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Differences in persistence between dogs and wolves in an unsolvable task in the absence of humans.

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1 Abstract

Despite being closely related, dogs consistently perform worse than wolves in independent problem-solving tasks. These differences in problem-solving performance have been attributed to dogs' greater reliance on humans, who are usually present when problem-solving tasks are presented. However, more fundamental motivational factors or behavioural traits such as persistence, behavioural variety and neophobia may also be responsible for differences in task performance. Hence, to better understand what drives dogs' and wolves' different problem-solving performance, it is essential to test them in the absence of humans. Here, we tested equally raised and kept dogs and wolves with two unsolvable tasks, a commonly used paradigm to study problem-solving behaviour in these species. Differently from previous studies, we ensured no humans were present in the testing situation. We also ensured that the task was unsolvable from the start which eliminated the possibility that specific manipulative behaviours was reinforced. This allowed us to measure both persistence and behavioural flexibility more accurately. In line with previous studies, we found wolves to be more persistent than dogs. We also found behavioural variety to be linked to persistence and persistence to be linked to contact latency. Finally, subjects were consistent in their performance between the two tasks. These results suggest that fundamental differences in motivation to interact with objects drive the performance of wolves and dogs in problem solving tasks. Since correlates of problem-solving success i.e. persistence, neophobia, and behavioural variety are influenced by species' ecology, our results support the social ecology hypothesis which postulates that the different ecological niches of the two subspecies (dogs have evolved to primarily be scavengers and thrive on and around human refuse, while wolves have evolved to primarily be group hunters and have a low hunting success rate) at least partly shaped their behaviours.

2 Introduction

Animals need to solve various ecological and social problems to survive. Studies across taxa have found problem-solving success to depend on several psychological propensities (also referred to as the "correlates of problem-solving success"). These include neophobia (the fear of new situations or objects), behavioural variety and flexibility (the repertoire of problem-solving behaviours an animal displays, and its ability to find novel solutions to already known problems, or use known solutions to solve novel problems) and, most importantly, persistence (Lefebvre, Reader & Sol, 2004; Biondi, Bó & Vassallo, 2010; Hiestand, 2011; Cole, Cram & Quinn, 2011; Morand-Ferron et al., 2011; Thornton & Samson, 2012; Benson-Amram & Holekamp, 2012; Griffin & Guez, 2014; Moretti et al., 2015; Griffin & Diquelou, 2015; Huebner & Fichtel, 2015; Udell, 2015; Borrego & Gaines, 2016) (defined as task directed motivation and quantified as the amount of time an animal spends tackling a task). These correlates are interconnected among themselves, with behavioural flexibility being positively correlated with persistence (Morand-Ferron et al., 2011; Benson-Amram & Holekamp, 2012; Griffin & Guez, 2014; Huebner & Fichtel, 2015; Borrego & Gaines, 2016) and both being negatively correlated with neophobia (Bouchard, Goodyer & Lefebvre, 2007; Biondi, Bó & Vassallo, 2010; Thornton & Samson, 2012; Sol, Griffin & Bartomeus, 2012; Benson-Amram & Holekamp, 2012; Griffin & Guez, 2014; Moretti et al., 2015; Borrego & Gaines, 2016). They are influenced by a

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species' ecology, social structure and living conditions (Webster & Lefebvre, 2001; Lefebvre, Reader & Sol, 2004; Cauchard et al., 2013; Griffin, Diquelou & Perea, 2014). For example, birds in variable environments and habitats were found to be less neophobic and have more behavioural variety and flexibility than conspecifics in more stable environments (Mettke-Hofmann, Winkler & Leisler, 2002; Sol, Lefebvre & Rodriguez-Teijeiro, 2005; Sol et al., 2011; Kozlovsky, Branch & Pravosudov, 2015). Persistence was higher in social carnivores than in closely related non-social ones, as well as in captive hyenas than in wild conspecifics (Benson-Amram, Weldele & Holekamp, 2013; Borrego & Gaines, 2016). Personality (or behavioural type), has also been shown to play a role in problem solving styles (Sih & Del Giudice, 2012). For instance, in certain contexts, a reactive behavioural type is associated with slower, less exploratory behaviour and less persistence, while a proactive behavioural type, with faster exploratory behaviour and higher persistence (Sih & Del Giudice, 2012). Performing multiple problem-solving experiments over time can help understand consistency in animals' performance and hence, the effect behavioural types have on the correlates of problem-solving success.

Dogs and their closest living ancestors, wolves (Frantz et al., 2016) differ strongly in their problem-solving success in various paradigms (Frank & Frank, 1982; Frank et al., 1989; Miklósi et al., 2003; Udell, Dorey & Wynne, 2008; Hiestand, 2011; Range & Virányi, 2014; Marshall-Pescini, Virányi & Range, 2015; Udell, 2015; Heberlein et al., 2016; Rao et al., 2017; Brubaker et al., 2017; Marshall-Pescini et al., 2017a,b). For instance, wolves were more task-focussed, showed more behavioural variety, were more persistent and were able to generalise better than dogs in a string-pulling task (Hiestand, 2011). They were faster and more successful at obtaining food from puzzle boxes (Frank & Frank, 1982; Udell, 2015; Rao et al., 2017; Brubaker et al., 2017) and performed better at a visual discrimination task than dogs (Frank et al., 1989). These differences have partly been attributed to the different ecological niches they live in (Virányi et al., 2008; Range & Virányi, 2013, 2014; Marshall-Pescini, Virányi & Range, 2015; Werhahn et al., 2016; Marshall-Pescini et al., 2017c,a; Brubaker et al., 2017). Unlike wolves, dogs live in a human dominated niche (Marshall-Pescini et al., 2017a). They may hence rely on humans more than wolves do, both, in terms of social support (Gácsi et al., 2005), and possibly as 'problem-solvers'. Authors often describe dogs displaying copious amounts of human directed behaviours during problem-solving experiments. There is ample evidence that when confronted with a problem in the presence of a human, dogs are more likely than wolves to look towards and/or interact with the human instead of engaging in the task (Miklósi et al., 2003; Passalacqua et al., 2011; Udell, 2015; Brubaker et al., 2017).

