterinary Medicine, Vienna, Austria
[b] Comparative Cognition, Messerli Research Institute, University of Veterinary Medicine, Vienna, Austria
[c] Comparative Cognition, University of Neuchâtel, Rue Emile-Argand 11, 2000 Neuchâtel, Switzerland

ARTICLE INFO

ABSTRACT

The aim of this pilot 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 human 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. Here we tested if wolves and dogs are prosocial in a novel paradigm and, secondly, whether prosociality in dogs is a by-product of domestication or an ancestral trait shared with wolves. With the exception of one wolf, the current task did not reveal a prosocial response in either species, despite the same subjects showing prosocial tendencies in other tasks. Prosociality has been difficult to experimentally observe and it presents a methodological challenge. We are still at the beginning of this journey in Canids and this study adds another piece to the puzzle of how best to investigate this behaviour.

1. Introduction

Prosociality can be defined as "*a voluntary behaviour that benefits others*" (Jensen et al., 2014). To determine the evolutionary origins of prosociality, researchers have primarily focused on our closest living relative, chimpanzees (*Pan troglodytes*). Indeed, as they live in groups, share food, defend territories, hunt collectively, and show evidence of empathy (Gruber and Clay, 2016; Preston and de Waal, 2002), chimpanzees are likely candidates to show prosocial behaviours. At first, studies revealed negative results (Jensen et al., 2006; Silk et al., 2005; Vonk et al., 2008). However, subsequent studies with different methodologies suggest that chimpanzees do behave prosocially in some tasks (Horner et al., 2011; House et al., 2014).

On the other hand, other species have shown more consistent prosocial responses across tasks such as capuchins (*Cebus paella*; Lakshminarayanan and Santos, 2008, *Cebus apella*; de Waal et al., 2008) and common marmosets (*Callithrix jacchus*; Burkart et al., 2007; Burkart and van Schaik, 2013). These findings opened up the possibility that specific traits linked to a species' social organization, rather than their phylogenetic closeness to humans, may be more clearly related to prosociality (Burkart et al., 2014; Marshall-Pescini et al., 2016), thus

leading the way to also testing non-primate species (e.g. Amici et al., 2017; Horn et al., 2016).

One species to have shown prosocial responses is the domestic dog (*Canis lupus familiaris*). Recently two studies tested pet dogs on a simplified prosocial choice test (PCT; Colman et al., 1969). Typically in this task the subject has the choice between a "selfish" option, in which only the actor is rewarded with food (1/0) and a prosocial option, in which both the actor and a partner get rewarded (1/1). In the simplified version with the dogs they could choose between an option which gave only the partner a reward (0/1) and an option which gave no reward at all (0/0). The first study used a bar-pull apparatus in which the dogs chose between an upper or lower shelf, one of which was baited, to pull towards them (Quervel-Chaumette et al., 2015). In this task the dogs pulled the giving shelf (0/1) more often for a familiar partner than for a stranger. Crucially, they also pulled more for the familiar partner than in a non-social control where no partner was present, and than in a social-facilitation control where the partner was present but unable to access the reward. In the second study the dogs could select between two tokens to press with their noses; one which provided the partner enclosure a reward and one which gave no reward (Dale et al., 2016). Again the dogs chose the 'giving' token more for the familiar partner

than for a stranger or in the non-social control. However, in this task there was no difference in the number of rewards delivered between when the partner accessed the reward and when the same partner was present but unable to access the food.

These findings, taken together with those from primates, suggest that the methodology employed can impact on the prosocial response demonstrated by the subjects. Therefore the current study again employed a prosocial choice task with dogs, but using a different method.

Recently, Hernandez-Lallement et al. (2015) designed a PCT experiment for rats (*Rattus norvegicus*) using a double T-maze, whereby once released into the apparatus they could choose between two compartments, one of which was prosocial (1/1, termed BR by the authors for "both reward") and the other was selfish (termed OR for "own reward"). In fact, Hernandez-Lallement et al. found that the rats, made on average 55% of prosocial choices in this test condition. As a control 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 maintained them after repetition.

However, the authors additionally noticed that the preference for either the prosocial or asocial compartment greatly varied across individuals. 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 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). Overall these results support those obtained in other experiments with rats (Ben-Ami Bartal et al., 2011; Ben-Ami Bartal et al., 2014) suggesting that rats are prosocial animals (Hernandez-Lallement et al., 2015) but they also highlight the importance of taking individual variation in prosociality into account.

