Master Thesis

OBSERVATIONAL SPATIAL MEMORY
IN THE WOLF (*Canis lupus*)

Submitted by:

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Date: 12.03.2015

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Acknowledgements

ABSTRACT

Observational Spatial Memory (OSM) is the ability to remember the location of food caches by observing other individuals during the caching process. Many corvid species have shown to possess very good OSM and use it to find and pilfer caches of others. When surplus food is available, canids, such as the wolf, also cache for delayed consumption and have been observed to raid caches of conspecifics. To explore whether wolves have a similar well-developed OSM as corvids, we tested them in an experimental setting. Subjects (n=9) could recover 4, 6 or 8 food caches respectively that were hidden by a human experimenter. The results show that wolves were significantly more successful in finding caches and needed shorter time if they had observed the caching process in comparison to a control situation where they did not observe this process, indicating OSM abilities. However, wolves also found all available caches in 45% of control trials, suggesting that they might rely to a large extent on their sense of smell in addition to OSM to relocate caches. In comparison to most corvid species, their OSM abilities seem to be limited as they had problems recovering all caches and the length of their search route did not differ significantly between test and control trials. All results combined, this study concludes only basic OSM skills in wolves.

ZUSAMMENFASSUNG

Observational Spatial Memory (OSM) ist die Fähigkeit, sich genaue Positionen von Futterverstecken zu merken, indem man andere beim Anlegen dieser Verstecke beobachtet. Viele Corviden haben ein sehr gut ausgeprägtes OSM und nutzen es, um die Verstecke anderer Tiere zu finden und auszurauben. Wenn ein Übermaß an Nahrung vorhanden ist, legen auch Wölfe Futterverstecke für den späteren Gebrauch an und rauben die Verstecke anderer aus. Um herauszufinden, ob sie daher auch ein gut entwickeltes OSM haben, wurden Wölfe in einem experimentellen Versuchsaufbau getestet. Die Versuchstiere in dieser Studie (n=9) mussten 4, 6 oder 8 Futterverstecke finden, die von einem Menschen angelegt wurden. Bei Testversuchen konnten die Wölfe den Versteckvorgang beobachten, bei Kontrollversuchen nicht. Die Ergebnisse der Studie zeigen, daß Wölfe bei Testversuchen signifikant höhere Sucherfolge hatten und weniger Zeit zum Auffinden der Verstecke benötigten, als bei Kontrollversuchen, was auf OSM schließen lässt. Allerdings fanden die Wölfe auch bei Kontrollversuchen in 45% der Versuche alle vorhandenen Verstecke, was darauf hinweist, dass Wölfe neben OSM mehrheitlich ihren Geruchssinn einsetzen, um Futterverstecke anderer aufzuspüren. Im Vergleich zu den meisten Corviden scheinen sie beschränkte OSM-Fähigkeiten aufzuweisen, da sie nicht immer alle Verstecke fanden und die zurückgelegte Wegstrecke in Test- und Kontrollversuchen keinen statistisch signifikanten Unterschied aufwies. Zusammengefasst zeigt diese Studie grundlegende OSM-Fähigkeiten beim Wolf auf.

INTRODUCTION

Many animal species cache excess food to store it safely for later consumption (Phillips et al. 1990). Clark's nutcracker (*Nucifraga columbiana*), a corvid, stores between 35.000 and 98.000 seeds per year (Hutchins and Lanner 1982, Vander Wall and Balda 1977) and relies heavily on them during winter and breeding season (Vander Wall 1982, Olsen et al. 1995). White-Breasted Nuthatches, *Sitta carolinensis*, cache seeds and insects intensively to recover them after hours or days (Waite 1988). A lot of rodents show caching behaviour too, such as Grey squirrels (*Sciurus carolinensis*), which cache up to 3000 nuts per season (Smulders et al. 2010). Among the canid family coyotes (*Canis latrans*) (Fentress and Godbois 2001), red foxes *(Vulpes vulpes)*, (Fisher 1951, MacDonald 1976), arctic foxes (*Alopex lagopus)* (Careau et al. 2007), African wild dogs (*Lycaon pictus*) (Malcolm 1980) and wolves, (*Canis lupus*) (Harrington 1981, Mech and Adams 1999, Murie 1944, Mech et al. 1998) are known to make food caches.