Two hypotheses might explain why dogs engage and persist less than wolves in these situations. First, it is possible that previous experience with humans, who often solve problems for dogs, drives the dogs' behaviour. In the human-dominated niche that dogs live in, humans often provide support in all important domains including providing access to resources such as food (Marshall-Pescini et al., 2017a). Hence, dogs might expect humans to solve problems for them and thus turn to humans for help without trying very hard to solve problems by themselves. However, differences in problem-solving success are visible even in dogs and wolves that have identical experience with humans (Gácsi et al., 2009; Virányi & Range, 2011; Range & Virányi, 2014; Marshall-Pescini, Virányi & Range, 2015; Marshall-Pescini et al., 2016, 2017c; Heberlein et al., 2016; Rao et al., 2017). The

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second, likelier hypothesis that may explain differences in dogs' and wolves' problem-solving performance, is that adaptations to their respective feeding ecologies (Fleming et al., 2017) have resulted in dogs and wolves evolving differences in their correlates of problem-solving success, particularly in persistence. Wolves are primarily hunters (Fleming et al., 2017) with low success rates (between 10% and 49%) and need to be highly persistent to survive (Mech, Smith & MacNulty, 2015). Dogs, however, are primarily scavengers (Marshall-Pescini et al., 2017a; Fleming et al., 2017), dependant mostly on human refuse (Atickem, Bekele & Williams, 2009; Vanak & Gomper, 2009; Newsome et al., 2014; Marshall-Pescini et al., 2017a; Fleming et al., 2017) and may not need to be as persistent. Accordingly, in a problem-solving experiment with a human present, dogs might be less persistent, give up earlier than wolves, and then, turn towards the human as there is nothing else to do. Following this reasoning, turning to humans would not be a strategic choice to obtain help or support instead of solving the task independently, as has been suggested previously (Miklósi et al., 2003; Gácsi et al., 2005; Persson et al., 2015; Konno et al., 2016) but rather a consequence of reduced persistence. Overall, while the ecology-based hypothesis postulates fundamental differences in motivation (regardless of human presence), the human reliance hypothesis suggests that, while dogs and wolves might have similar problem-solving skills (when alone), dogs turn towards humans as an alternative strategy to solving problems by themselves.

A first step towards teasing these hypotheses apart and better quantifying persistence without direct human influence on dogs' and wolves' performance is to conduct problem-solving tasks in the absence of humans. Udell (2015) headed in this direction by testing subjects in three conditions - alone, with a silent human, and with an encouraging human. While wolves were more persistent than pet dogs in the task even when alone suggesting that dogs' may have a "generalized dependence on humans" (Pg. 1), authors also highlight that such dependence may be a result of differences in the life experiences that the pet dogs and hand-reared wolves had. Pet dogs may have been discouraged by their owners to 'problem-solve' the trash-can or kitchen drawers, which may have resulted in dogs being inhibited when confronting a novel object. Differences in life experience are in fact known to affect problem-solving in dogs: highly trained dogs (agility, retriever, search and rescue) showed more independent problem-solving abilities than untrained pet dogs, who conversely looked towards the owner longer (Marshall-Pescini et al., 2008) in such tasks.

Here, we presented equally raised and kept pack-living dogs and wolves with two different unsolvable tasks in the absence of humans on two separate occasions. Each task consisted of an object baited with food that was inaccessible to the animal. To avoid animals' expectations regarding the role of a human in the task, we presented the object in their home enclosure where humans rarely enter. Humans entering the enclosure is instead associated with a routine enrichment procedure where the animals are shifted out of the home enclosures, humans scatter food in the enclosures, leave and then shift the animals back in. Apart from removing the expectation of human presence, using an enclosure associated with the enrichment procedure (which is familiar to all animals) guaranteed a similar motivational state for all subjects. Furthermore, since food motivation is known to influence problem-solving behaviour (Laland & Reader, 1999; Sol, Griffin & Bartomeus, 2012; Griffin, Diquelou & Perea, 2014; Griffin & Guez, 2014), we tested subjects early in the morning without feeding them the evening prior to the test. Finally, as food motivation is influenced by food

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quality (Fontenot et al., 2007; Dufour et al., 2012; Hillemann et al., 2014); we used high value food (based on a previously performed preference test) for testing (Rao, et al. *submitted*).

We measured persistence as the time spent manipulating the presented objects. We predicted that if human presence during testing and/or general differences in wolf-dog experiences with humans (Udell, 2015) are the main factors responsible for wolves' greater persistence in problem-solving experiments, dogs and wolves would not differ significantly in their persistence in the current study. If, however, adaptations to the respective feeding niches play a bigger role than their experience with humans, wolves would be significantly more persistent than dogs.

Although several studies have compared species (Griffin & Guez, 2014) and evaluated the effect of different environments on problem solving behaviours, fewer studies have also examined how problem-solving correlates relate to each other (birds: (Griffin & Guez, 2014), mammals: (Thornton & Samson, 2012; Benson-Amram & Holekamp, 2012; Borrego & Gaines, 2016)). Therefore, in the current study, apart from persistence, we also measured behavioural variety (the number of different object-directed manipulative behaviours exhibited) when subjects attempted to extract the food from the presented objects, the latency for subjects to contact each object (contact latency; typically used as a measure of neophobia (Griffin & Guez, 2014)) and the body posture (low-fearful vs. high-confident) exhibited during approach and manipulation.

Based on literature, we predicted a positive correlation between persistence and behavioural variety. The relationship between persistence and contact latency may be more multifaceted, as contact latency could be a measure of neophobia but also a measure of (dis)interest in an object. To try teasing these possibilities apart, we included body postures when analysing the data for contact latency. If contact latency was a measure of neophobia, we expected it to be higher in subjects that show an unsure body posture (known to be related to fear and insecurity (Marshall-Pescini et al., 2017c)) during approach. If no such relationship emerged, it may be that contact latency was a measure of the animal's interest in the task.

Independently of whether contact latency is a measure of neophobia or interest, we expected a negative correlation between contact latency and persistence based on previous literature (Sih & Del Giudice, 2012) in both species. Finally, we evaluated whether individual consistency in persistence and in contact latency would emerge across the two tasks. Based on literature suggesting that both are personality traits (Sih & Del Giudice, 2012) and thus stable over time and context (Réale et al., 2007), we predicted that our subjects would be consistent in their persistence and contact latency between the two tasks.

To sum up, our study had three aims: (1) to test hypotheses about why dogs and wolves differ in their persistence, (2) to assess relationships between the correlates of problem-solving success and (3) test subjects' consistency in performance across tasks.

3 Materials and methods

3.1 Ethics Statement

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Special permission to use animals (wolves) in such cognitive studies is not required in Austria (Tierversuchsgesetz 2012—TVG 2012). The “Tierversuchskommission am Bundesministerium für Wissenschaft und Forschung (Austria)” allows research without special permissions regarding animals. We obtained ethical approval for this study from the ‘Ethik und Tierschutzcommission’ of the University of Veterinary Medicine (Protocol number ETK-07/08/2016).

3.2 Subjects

We tested 17 adult dogs (7 F, 10 M; mean age + SD = 4 + 1.6 years) and 12 adult wolves (4 F, 8 M; mean age + SD = 6.3 + 1.7 years) similarly raised and kept in conspecific packs at the Wolf Science Centre, Austria, from October 2016 to February 2017 (Table 1) (see Range and Virányi 2014 for a full description of raising procedures). All subjects have contact with humans through daily training and participate in behavioural and cognitive tests conducted at the centre. The subjects also participate in weekly touristic events, which involve walking through the park on leash with a trainer and visitor and having occasional group social interactions with visitors and trainers in their home enclosures.