The current study adapted the paradigm created by Hernandez-Lallement et al. for use with Canids. This task was chosen due to its simple design and because it does not require apparatus manipulation, but merely the choice of one location over another. Object manipulation is a factor, which might make species comparisons difficult as, for example, wolves are more inclined to manipulate objects than dogs (Marshall-Pescini et al., 2017a;b; Moretti et al., 2015). Accordingly, compared to the more 'traditional' prosocial choice tasks, the advantage of the location task is that it avoids this potential confounding factor. The general procedure remained mostly the same with the exception that in the control condition, instead of using a toy rat, in our study the partner was present but was never rewarded, even when the actor entered the BR compartment. Additionally, we added comprehension sessions at the end of the testing to assess whether the animals had understood the set-up of the task.

Furthermore, the origins of dog prosociality are still an open question. It is possible that due to selection for reduced fear and aggression (Hare et al., 2002), dogs have developed more prosocial tendencies during the process of domestication. Alternatively it may be that wolves, the closest living relatives of dogs, have prosocial tendencies to help maintain their cooperative social organisation (MacNulty et al., 2014; Mech and Boitani, 2003; Packard, 2003). As such, dogs may have retained this trait from their ancestors (Range and Virányi, 2015). Therefore, the current study also tested wolves on the same task.

Based on the performance of the rats and the positive results of dog prosociality in other tasks, we predicted that dogs would also be prosocial in the current set-up by choosing the BR compartment more often

Table 1
Information on the species and sex composition of each dyad.

Actor	Partner	Species	Sex composition
Chitto	Kaspar	Wolf	M-M
Shima	Aragorn	Wolf	F-M
Yukon	Geronimo	Wolf	F-M
Maisha	Binti	Dog	M-F
Pepeo	Nuru	Dog	M-M
Nia	Sahibu	Dog	F-M
Meru	Hiari	Dog	M-M

in the test than in the control condition. Since wolves have never been experimentally tested in a prosocial task before, we propose two hypotheses, 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. 2. Both wolves and dogs show prosociality. If the results confirm this latter prediction, this would suggest that the basis for dog-human cooperation is grounded in wolves' cooperative/prosocial behaviour towards conspecifics (see the Canine Cooperation hypothesis; Range and Virányi, 2015).

2. Methods

2.1. Subjects

All testing was carried out at the Wolf Science Center (WSC), Austria. The dogs (actors N = 4, partners N = 4; see Table 1) were mixed breeds and came from Hungarian shelters or were born at the WSC. All wolves (actors N = 3, partners N = 3; see Table 1) used in this study were born in captivity in North America. Ten days after birth, all of the wolves and the dogs from the Hungarian shelters were taken 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 6 h 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 but also integrated into their conspecific packs. After these first five months they were moved to 2000-8000 m^2 enclosures, where they were integrated into existing packs according to their temperament and bonds. From this time, humans are not continuously present in their enclosure anymore. Dogs and wolves participate in multiple behavioural tests every week but all were naïve to the current set-up. Their participation in each testing and training session is voluntary.

The dyads for this experiment were all adult animals and were chosen semi-randomly, with the criteria that the donor had to be motivated to perform the task for the required number of trials per session and the partner had to be comfortable in the partner compartment for the duration of the session. Since this was a pilot study and the sample size was kept small, dyads were also selected randomly according to sex composition and social relationship factors such as hierarchy and these factors were not considered in the analyses.

2.2. 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 closed with the partner inside (see Fig. 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

Fig. 1. This figure represents the test enclosures 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, held on its collar by a trainer (yellow dot). 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). A camera (pink rectangle) recorded 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 and moved to open and close the slides (blue lines) 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).

actor would go back to its start position and a new trial would start.

2.3. Experimental set-up

It was crucial to ensure that the actor could see that its' partner was present. 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 have influenced the side the actor chooses due to the actor seeking, or indeed avoiding, proximity with the partner (e.g. Amici et al., 2014; Massen et al., 2010). 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 Fig. 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 reducing the chance that their location influenced the

actor's choice.

An experimenter and two helpers, hidden from both actor and partner by a visual occluder, were standing 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 moved to a slide each and closed and opened them again, via a pulley system, to bring the animal's attention to the task and to alert them that the next trial was starting.

The trainer called the actor back to the starting point (2.1–2.4 meters from the compartments) after each trial and held it by its collar, a procedure these animals are accustomed to from an early age on. Trials were recorded using cameras placed behind the actor's starting point on the other side of a fence (see Fig. 1) and at the top of the compartments (see Fig. 1).

2.4. Schedule

The general testing schedule 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 non-prosocial choice) and experimental sessions (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 carried out prior to every experimental session (regardless of whether it was a test or control condition) to ensure that animals had experience of the task contingencies (see supplementary materials for example schedule). For each dyad, the side of OR and 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 sessions and the OR/BR sides was counterbalanced across dyads (see supplementary materials S1).