To retrieve their caches, storers can theoretically rely on various mechanisms: (1) dig and probe at random, which is rather ineffective or (2) they could use cues like soil-disturbances or a distinct smell that emanates from the food (Vander Wall, 1982). (3) Alternatively animals might have a preference for certain caching sites and search at these caching sites randomly. This strategy would increase the probabilities that a cache is recovered as it narrows down the number of possible cache locations. Corvid species, for example, like to store their food next to landmarks but the recovery rates of food caching corvids (50 – 99%) are too high to make this strategy likely (de Kort et al. 2009). (4) The most effective strategy is to remember exactly where the cache is located using visual cues. This strategy requires a good spatial memory, which seems to be the case for most food-caching animals (reviewed in Shettleworth 2010, Clayton and Dickinson 1998, Vander Wall 1990).
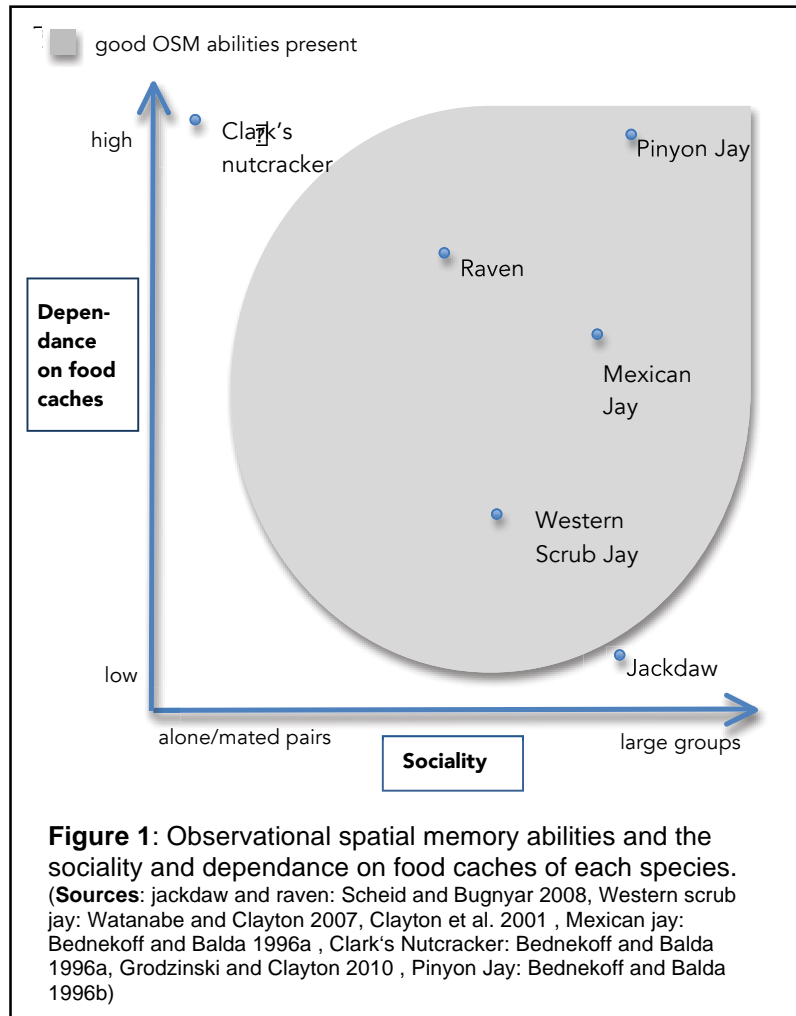
Spatial memory for cache recovery is especially important for species with no or little sense of smell, such as jays and nutcrackers (Vander Wall and Jenkins 2003). But olfactory cues, emanating from the food caches, can potentially be very important in regard to cache retrieval in mammals. Under wet conditions Yellow pine chipmunks (*Neotamias amoneus)* and deer mice (*Peromycus*) use olfaction to find hidden seeds, whereas spatial memory is very important for the retrieval of caches under dry conditions, when seeds do not emit strong odours (Vander Wall 2000).

Apart of having to find their own caches to retrieve the food, food storers often also bare the risk of caches being stolen by other animals. Like storers, cache pilferers use different methods to recover the caches made by others: (1) They can raid caches right after the caching individual created the cache – this is however mainly limited to dominant individuals (Waite 1992, Bednekoff and Balda 1996b). (2) They can use visual cues, such as soil

disturbances (Krebs 1977) or olfactory cues (Vander Wall 1998) emanating from the food. (3) Some animal species can remember the exact location of caches made by others by observing the caching event. This ability is called observational spatial memory (OSM) and gives the pilferer the opportunity to approach the cache location after the caching animal has left, enabling also subordinate group members to pilfer caches at a relatively low risk.