Table 1: Subjects

Subject	Species	Sex	Date of Birth	Age when tested
Amarok	Wolf	M	04/04/2012	4.7
Aragorn	Wolf	M	04/05/2008	8.3
Chitto	Wolf	M	04/04/2012	4.3
Geronimo	Wolf	M	02/05/2009	7.3
Kaspar	Wolf	M	04/05/2008	8.6
Kenai	Wolf	M	01/04/2010	6.6
Nanuk	Wolf	M	28/04/2009	7.3
Shima	Wolf	F	04/05/2008	8.4
Tala	Wolf	F	04/04/2012	4.3
Una	Wolf	F	07/04/2012	4.3
Wamblee	Wolf	M	18/04/2012	4.5
Yukon	Wolf	F	02/05/2009	7.3
Asali	Dog	M	15/09/2010	5.9
Banzai	Dog	M	02/04/2014	2.4
Binti	Dog	F	15/09/2010	5.9
Bora	Dog	F	02/08/2011	5.0
Enzi	Dog	M	02/04/2014	2.3
Gombo	Dog	M	21/03/2014	2.4
Hiari	Dog	M	21/03/2014	2.4
Imara	Dog	F	21/03/2014	2.4
Layla	Dog	F	03/08/2011	5.1
Maisha	Dog	M	18/12/2009	6.6

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Meru	Dog	M	01/10/2010	5.8
Nia	Dog	F	22/07/2011	5.0
Nuru	Dog	M	24/06/2011	4.9
Panya	Dog	F	02/04/2014	2.4
Pepeo	Dog	M	02/04/2014	2.3
Sahibu	Dog	M	21/03/2014	2.4
Zuri	Dog	F	24/06/2011	5.1

3.3 Apparatus

One object (henceforth referred to as the "ball") was a perforated, hard plastic sphere 24 cm in diameter, weighing 1.5 kg (commercially available "Lion Feeder Ball" from www.ottoenvironmental.com) (Figure 1), the other was a modified, perforated PVC sewage pipe (22 cm in diameter, 40 cm in length henceforth referred to as the "pipe") (Figure 2). Prior to the test, each object was baited with large chunks of strongly smelling sausage and meat out of sight of the subject.

Figure 1: Commercially available "Lion Feeder Ball"

Figure 2: Modified sewage pipe

3.4 Experimental Setup

Before a test session began, we anchored one of the objects using a 30-cm long metal chain to a camping peg driven into the ground in the subjects' home enclosure. This was done out of sight of the test subject. The peg was positioned such that we could record any interactions the subject had with the object from two different angles without any visual obstructions. We mounted two video cameras (recording at 1920 × 1080 pixels at 50 progressive frames per second) on tripods outside the enclosures. We marked a two-meter radius around the object using a commercially available bright

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red timber marking spray. We mounted a smartphone at a third angle and used "IP Webcam", a freely available app, to remotely monitor the trial, whilst staying out of sight of the subject during the entire procedure.

We tested subjects in their home enclosure as the subjects least expect a human to be present inside. Tests are normally conducted in specific "testing enclosures" at the Wolf Science Centre and humans (including trainers) only visit the animals in the home enclosures in very specific contexts (i.e. pack visits, animal care and short, training demonstrations during public guided tours).

3.5 Procedure

We tested subjects individually between 7:00 and 10:00 a.m. To ensure high food motivation, we did not feed the subjects the evening before the test. We tested one animal per pack per session and conducted two to three sessions per week, never on consecutive days. We shifted the entire pack out of their home enclosure into an empty enclosure such that their home enclosure was out of sight. We placed the test object in the subjects' home enclosure, and then led the focal subject back into the enclosure. We started the test session when the animal entered the 2m-radius (see "Start" in Table 2) and ended the test five minutes after the focal individual had stopped interacting with the object (see "End" in Table 2). We carefully washed the objects after each session to remove any possible odour cues left by the previously tested subject. We tested each subject first with the ball and re-tested them with the pipe one and a half to three months later. Two wolves, Chitto and Tala, had to be tested with the pipe six months after their test with the ball due to the onset of the mating season. As we needed to keep our study comparable to a complementary study with free ranging and pet dogs which were only presented with the ball (Lazzaroni et al. in prep), we were unable to counterbalance the presentation order of the two objects. We tested each subject only once per task to avoid object-specific learning effects.

3.6 Behavioural Coding

We recorded all tests on video and coded behaviours using Solomon Coder beta 100926 (a behaviour coding software developed by András Péter, Dept. of Ethology, Budapest, www.solomoncoder.com). Coded behaviours and definitions are summarized in Table 2. See the supplementary video for an example of each behaviour. We defined "Persistence" as the time (in seconds) a subject spent in the "Manipulating" behavioural state. We defined "Contact Latency" as the time (in seconds) a subject took from "Start" to First contact the object (Defined as the first time a subject touched or sniffed the object; in case of a sniff, the nose was within 5 cm of the object). We defined "Behavioural Variety" as the number of unique "Manipulative Behaviours" shown by a subject.

Table 2: Definitions of coded behaviours

Behaviour	**Definition**
Approach Posture	
Neutral	Body relaxed, tail relaxed below the plane of the back.

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Confident	Body rigid or relaxed, tail above or at the same level of the plane of the back.
Insecure	Tail between the legs (and wagging), and/or back (slightly) lowered, ears can be rearward, and the head can be lowered, approach can be jerky and /or cautious.
Friendly	Body relaxed, tail wagging horizontal or below the plane of the back
Manipulation Posture	
Insecure	Tail between the legs, even wagging, or back lowered, ears can be rearward, and the head can be lowered, body can be rigid, and movement can be jerky.
Friendly	Tail wagging, not between the legs.
Confident	Body rigid or relaxed, tail above or at the same level of the plane of the back.
Behavioural States	
Sniff	The subject smells or attempts to smell the object with its snout less than 10 cm from the object.
Manipulating	The subject physically manipulates the object using its paws, snout, mouth or any combination of the three and shows any of the “Manipulative Behaviours”.
Markers	
Start	The subject places a paw inside the marked 2-meter radius
End	1. The subject stops manipulating the object for 5 minutes or 2. The subject has not started manipulating the object for 5 minutes after making “First Contact” or 3. The subject has not made “First Contact” 5 minutes after “Start”.
Manipulative Behaviours	
Lift	The subject raises the object off the ground by holding it with its mouth by the chain, the object’s surface or edges, or screws. Additional behaviours while the object is lifted are not coded.
Nose	The subject moves the apparatus or tries to lift it with only its nose.
Bite	The subject bites the object.
Paws On	The subject places both paws on the top of the object and presses the object down.
Hold	The subject holds the object with both paws on the sides of it or on the top of it for the pipe, while biting it on top.
Hold Ground	The animal holds the object between both paws (which are on the ground) and stabilises the object while simultaneously biting it.
Dig	The subject uses both its paws to dig at the ground in immediate proximity of the object.
Pull	The subject pulls either the chain, the screws or the object’s surface or edges with its mouth.
Scratch	The subject scratches the object’s surface with its paws by alternating them (without its paws touching the ground).
Paw on	The subject places its paw on the object without scratching it.
Paw & Nose	The subject pushes or tries to lift the object with its nose while manipulating the object with its paw.
Paw Hold Chain	The subject holds the chain on the ground with its paw, while biting, licking, or sniffing the object, and may simultaneously paw at the object with another paw.