Each subject received a total of 28 sessions per dyad (see supplementary materials for an example).

2.5. Procedure

2.5.1. Exposure sessions

In exposure trials (24 trials per session) actors were exposed to a forced choice; only one door, selected in a pseudo-randomized order (the same side presented not 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) and therefore learn which side was OR and which was BR. 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. During the first session, the experimenter called the actor to the open compartment when she/he failed to enter it within 30 s.

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 two 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 and after an OR choice the partner was never rewarded which may have led to negative reactions towards the experimenter. Therefore for safety reasons, the partner was rewarded after each trial, but only after the actor had returned to its start location and was unable to see or hear its partner getting rewarded.

2.5.2. Experimental sessions

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.

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). We conducted this control condition, because in the test condition actors could prefer the BR side because there were two pieces of meat, which was visually attractive, regardless of whether his partner was getting one or not, or alternatively they may become frustrated when entering the BR side because two rewards are visible but they could only consume one and thus start to avoid the BR compartment. Therefore, this control was conducted to assess whether the actor was making his choices based solely on their outcome, or whether they were influenced by the quantity of visible rewards. To avoid any frustration 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 six control condition sessions were presented to each subject (see supplementary materials for an example testing order).

2.5.3. Comprehension sessions

After the testing phase, the subjects completed two comprehension sessions of 18 trials each. During these comprehension sessions, the partner was absent. As in the test, the actor chose to enter either the OR or BR enclosure and received the reward distribution of the enclosure they entered, but now the doors between the 3 compartments (OR, BR and partner compartments) were open, to allow the actor to move between the three enclosures. Therefore, if the actor understood the outcome of each enclosure, they should choose to go to the BR enclosure to get two rewards (actor and receiver enclosures) instead of only one, which they would receive if OR is chosen. The prosocial (BR) side was on the same side as that of the last testing session.

2.6. Analyses

Firstly, we tested whether subjects chose the prosocial (BR) side more than the own-reward (OR) side in the test condition. Due to side biases and a relatively large amount of variation between individuals in the performance in both test and control, we used the control condition as a baseline for the test responses. Therefore, for each individual the scores were calculated as follows (Table 2):

$$BR\_choices_{(test)} - BR\_choices_{(control)} = BR\_delta$$

$$OR\_choices_{(test)} - OR\_choices_{(control)} = OR\_delta$$

By using the test responses relative to the control, this method means that even with a side bias, we can assess whether subjects may still be showing a more prosocial response in the test than in the control, which may not be apparent when comparing the number of BR choices to a 50/50 chance level. We then ran a Wilcoxon signed rank test to compare BR_delta with OR_delta.

Due to the small sample size, the Wilcoxon test was the primary analysis. However, in order to also assess whether learning or species affected our results, a linear mixed model was run using the lmer function of the lme4 package in R version 3.2.2 (R Core Team, 2015). Percentage of BR choices was the response variable, and session, species and condition were included as fixed effects. The identity of the subject and the human helpers were included as random variables.

Finally, we calculated a social bias score for each individual, according to the procedure of Hernanzez-Lallement et al (2015):

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

Whereby i represents an individual, SB = social bias score and BR = both-reward choices. A positive score indicates a tendency to choose the BR compartment more in the test relative to the control and vice versa for a negative score. These scores were then compared to upper and lower confidence interval limits generated via a bootstrapped permutation analysis to assess whether the subjects were more (or less) prosocial than would be predicted by chance. Specifically, the permutation distribution of social bias scores consisted of N = 5000 draws of 6×2 sessions, with the percentage of BR choices of these sessions randomly assigned to test and control. For each of these draws, the resulting social bias score was calculated, generating a distribution of 5000 permuted social bias scores that followed a normal distribution. Both the 95% and 90% percentile of this distribution were selected as benchmark social bias scores, and subsequently the actual social bias score of each animal was then tested for significance against these condition-randomized social bias benchmark values.

Finally we tested whether the subjects chose the BR side more than the OR side in the comprehension sessions using a Wilcoxon signed rank test.

3. Results

3.1. Prosocial versus asocial choices

A Wilcoxon signed rank test showed an overall trend for the animals to perform more BR choices than OR choices in the test, when using the control scores as a baseline (Z = 1.86, p = 0.07). As can be seen from the delta values in Table 2, only Meru and Pepeo performed more OR choices than BR choices, and in these cases both animals showed almost the same level of BR choice in test and control (i.e. a delta value of 0), suggesting they were choosing randomly. Yukon, Nia, Maisha, Shima and Chitto have BR_delta scores above 0, meaning that they chose the BR side more often in the test than in the control. Yukon in particular
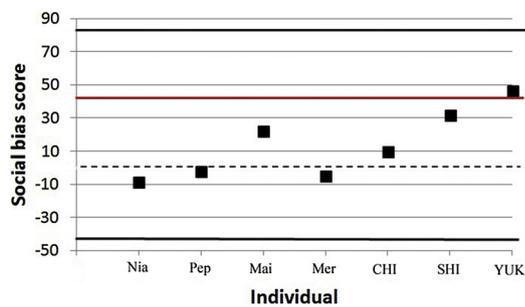
Table 2
The total number of BR and OR choices in test and control conditions across all sessions (72 trials per condition), the delta scores, and the social bias (SB) score of each individual.

Subject	Species	BR_test	OR_test	BR_control	OR_control	BR_delta	OR_delta	SB_score
Chitto	Wolf	38	33	34	38	4	−5	9.75
Shima	Wolf	23	49	18	54	5	−5	31.71
Yukon	Wolf	44	29	25	46	19	−17	46.41
Nia	Dog	37	34	29	43	8	−9	−8.67
Pepeo	Dog	38	34	39	33	−1	1	−2.43
Maisha	Dog	38	34	29	43	9	−9	21.9
Meru	Dog	34	38	36	36	−2	2	−4.89

Fig. 2. Social bias scores of each individual. The filled black lines represent undirected 95% confidence intervals. The red line shows the 90% directed confidence interval. The dashed line shows zero. Individuals in all caps are the wolves.

has a high score, suggesting she may have been acting somewhat prosocially.

The linear mixed model showed that overall, species (F (1) = 1.7, p = 0.2), condition (F (1) = 1.97, p = 0.16) and session (F (1) = 0.46, p = 0.5) had no effect on the subjects' prosocial choices.

3.2. Social bias score

The social bias scores of each animal are seen in Table 2. Using 95% undirected confidence intervals (black lines on Fig. 2), none of the individuals showed significant prosocial behaviour. However, when using a 90% directed confidence interval, predicting only prosociality and not "anti-sociality", Yukon showed significant prosociality (Fig. 2). This result corroborates with the delta scores, providing added support for a prosocial tendency in this individual. Despite the lack of significant prosociality overall, it is interesting to note that all wolves had a positive score but only one dog did.

3.3. Individual differences

By only looking at the values from the models and scores, it is difficult to assess exactly how the individual variation in responses was manifest. With a small sample size, more can be ascertained by looking at each individual descriptively.

For example, by looking at Yukon's performance over time (Fig. 3) it can be seen that her side bias was driving her response in the first three sessions, but in the final three she was able to overcome that bias. For the other individuals (Fig. S2), with the exception of a few sessions (Shima session 2, Chitto session 5, Nia sessions 1 & 6, Maisha session 1) the individual plots reveal that either side biases were driving their responses or they were acting randomly.

3.4. Comprehension

A Wilcoxon signed rank test showed that the subjects did not choose the BR side significantly more often than the OR side in the comprehension sessions (mean BR; 7.771, from 18 trials. Z = -5.05, p = 0.64).

4. 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 made prosocial choices in a single T-maze setup. Contrary to the findings with rats, our results did not show any conclusive evidence of prosociality by wolves or dogs in this task. However, there are a number of potential methodological issues, which may suggest that this paradigm was inadequate to test prosociality in these species.

In adapting the task to our infrastructure and species, a number of

potentially crucial changes were made to the paradigm. Firstly, the number of trials might not have been enough to mimic and compare with the study of Hernandez-Lallement et al. (2015), as our wolves and dogs only did 72 free-choice trials per condition versus 105–150 free-choice trials per condition for the rats. Furthermore, our animals completed 16 trials per session (4 forced-choice and 12 free-choice) compared to 23–25 trials in the rats (8–10 forced-choice and 15 free-choice). 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 due to the bigger set-up and resultant larger distances the animals needed to cover. Thus, only a few trials could be run at a time for each animal before a decrease in their motivation occurred. The additional trials for the rats, both within and across sessions, may have allowed more opportunities to learn the contingencies of the task and therefore subsequently demonstrate prosociality. This explanation is supported by the finding that the rats demonstrated an increase in their prosocial choices over trials (Hernandez-Lallement et al., 2016). The reduced number of sessions, and trials per session in the canids compared to the rats increased the variance of the bootstrapped reference distribution. Thus, the 95% upper confidence interval boundary, above which indicates significant prosociality, was much higher in the current task (86.3) compared to the rats (8). Therefore, it is not surprising that some rats, but no wolves, exceeded the upper boundary and were classified as prosocial.