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Paw on & Bite	The subject places its paw on the object and simultaneously bites the object.
Paw Scratch	The subject scratches at the top of the object with its paw while attempting to pull the object towards itself.
Scratch & Lick/Sniff	The subject scratches at the top of the object with its paw while simultaneously sniffing or licking the object.
Scratch & Bite	The subject scratches at the object with its paw while simultaneously biting it.
Scratch, Paw on & Bite	The subject scratches at the object with its paw, places its other paw on top of the object and bites the object.
Lift Paw	The subject lifts its paw over the object without touching it.
Paw Dig	The subject uses its paw to dig at the ground in immediate proximity of the object.
Paw Push	The subject moves the object away from itself with its paw.
Paw Slide	The subject moves the object laterally with its paw.
Other Behaviours	
Pee	The subject urinates on the object or on or inside the circle.
Lick	The subject licks the object.
Paw & Lick/Sniff	The subject licks or sniffs the object with its paw placed on the object.
Bark	The subject vocalizes at the object.
Jump back	The subject jumps back or withdraws from the object in a neutral or insecure posture after looking at it, approaching it, sniffing it, or manipulating it.
Lay down	The subject lays down or sits next to the object or inside the marked radius.

3.7 Analyses

We excluded one dog (Gombo) from the analyses for the pipe as he successfully extracted food from the object, thereby rendering the task solvable. We used Grubbs tests (Grubbs, 1950) R version 3.4.3 (R Core Team, 2017) to detect outliers (“outliers” version 0.14) (Komsta, 2006). We excluded one wolf (Una) from the latency analyses for the ball as her contact latency was an outlier (28 seconds; $G = 5.09$, $U = 0.007$, $P < 0.001$) (potentially because she was tested at the onset of the breeding season). We excluded one dog (Nuru) from the analyses of the pipe as he was overly persistent with the pipe, making his manipulation duration an outlier (1,361 seconds, $G = 3.10$, $U = 0.63$, $P = 0.008$). See the supplementary material for how results changed when these latter two individuals were included in the analyses. All other subjects were included in the analyses (Ball: $N = 11$ wolves, 16 dogs, Pipe: $N = 12$ wolves, 15 dogs). For calculating inter-observer reliability, we used inter-class correlations (“psych” version 1.7.8) (Revelle, 2017) in R version 3.4.3 (R Core Team, 2017).

We first carried out an exploratory data analysis for each object with Two-Step Cluster analysis in SPSS version 23. We used automatic clustering with a log-likelihood distance measure and extracted the optimal number of clusters based on AIC values. We chose a multivariate approach primarily because performing several univariate analyses may not have allowed us to understand the combined effect of all explanatory variables on our subjects’ task performance. We included persistence, behavioural variety, latency to contact, approach posture and likelihood of manipulation as explanatory variables. The clustering algorithm classified subjects based on these parameters. Species was included as evaluation field; it played no part in classification but helped us understand the composition of each cluster. The rationale behind this was to allow the clustering algorithm to classify subjects purely based on task performance without any pre-existing bias. This way, if, for example, there were distinct behavioural differences between the two species, it would result in clusters composed entirely of dogs and entirely of wolves, with each cluster having significantly different values of one or more behavioural variables. Not only did this analysis allow us to test our hypotheses (about why dogs and wolves differ in their persistence), it also revealed the correlates that were most important when understanding subjects' performance.

We ran a separate cluster analysis for each object. Including both species and both objects in one analysis made it difficult to meaningfully interpret the clusters' structures. Separating the two objects allowed us to analyse whether subjects performed similarly with both objects. While the analysis gave us useful insights into patterns in our data and allowed us to partially test our first hypothesis, we could not test whether there was a statistically significant difference in dogs' and wolves' performance when interacting with the two objects. Hence, we further analysed persistence, behavioural variety and contact latency individually using generalised additive models for location, scale and shape ("gamlss" version 5.0-6) (Stasinopoulos & Rigby, 2007) in R version 3.4.3. We used the "gamlss.Distr" package version 5.0-4 to fit distributions to our data. We evaluated the distribution of each response variable (including each time we split the data to better understand statistically significant interactions) and specified the best fitting distribution in the models (see the supplementary material for distribution fit plots). We evaluated model fits both by their generalised Akaike information criteria (Akaike, 1974) and by the distribution of the model residual quantile-quantile plots (see supplementary material for model diagnostic plots). This approach enabled us to analyse the data without major transformations, which could have affected our interpretations of the results (Feng et al., 2014; Lo & Andrews, 2015).

We used a Fisher's Exact Test in SPSS v23 to test whether dogs and wolves differed in their likelihood to manipulate the objects. To test whether wolves and dogs differ in their persistence, we used a GAMLSS model to evaluate the effects of explanatory factors: species, object type and a two-way interaction between them, on the response variable persistence. We included the individual as a random factor. To ensure model convergence, we added a miniscule constant (0.001) to all persistence values.

For our second aim, we focussed on understanding the relationships between the correlates of problem solving success within dogs and wolves. Hence, we analysed data for both species separately. We ran two GAMLSS models for dogs and wolves' separately. The first model included contact latency as the response variable and the following explanatory variables: object type, persistence, approach posture and the two-way interactions between object type and persistence, and object type and approach posture. The second model considered behavioural variety as response variable and the following explanatory variables: persistence, object type and a two-way interaction between persistence and object type. We included the individual as a random factor in both models.

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Finally, we scaled subjects' persistence and contact latency from 0 to 1 in each task separately using the following formula for both variables: $V_s = \frac{V_i - Min\,(V_{all})}{Max\,(V_{all}) - Min\,(V_{all})}$ where V_s = scaled value (persistence or contact latency), V_i = individual's unscaled value, Min / Max (V_{all}) = the minimum / maximum values for that object. We used a Spearman's rank correlation on the scaled persistence and scaled contact latency data to test whether subjects were consistent in their persistence and contact latency between the two objects. We calculated a consistency score for persistence and contact latency by taking the absolute value of the difference between subjects' scaled persistence scores (or scaled contract latency scores) for the ball and for the pipe. We used a GAMLSS model to assess the effect of species on the consistency scores.

To better understand interactions that were statistically significant in any of the analyses, we carried out post-hoc analyses using GAMLSS models on subsets of our data.

4 Results

4.1 Multivariate approach to wolf-dog comparison

The cluster analysis for the ball revealed 4 clusters (average silhouette = 0.5). The likelihood of manipulation and approach posture had the most influence on how individuals were classified. See Table 3 for details of the results of the cluster analysis for the ball.

Table 3: Summary of cluster structure for the ball

Clusters (Ball)		**1**	**2**	**3**	**4**
Cluster Size		7.4% (2)	14.8% (4)	29.6% (8)	48.1% (13)
Manipulation Likelihood	*1.00*	Yes = 0 No = 2	Yes = 4 No = 0	Yes = 8 No = 0	Yes = 13 No = 0
Approach Posture	*0.87*	Unsure = 1 Confident = 1	Unsure = 4 Confident = 0	Unsure = 0 Confident = 8	Unsure = 0 Confident = 13
Behavioural Variety	*0.61*	$\bar{x}$ = 0.00 M = 0.00	$\bar{x}$ = 7.25 M = 5.25	$\bar{x}$ = 10.00 M = 10.00	$\bar{x}$ = 3.62 M = 4.01
Persistence (sec)	*0.33*	$\bar{x}$ = 0.00 M = 0.00	$\bar{x}$ = 241.70 M = 12.94	$\bar{x}$ = 328.95 M = 302.23	$\bar{x}$ = 29.29 M = 15.29
Contact Latency (sec)	*0.32*	$\bar{x}$ = 1.70 M = 1.70	$\bar{x}$ = 0.95 M = 1.10	$\bar{x}$ = 1.25 M = 1.30	$\bar{x}$ = 0.88 M = 0.80
Species		Dogs = 2 Wolves = 0	Dogs = 2 Wolves = 2	Dogs = 1 Wolves = 7	Dogs = 11 Wolves = 2

Values in brackets indicate the number of individuals in each cluster and values in italics indicate predictor importance. Columns show cluster structure; cluster means are indicated by $\bar{x}$ and sample medians by M. Counts are shown for approach posture, manipulation likelihood and species.

Cluster 1 *"Uninterested"*: This cluster comprised of two dogs (one of which showed an unsure approach posture) that were slow to contact and never manipulated the ball.

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Cluster 2 *"Unsure & non-persistent"*: This cluster comprised of two dogs and two wolves that, while unsure, were still potentially interested in the ball. They did interact with it but showed low persistence and low behavioural variety.

Cluster 3 *"Slow & persistent"*: This cluster comprised of seven wolves and one dog that while confident, took longer to approach the ball. They showed the most persistence and behavioural variety of all subjects.

Cluster 4 *"Quick & non-persistent"*: This cluster comprised of eleven dogs and two wolves, that were confident and quick to approach the ball but did not persist very long and did not show very many behaviours.

The cluster analysis for the pipe revealed 3 clusters (average silhouette = 0.6). Unlike with the analysis for the ball (where the likelihood of manipulation and approach posture had a strong influence), persistence and behavioural variety had the most influence on how individuals were classified. See Table 4 for details of the results of the cluster analysis for the pipe.

Table 4: Summary of cluster structure for the pipe

Cluster Size		18.5% (5)	22.2% (6)	59.3% (16)
Persistence (sec)	*1.00*	$\bar{x}$ = 0.00 M = 0.00	$\bar{x}$ = 673.40 M = 684.43	$\bar{x}$ = 18.56 M = 6.54
Behavioural Variety	*0.86*	$\bar{x}$ = 0.00 M = 0.00	$\bar{x}$ = 12.33 M = 13.5	$\bar{x}$ = 3.50 M = 3.00
Manipulation Likelihood	*0.58*	Yes = 0 No = 5	Yes = 6 No = 0	Yes = 7 No = 0
Approach Posture	*0.10*	Unsure = 1 Confident = 4	Unsure = 0 Confident = 7	Unsure = 0 Confident = 16
Contact Latency (sec)	*0.08*	$\bar{x}$ = 1.20 M = 1.20	$\bar{x}$ = 0.77 M = 0.81	$\bar{x}$ = 1.39 M = 1.00
Species		Dogs = 5 Wolves = 0	Dogs = 2 Wolves = 4	Dogs = 8 Wolves = 8

Values in brackets indicate the number of individuals in each cluster and values in italics indicate predictor importance. Columns show cluster structure; cluster means are indicated by $\bar{x}$ and sample medians by M. Counts are shown for approach posture, manipulation likelihood and species.

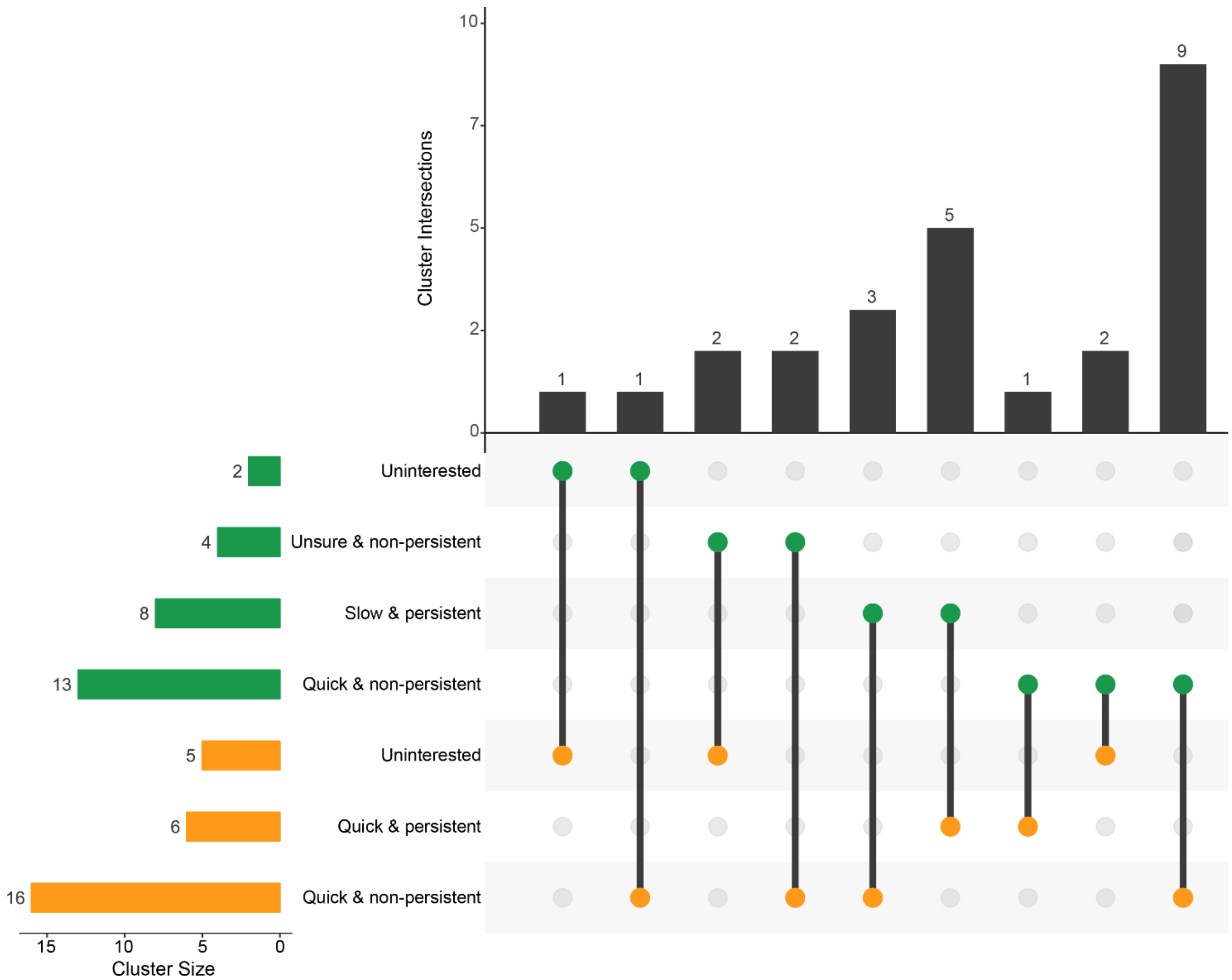
Cluster 1 *"Uninterested"*: This cluster was comprised of five dogs (one of which showed an unsure approach posture) that were slow to contact and never manipulated the pipe.