Another factor that changed between the two studies is that rather than using a toy animal in the control condition, we used the same partner as in the test, but in the control they had no access to rewards on either the BR or OR side. The presence of the partner was designed to be a stricter control, since we felt a toy animal would not represent another individual to the animals and therefore would not have been different from an empty enclosure. Furthermore, in order to make sure the animals were paying attention to the task contingencies and didn't fall into acquired habits from repeated testing, we alternated the presentation of test and control. However, this, combined with the presences of the partner in the control, may have influenced the animals' ability to discriminate between test and control conditions. This does raise the issue as to whether the toy condition in the rat study was an adequate control. Although it controls for non-social motivating factors such as secondary reinforcing properties of reward delivery, it does not control for potential social (but non-prosocial) motivating factors. Furthermore, the few studies to include social controls in previous PCTs have suggested that social facilitation, whereby the mere presence of a conspecific can increase, or inhibit, an individual's performance, may at least be partly driving the prosocial response (Dale et al., 2016; Jensen et al., 2006). Given that contact seeking is a motivating factor for rats to release a conspecific from a tube (Silberberg et al., 2013), social facilitation may also have impacted the performance of the rats.

Finally, it is of course possible that the wolves and dogs of the current sample are simply not prosocial. However, a number of lines of evidence suggest the negative results to be methodological rather than social. Firstly, it appears that the subjects in this study failed to fully understand the task as they did not perform above chance in the comprehension sessions. Specifically, when given access to the partner enclosure as well, therefore having the opportunity to gain two rewards if the BR side was chosen, they did not choose the BR side more than the OR side. This suggests that the adaptations we were required to make for this paradigm to work with a larger species made the task ultimately too challenging for the animals to understand.

Furthermore, this study was part of a bigger project to assess prosociality in wolves and dogs and was therefore one of multiple paradigms that was tested to investigate this topic in canids. More specifically, dogs have been found to show prosociality to familiar partners in two simplified prosocial choice tests (bar pull: Quervel-Chaumette et al., 2015 ; token choice: Dale et al., 2016). In a version of the token choice task (Dale et al., 2016) using a touch screen, wolves tested demonstrated prosocial responses in test, but not control conditions (R
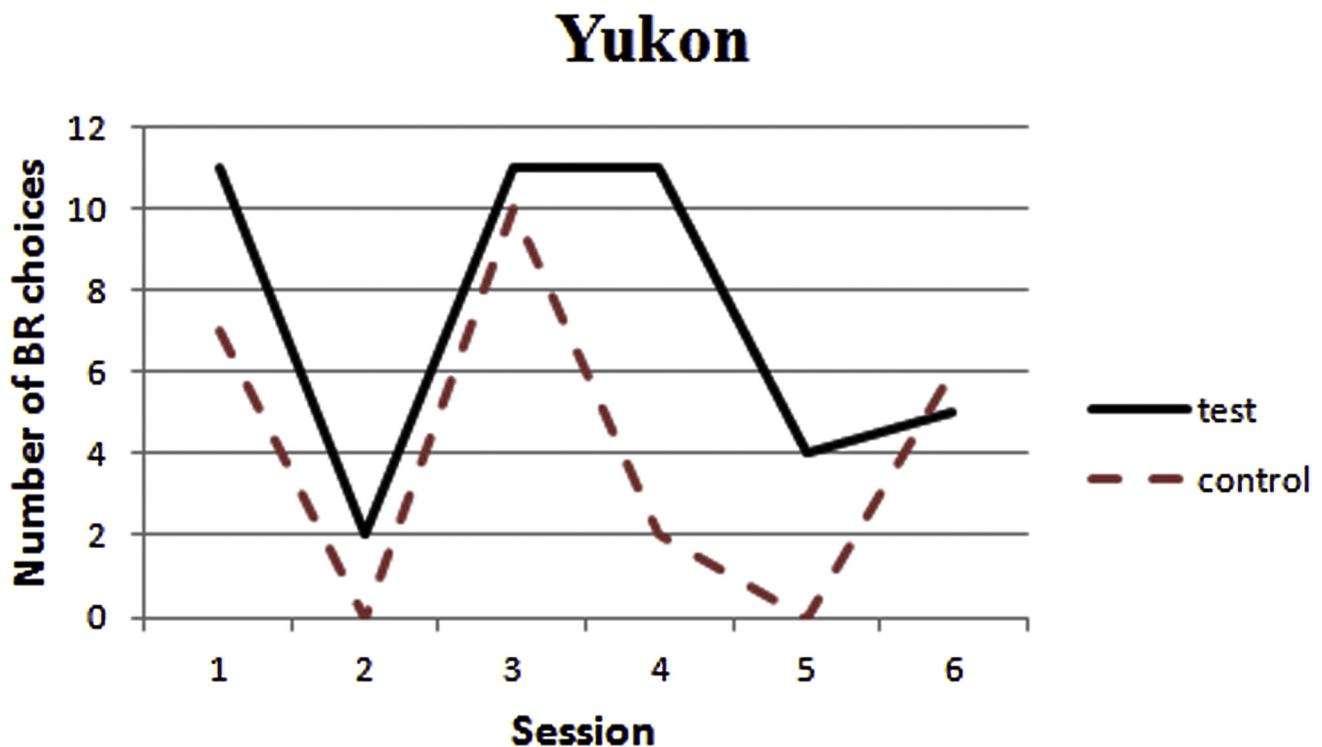
Yukon

Fig. 3. The BR choices of Yukon across sessions in the test (black) and control (dashed red).

Dale et al., unpublished data) suggesting wolves will act prosocially in an experimental prosocial choice task. Furthermore, wolves and dogs have been found to share in the feeding context. Although dogs appear to be more dependent on suitable social circumstances being present (e.g. breeding season: Dale et al., 2017a, 2017b, or high affiliation with the partner: Dale et al., 2017a, 2017b) than wolves, both demonstrate sharing of resources in natural settings. Overall, these results suggest that both wolves and dogs do act prosocially under certain conditions.

These previous findings, combined with the current study, support suggestions from a number of recent studies that methodology plays a crucial role in whether prosociality will be observed in a species or not (see also (Claidière et al., 2015; Dale et al., 2016; House et al., 2014). For example, in a direct comparison of paradigms, House et al (2014) tested chimpanzees on two different prosociality tasks and found positive results in one but not the other. Furthermore, it appears that results from experimental tests are not always congruent with more natural prosocial behaviours such as food sharing, as seen here with wolves, and with a recent failure to detect prosociality in an experiment with meerkats, a species which regularly shows helping and sharing behaviours towards conspecifics (Amici et al., 2017). The emergent picture appears to be that prosociality is a somewhat challenging behaviour to detect experimentally, and this appears to be no different in canids.

Additionally, we also did not set out to investigate individual differences in partner behaviour. Furthermore, since we fed the partner after every trial for safety reasons (see methods), this may have affected their behaviour. Pet dogs did not show an effect of partner behaviour in their prosocial responses (Quervel-Chaumette et al., 2015), and thus we do not believe this to be a strongly influencing factor. However, effects of partner behaviour have been found in other species and therefore this should be a consideration in larger scale studies.

Some authors have begun to highlight individual differences in regard to prosocial behaviours, suggesting some individuals are simply more prosocial than others (Hernandez-Lallement et al., 2015). In fact even in primate studies that demonstrate prosocial responses at the group level, typically not every individual is indeed prosocial (e.g. chimpanzees (Horner et al., 2011), marmosets (Burkart et al., 2007),

capuchins; (de Waal et al., 2008; Lakshminarayanan and Santos, 2008; Takimoto et al., 2010)). This study was designed as a small pilot to investigate the suitability of the paradigm, and therefore we did not investigate individual differences. However, it is interesting to note that the only subject in the current study to show a tendency for prosocial behaviour (when using a 90% directed confidence interval) was Yukon, who was also one of the prosocial subjects in the touch screen PCT, lending tentative support to this notion and suggesting her response was in fact prosocial, but perhaps dampened by side bias or task comprehension in the current setting. Since prosociality is apparently hard to observe experimentally at the group level, it may be that the more prosocial individuals are, the better able they are to overcome challenging experimental situations to show prosocial behaviour where other individuals do not.

4.1. Conclusions

It is necessary to try many methodologies to understand the circumstances under which animals do, and do not, show prosociality. Since dogs and wolves show prosociality to familiar conspecifics in other tasks, and wolves often show food sharing in natural contexts, we conclude these negative results to be largely methodological in nature. Although the location choice task is a simple design without the need for object manipulation, the inability to execute this task under such strictly controlled conditions and with so many trials as the rat study are the likely reasons for the lack of prosociality in the current setting and suggests that this is not the most suitable methodology, at least for our sample. This study adds an extra piece to the puzzle of how to test for prosociality in non-human animals.

Conflict of interest

The authors declare that they have no conflict of interest.

Ethical statement

All applicable international, national, and/or institutional

guidelines for the care and use of animals were followed. The research was discussed and approved by the institutional ethics committee at the University of Veterinary Medicine, Vienna, in accordance with GSP guidelines and national legislation (ETK-17/07/2015)

References

Amici, F., Visalberghi, E., Call, J., 2014. Lack of prosociality in great apes, capuchin monkeys and spider monkeys : convergent evidence from two different food distribution tasks. Proc. R. Soc. B 281 (1793) 20141699.