Cluster 2 *"Quick & persistent"*: This cluster was comprised of two confident dogs and four confident wolves that were fast to contact the pipe and showed the highest persistence and most number of behaviours.

Cluster 3 *"Quick & non-persistent"*: This was the largest cluster, comprised of eight confident dogs and eight confident wolves that were faster to contact the pipe than those in the first cluster but did not persist long and did not show very many behaviours.

To better understand the distribution of individuals across clusters in the two tasks, we calculated how many individuals in each cluster identified in the ball analysis, fell into the same or other clusters in the pipe analysis (Figure 3).

Figure 3: Degree of overlap between clusters



Green bars and dots represent clusters from the analysis for the ball and orange bars and dots represent those from the analysis for the pipe. Vertical bars show how many individuals were common between clusters connected with black lines (Only individuals that were included in the cluster analysis for both objects are shown). Cluster size is shown by the length of the green and orange bars next to each cluster name (left). E.g. The "uninterested" clusters from the ball and the pipe had one individual in common between them.

4.2 Model approach to the wolf-dog comparison

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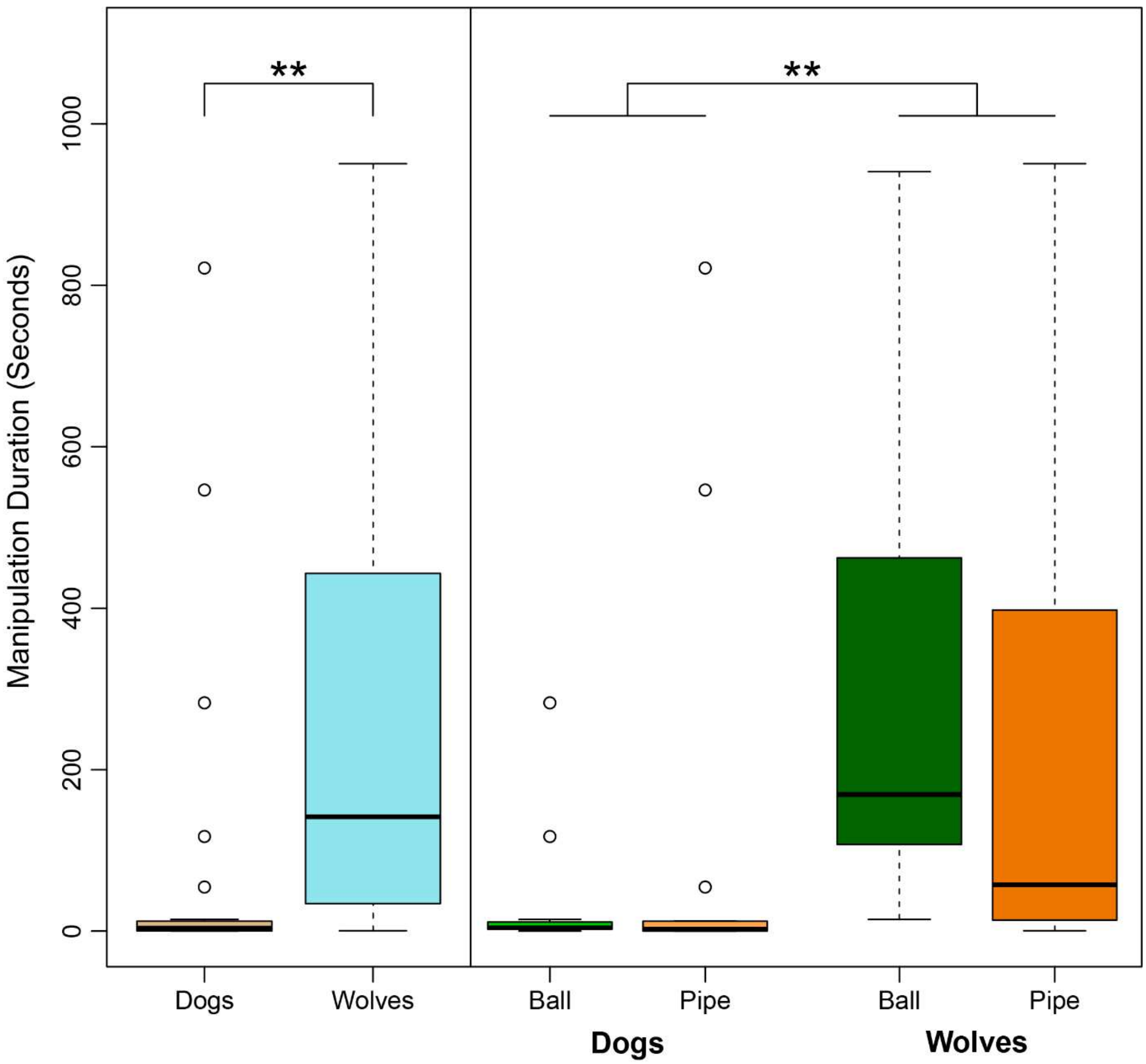
Overall, 14 out of 16 dogs manipulated the ball and 10 out of 15 dogs manipulated the pipe. In contrast, all 11 wolves manipulated the ball and all 12 wolves manipulated the pipe. Wolves were significantly more likely to manipulate objects than dogs (Fisher's Exact Test, Odds Ratio = 0.774, 95% conf. interval 0.64 – 0.94, P = 0.016). Regardless of object-type, wolves were more persistent than dogs (GAMLSS: t = 0.99, P = 0.006) in their manipulation of the objects (i.e. the interaction between species and object was not significant, GAMLSS: t = -1.34, P = 0.19) (Figure 4, panel A). Object type did not affect persistence in dogs (GAMLSS: t = 1.44, P = 0.16) or wolves (GAMLSS: t = -0.85, P = 0.41) (Figure 4, panel B).