Amici, F., Mimo, M.C., von Borell, C., Bueno-Guerra, N., 2017. Meerkats (Suricata suricatta) fail to prosocially donate food in an experimental set-up. Anim. Cogn. https://doi.org/10.1007/s10071-017-1122-6.

Bartal, I.B.A., Decety, J., Mason, P., 2011. Empathy and pro-social behavior in rats. Science 334 (6061), 1427–1430.

Bartal, I.B.A., Rodgers, D.A., Sarria, M.S.B., Decety, J., Mason, P., 2014. Pro-social behavior in rats is modulated by social experience. Elife 3, e01385.

Burkart, J.M., van Schaik, C., 2013. Group service in macaques (Macaca fuscata), capuchins (Cebus apella) and marmosets (Callithrix jacchus): a comparative approach to identifying proactive prosocial motivations. J. Comp. Psychol. 127 (2), 212–225. https://doi.org/10.1037/a0026392.

Burkart, J.M., Fehr, E., Efferson, C., van Schaik, C.P., 2007. Other-regarding preferences in a non-human primate: common marmosets provision food altruistically. Proc. Natl. Acad. Sci. 104 (50).

Burkart, J.M., Allon, O., Amici, F., Fichtel, C., Finkenwirth, C., Heschl, A., et al., 2014. The evolutionary origin of human hyper-cooperation. Nat. Commun. 5, 4747. https://doi.org/10.1038/ncomms5747.

Claidière, N., Whiten, A., Mareno, M.C., Messer, E.J.E., Brosnan, S.F., Hopper, L.M., et al., 2015. Selective and contagious prosocial resource donation in capuchin monkeys, chimpanzees and humans. Sci. Rep. 5, 7631. https://doi.org/10.1038/srep07631.

Colman, A., Liebold, R., Boren, J., 1969. A method for studying altruism in monkeys. Psychol. Rec. 401–405.

Dale, R., Quervel-Chaumette, M., Huber, L., Range, F., Marshall-Pescini, S., 2016. Task differences and prosociality; Investigating pet dogs' prosocial preferences in a token choice paradigm. PLoS One. https://doi.org/10.1371/journal.pone.0167750.

Dale, R., Marshall-Pescini, S., Range, F., 2017a. Do females use their sexual status to gain resource access? Investigating food-for-sex in wolves and dogs. Curr. Zool. 1–8. https://doi.org/10.1093/cz/zow111.

Dale, R., Range, F., Stott, L., Kotrschal, K., Marshall-Pescini, S., 2017b. The influence of social relationship on food tolerance in wolves and dogs. Behav. Ecol. Sociobiol. 71 (107). https://doi.org/10.1007/s00265-017-2339-8.

de Waal, F.B.M., Leimgruber, K., Greenberg, A.R., 2008. Giving is self-rewarding for monkeys. Proc. Natl. Acad. Sci. 105 (36), 13685–13689.

Gruber, T., Clay, Z., 2016. A comparison between bonobos and chimpanzees: a review and update. Evol. Anthropol.: Issues News Rev. 25 (5), 239–252. https://doi.org/10.1002/evan.21501.

Hare, B., Brown, M., Williamson, C., Tomasello, M., 2002. The domestication of social cognition in dogs. Science 298 (5598), 1634–1636. https://doi.org/10.1126/science.1072702.

Hernandez-Lallement, J., van Wingerden, M., Marx, C., Srejic, M., Kalenscher, T., 2015. Rats prefer mutual rewards in a prosocial choice task. Front. Neurosci. 8, 1–9. https://doi.org/10.3389/fnins.2014.00443.

Hernandez-Lallement, J., van Wingerden, M., Schäble, S., Kalenscher, T., 2016. A social reinforcement learning hypothesis for mutual reward preference in rats. Curr. Topic Behav. Neurosci. 289–320.

Horn, L., Scheer, C., Bugnyar, T., Massen, J.J.M., 2016. Proactive prosociality in a co-operatively breeding corvid, the azure-winged magpie (Cyanopica cyana). Biol. Lett. 12 (10). https://doi.org/10.1098/rsbl.2016.0649.

Horner, V., Carter, J.D., Suchak, M., de Waal, F.B.M., 2011. Spontaneous prosocial choice by chimpanzees. Proc. Natl. Acad. Sci. 1–5. https://doi.org/10.1073/pnas.1111088108.

House, B.R., Silk, J.B., Lambeth, S.P., Schapiro, S.J., 2014. Task design influences prosociality in captive chimpanzees (Pan troglodytes). PLoS One 9 (9). https://doi.org/10.1371/journal.pone.0103422. e103422.

Jensen, K., Hare, B., Call, J., Tomasello, M., 2006. What's in it for me? Self-regard precludes altruism and spite in chimpanzees. Proc. Biol. Sci. R. Soc. 273 (1589), 1013–1021. https://doi.org/10.1098/rspb.2005.3417.

Jensen, K., Vaish, A., Schmidt, M.F.H., 2014. The emergence of human prosociality: aligning with others through feelings, concerns, and norms. Front. Psychol. 5, 1–16. https://doi.org/10.3389/fpsyg.2014.00822.

Lakshminarayanan, V.R., Santos, L.R., 2008. Capuchin monkeys are sensitive to others' welfare. Curr. Biol. 18 (21), 999–1000.

MacNulty, D.R., Tallian, A., Stahler, D.R., Smith, D.W., 2014. Influence of group size on the success of wolves hunting bison. PLoS One 9 (11), 1–8. https://doi.org/10.1371/journal.pone.0112884.

Marshall-pescini, S., Schwarz, J.F.L., Kostelnik, I., Virányi, Z., Range, F., 2017a. Importance of a species' socioecology: wolves outperform dogs in a conspecific co-operation task. Proc. Natl. Acad. Sci. 114, 11793–11798. https://doi.org/10.1073/pnas.1709027114.

Marshall-Pescini, S., Dale, R., Quervel-Chaumette, M., Range, F., 2016. Critical issues in experimental studies of prosociality in non-human species. Anim. Cogn. 1–27. https://doi.org/10.1007/s10071-016-0973-6.

Marshall-Pescini, S., Virányi, Z., Kubinyi, E., Range, F., 2017b. Motivational factors underlying problem solving: comparing wolf and dog puppies' explorative and neophobic behaviors at 5, 6, and 8 weeks of age. Front. Psychol. 8, 1–11. https://doi.org/10.3389/fpsyg.2017.00180.

Massen, J.J.M., van den Berg, L.M., Spruijt, B.M., Sterck, E.H.M., 2010. Generous leaders and selfish underdogs: pro-sociality in despotic macaques. PLoS One 5 (3), e9734. https://doi.org/10.1371/journal.pone.0009734.

Mech, L.D., Boitani, L., 2003. Wolves: Behavior, Ecology, and Conservation. University of Chicago Press, Chicago.

Moretti, L., Hentrup, M., Kotrschal, K., Range, F., 2015. The influence of relationships on neophobia and exploration in wolves and dogs. Anim. Behav. 107, 159–173. https://doi.org/10.1016/j.anbehav.2015.06.008.

Packard, J.M., 2003. Wolf behavior: reproductive, social and intelligent. In: Mech, L.D., Boitani, L. (Eds.), Wolves: behavior, ecology, and conservation. The University of Chicago Press, Chicago, pp. 35–65.

Preston, S.D., de Waal, F.B.M., 2002. Empathy: its ultimate and proximate bases. Behav. Brain Sci. 25 (1) 1-20-71.

Quervel-Chaumette, M., Dale, R., Marshall-Pescini, S., Range, F., 2015. Familiarity affects other-regarding preferences in pet dogs. Sci. Rep. 5, 18102. https://doi.org/10.1038/srep18102.

R Core Team, 2015. R: A Language and Environment for Statistical Computing. Vienna, Austria.

Range, F., Virányi, Z., 2015. Tracking the evolutionary origins of dog-human cooperation: the canine cooperation hypothesis. Front. Psychol. 5, 1–10. https://doi.org/10.3389/fpsyg.2014.01582.

Silberberg, A., Allouch, C., Sandfort, S., Kearns, D., Karpel, H., Slotnick, B., 2013. Desire for social contact, not empathy, may explain "rescue" behavior in rats. Anim. Cogn. 17 (3), 609–618. https://doi.org/10.1007/s10071-013-0692-1.

Silk, J.B., Brosnan, S.F., Vonk, J., Henrich, J., Povinelli, D.J., Richardson, A.S., et al., 2005. Chimpanzees are indifferent to the welfare of unrelated group members. Nature 437 (7063), 1357–1359. https://doi.org/10.1038/nature04243.

Takimoto, A., Kuroshima, H., Fujita, K., 2010. Capuchin monkeys are sensitive to others' reward: an experimental analysis on food-choice for conspecifics. Anim. Cogn. 13 (2), 249–261.

Vonk, J., Brosnan, S.F., Silk, J.B., Henrich, J., Richardson, A.S., Lambeth, S., et al., 2008. Chimpanzees do not take advantage of very low cost opportunities to deliver food to unrelated group members. Anim. Behav. 75 (5), 1757–1770. https://doi.org/10.1016/j.anbehav.2007.09.036.