Figure 4: Differences in persistence between dogs and wolves



*Panel A shows the time (in seconds) dogs and wolves spent manipulating both apparatuses combined. Panel B shows the time (in seconds) dogs and wolves spent manipulating each object separately. Circles indicate outliers, ** indicates a P value under 0.01 at α = 0.05.*

4.3 Relationship between correlates of problem-solving

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In dogs, contact latency affected persistence differently depending on object-type (GAMLSS: t = 2.20, P = 0.04). Dogs that were slower to contact the ball (GAMLSS: t = -2.34, P = 0.03) were also less persistent when interacting with it. However, contact latency did not affect dogs' persistence with the pipe (GAMLSS: t = -1.67, P = 0.13). In wolves, regardless of object-type (no object-type by persistence interaction: GAMLSS: t = -0.61, P = 0.55) animals that were slower to contact the object were also less persistent (GAMLSS: t = -3.94, P < 0.001) (Supplementary Figure 5).

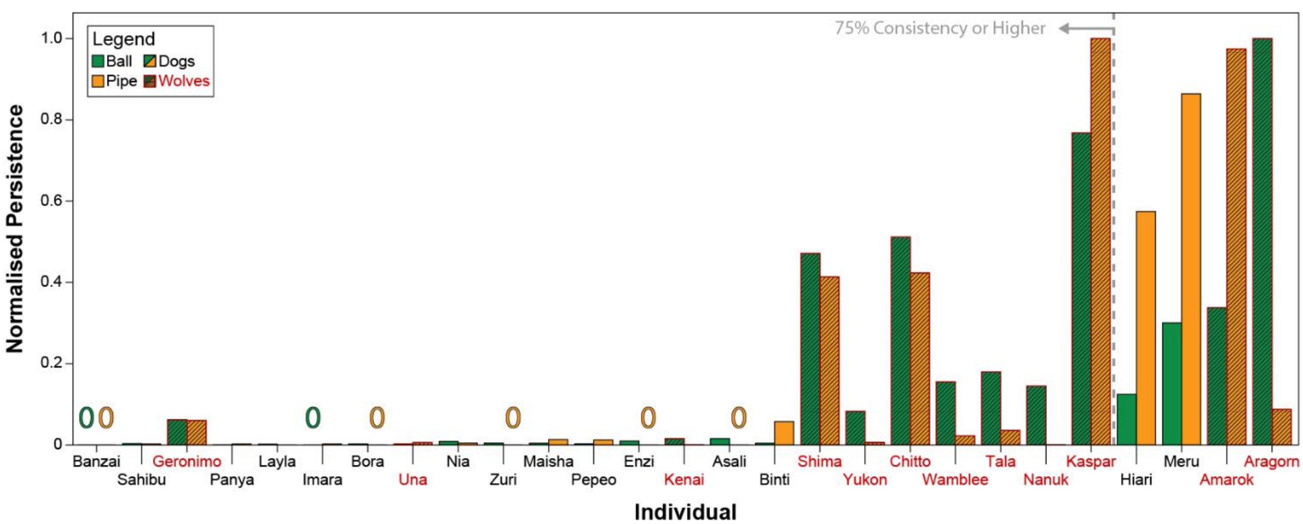
The effect of the interaction between object type and approach posture on contact latency was not significant (GAMLSS; Dogs: t =-0.97, P = 0.34, Wolves: t = -1.17, P = 0.55). There was no effect of approach posture on contact latencies in either wolves or dogs (GAMLSS; Dogs: t = 0.59, P = 0.56, Wolves: t = -1.10, P = 0.29).

In dogs, the interaction between persistence and object type had a significant effect on behavioural variety (GAMLSS: t = -2.57, P = 0.02). Persistence significantly affected behavioural variety with the ball (GAMLSS: t = 20.92, P < 0.001), but this effect was only marginally significant with the pipe (GAMLSS: t = 2.16, P = 0.05). In wolves, persistence significantly affected behavioural variety (GAMLSS: t = 5.91, P < 0.001) regardless of object-type (GAMLSS: t = 1.90, P = 0.074) (Supplementary Figure 15).

4.4 Individual consistency

Both subjects' persistence (Spearman's ρ = 0.71, P < 0.001) and contact latency (Spearman's ρ = 0.64, P < 0.001) across tasks were significantly correlated. Figure 5 shows individuals' scaled persistence in both tasks. Overall, dogs were significantly more consistent both, in their persistence (GAMLSS: t = -5.79, P < 0.001) as well as in their contact latency (GAMLSS: t = -5.5, P < 0.001) than wolves.

Figure 5: Every individual's persistence in both tasks, re-scaled from 0 to 1 for comparability



Green bars indicate persistence with the ball, orange bars indicate persistence with the pipe. Zeros indicate that the individual did not manipulate the object at all. Individuals with red names and hashed bars are

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wolves, individuals with black names and non-hashed bars are dogs. Individuals are arranged from left to right in descending order of consistency in persistence across tasks.

For descriptive statistics of both groups' performance in each task and for complete model information, see the supplementary material.

5 Discussion

We tested similarly raised dogs and wolves with two unsolvable tasks in the absence of humans on two separate occasions with three aims: First, to test hypotheses about why dogs and wolves differ in their persistence in an independent problem-solving task; second, to evaluate relationships between correlates of problem-solving success in our subjects and third, to assess our subjects' consistency in task performance.

We used two approaches when analysing our data: a bottom-up descriptive approach which allowed us to categorize animals based on their behaviours, and a direct comparison between wolves and dogs on measures of persistence. With both objects, dogs were always a part of low persistence and low behavioural variety clusters. Wolves were mainly part of the high persistence and behavioural variety cluster with the ball but were part of the low persistence and behavioural variety clusters with the pipe. This discrepancy may be due to wolves' ability to generalise (Hiestand, 2011). They may have learned that trying to solve a task presented in that specific setting was futile and did not persist as long with the pipe which was presented as the second task. Alternatively, it is possible that a neophobic response may have affected wolves' persistence and behavioural variety negatively (Sol et al., 2011; Thornton & Samson, 2012; Griffin & Guez, 2014) with the pipe. However, this is unlikely as we found no evidence for contact latency to be an indicator of neophobia based on approach postures. This lack of neophobic response may either be due to the objects themselves not being "intimidating" enough, or due to our subjects' experience with several novel objects over their lives. It is possible that like Moretti et al. (2015), contact latency was a measure of interest in novel objects rather than neophobia. While counterbalancing the order in which the two objects were presented would have allowed better control over this aspect, we had to ensure that all subjects interacted with the ball first to keep this study comparable to a parallel one being run on free-ranging dogs (where testing an individual repeatedly with a gap of two or more weeks was impossible). Crucially, however, the difference in wolves' persistence between the ball and pipe was not statistically significant when each correlate was analysed individually.

When directly comparing wolves' and dogs' persistence in the two tasks, our results confirm numerous other studies (Hiestand, 2011; Frank, 2011; Udell, 2015; Marshall-Pescini et al., 2017c,a,b; Rao et al., 2017) that have found wolves to be more persistent than dogs in object manipulation. We found these differences to hold even in the absence of humans during testing, and importantly, with dogs and wolves that have the same level of experience with both, humans and with interacting with different objects. Hence, it seems that these results can be explained neither by dogs' (but not wolves) having been inhibited from interacting with objects in their daily lives (e.g. pet dogs), nor by dogs preferring to use a social problem-solving strategy in the presence of a human (i.e. by asking for

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help instead of solving the problem alone). We suggest that the data are in line with the hypothesis that differences in dogs' and wolves' problem-solving performance is due to adaptations to their respective feeding ecologies. Dogs have been proposed to be selected against directly manipulating their environment and potentially for lower persistence (Hiestand, 2011) with humans being intermediaries between dogs and their environment (Frank & Frank, 1985). Wolves, however, require high levels of persistence to survive in the wild (David Mech, 1966; Mech & Korb, 1978; Mech, Smith & MacNulty, 2015). Further, wolves are more sensitive to their environment (Hiestand, 2011); while they are more neophobic, they are also more explorative than dogs (Moretti et al., 2015; Marshall-Pescini et al., 2017c). Considering animals in the current study had the same experience of human provisioning and interaction during object manipulation, we suggest that differences in persistence are more likely due to dogs' and wolves' adaptations to their respective ecological niche. The current results cannot reveal the extent to which dogs' persistence is affected by their generalist-foraging style and by the active role being played by humans in their feeding ecology (such as humans providing dogs with food (Sen Majumder et al., 2016) or actively inhibiting them from interacting with objects, which may be the case with pet dogs). Comparing dog populations with varying levels of experience with humans (such as pet dogs and free-ranging dogs) may help better understand whether dogs' reduced persistence could be a result of humans inhibiting their interactiveness with objects.

In line with previous studies (Morand-Ferron et al., 2011; Benson-Amram & Holekamp, 2012; Huebner & Fichtel, 2015; Borrego & Gaines, 2016), we found behavioural variety to be positively linked to persistence in both tasks, in both dogs and wolves. Behavioural variety and flexibility is important during foraging. Being able to employ and switch between different strategies both when hunting and when scavenging may increase success rates regardless of foraging style. While we found a positive trend in dogs with both objects, the difference in the strength of the effect between the two objects may have been due to several dogs not manipulating the pipe at all. We found persistence and contact latency to be negatively correlated. Our results are in line with predictions based on the concept of behavioural types (Sih & Del Giudice, 2012). Individuals that were faster to contact the apparatus, presumably were more interested and proactive in their approach and were persistent. The absence of this effect with the pipe in dogs may be since almost half our dogs did not manipulate the pipe at all.

Finally, we found that our subjects were consistent in their persistence and contact latency between the two tasks. Persistence is an important aspect of animal personality (Gosling, 1998; Svartberg, 2002; Range, Leitner & Virányi, 2012; Sih & Del Giudice, 2012; Massen et al., 2013). We found dogs to be more consistent in their persistence (or lack thereof) and their contact latency than wolves. A likely explanation for this could be that selection against persistence (Hiestand, 2011) and direct manipulation of the environment (Moretti et al., 2015; Brubaker et al., 2017) may have resulted in a more consistent reactive-type personality. Wolves, having faced no such selection, may be more variable in their behaviour. Alternatively, wolves' ability to better generalise and understand that the task is unsolvable may have influenced the consistency in their performance. To disentangle these possibilities, it would be necessary to test subjects in tasks that are similar in concept but in different

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test settings. Further, utilising multiple tests would provide a better insight into inter-task performance consistency.

Our study was the first to test differences in persistence between similarly raised and experienced dogs and wolves in an unsolvable task in the absence of humans. Past studies have used tasks that have initially been solvable and later become unsolvable. It is possible that persistence may differ between these two designs. The "unsolvable task" paradigm has been widely used with dogs and wolves (Miklósi et al., 2003; Gácsi et al., 2005; Passalacqua et al., 2011; Smith & Litchfield, 2013; Marshall-Pescini et al., 2013; D'Aniello et al., 2015; Udell, 2015; Rao et al., 2017). It involves repeatedly allowing a subject to find a solution to a simple foraging task, and then modifying the task to make it unsolvable. Data about persistence are usually collected in the unsolvable trial. This approach has certain drawbacks when studying the correlates of problem-solving success. First, it reinforces certain manipulative behaviours, potentially reducing the behavioural variety that the subject would show in the unsolvable trial. Second, reinforcing task-engagement with solvable trials may potentially increase persistence in the unsolvable trial. A task that is unsolvable from the start may provide a more reliable measure of persistence. Third, as human presence affects dogs' and wolves' behaviour differently during the test, testing subjects in the presence of a human may make directly comparing wolves' and dogs' persistence difficult.

While several studies have investigated problem-solving behaviour in dogs and wolves, few have analysed consistency in problem-solving success in dogs (Svartberg & Forkman, 2002; Svartberg, 2005), and none have done so in wolves. By testing dogs and wolves in independent problem-solving tasks with and without the presence of a human, using tasks that offer either controlled or random reinforcement and by using a battery of various physical problem-solving tasks, future studies could improve our understanding of how the domestication process has affected the problem-solving behaviour in the two canids, and the role personality traits play in their problem-solving behaviour. Our study provides an interesting starting point in this direction.

6 Conclusions

We compared equally raised and kept pack-living wolves and dogs in independent problem-solving task using an unsolvable task in the absence of humans. Wolves were more likely than dogs to engage in the presented tasks and were more persistent at attempting to extract food from the objects. Further, persistence and behavioural variety were positively correlated, and subjects were consistent in their persistence and approach latency across tasks, dogs more so than wolves. Results from this study support the ecology-based hypothesis, suggesting that fundamental differences in dogs' and wolves' correlates of problem solving success that have evolved due to differences in their feeding ecologies and are responsible for differences in their problem-solving performance.

Comparing dog populations that have different experiences with humans (e.g. pets and free-ranging dogs) and testing subjects in identical tasks both, with and without humans present in the test setting may help further disentangle the human-reliance and ecology-based hypotheses. Using a battery of

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conceptually similar tests across varying test settings may provide better insight into the role of behavioural types or personality in problem-solving success.

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