OSM abilities have been found in many corvid species. They are, however, not evenly well developed among the different corvid species (e.g.: Scheid and Bugnyar 2008, Olsen et al. 1995, Bednekoff and Balda 1996a, deKort et al. 2006). Knowledge about ultimate questions, such as evolution and survival value can help to predict ontogenetic or mechanistic abilities, such as Observational Spatial Memory abilities (Smulders et al. 2010). For example, the social structure the birds live in and the reliance on food caches seem to have an influence on OSM abilities (Grodzinski and Clayton 2010). According to recent research in corvids, animals

Figure 1: Observational spatial memory abilities and the sociality and dependance on food caches of each species. (**Sources**: jackdaw and raven: Scheid and Bugnyar 2008, Western scrub jay: Watanabe and Clayton 2007, Clayton et al. 2001 , Mexican jay: Bednekoff and Balda 1996a , Clark's Nutcracker: Bednekoff and Balda 1996a, Grodzinski and Clayton 2010 , Pinyon Jay: Bednekoff and Balda 1996b)

that have good OSM are at least moderate cachers and are a social living species (figure 1). Put differently, a good indicator for OSM might therefore be how often individuals have the opportunity to observe caching behaviour of others in ontogeny and phylogeny (Grodzinski and Clayton 2010), which requires group living and caching behaviour to some extend. For example, in a comparison of ravens (*Corvus corax*) and jackdaws (*Corvus monedula*) birds had to remember 2, 4 or 6 food caches out of 10 possible locations (Scheid and Bugnyar 2008). Ravens live in a socially dynamic environment and compete heavily for food caches whereas the closely related jackdaw is a highly social species that does only cache very rarely. Ravens performed more accurately than expected by chance in cache retrieval of 2, 4 and 6 caches whereas jackdaws did not.

In mammals, another important predictor of OSM abilities is the sense of smell (Smulders et al. 2010). Rodents are very successful inter- and intraspecific pilferers (Van der Wall 2003) and as mentioned above, they are known to use their sense of smell as well as their spatial memory abilities for the relocation of caches depending on environmental conditions (Vander Wall 1998, 2000). In a direct comparison of the inter- and intraspecific pilfering success between rodents and corvids, Yellow pine chipmunks were much better pilferers than Steller's jay (*Caynocitta stelleri*) because they also use olfaction to relocate caches (Thayer and Vander Wall 2005).

In comparison to corvids, nearly all food-caching rodents do not live in groups after reproduction, which makes food-caching a solitary task. Maybe this is the reason why, to our knowledge, there have been no scientific tests for OSM in rodents so far. Applying the assumptions mentioned for OSM in corvids, OSM might be expected to not having developed that strongly in food-caching rodents because they do rarely have the chance to observe caching individuals during ontogeny and can also rely on their excellent sense of smell for cache retrieval under certain environmental conditions.

Canids also have a great sense of smell (Sillero-Zubiri 2013) and at least the wolf relies strongly on it to gain information about food (Harrington and Asa 2003) but at the same time, several canid species live in social groups and seem to rely on caching at least to a certain degree: Wolves, for example, live in packs usually consisting of a mated pair and its offspring (Mech and Boitani, 2003). Pack sizes vary greatly between 3 and over 20 members, depending on prey size, prey densities and habitat (Mech and Boitani, 2003). Wolves hunt large prey, which often cannot be consumed at once. Since they live in a stochastic environment, they kill when they encounter prey, which can result in a surplus of food (e.g. Kreeger et al. 1997). Accordingly, wolves in the wild and in captivity have been repeatedly observed to make several food caches with a total weight of up to 90kg (Mech and Adams 1999). Mech (1999) observed caching behaviour of one individual after the killing of a muskox. The wolf made 2 caches, which contained regurgitated food and probably made more caches afterwards. Later that same wolf was observed burying walnut-sized pieces of meat and a leg of the muskox. Murie (1944) observed wolves caching a sheep horn, the head of a ram, sheep meat and a whole caribou calf. Phillips (et al. 1990) observed captive timber wolves from 1983 to 1986 and videotaped 126 caching events in that time. Pups in the wild have also been observed making food caches around the den when there was a surplus of food (Packard 2003). Mech observed a wolf eating a hare that had been cached for at least a year (Peterson and Ciucci 2003) on Ellesmere Island, where the ground is frozen for 9 to 10 months a year. Thus, although most food-caching records are anecdotal in nature, food caching seems to occur regularly (see for example Mech 1999) and to be more

important in summer than winter, when wolves forage alone or in small groups (Murie 1944, Cowan 1947).

Still, due to the limited information, it is currently unclear how high the survival value of food caches is for the wolf.

Moreover, it is not known how often pack-mates pilfer caches from each other although this behaviour has been observed in the wild (Mech D., personal communication in Range and Virányi, 2013). From an experimental study we know that wolves do pay attention if conspecifics hide a food reward and can retrieve the reward based on the social information provided (Range and Virányi, 2013). However, it is unknown, how many caches they could potentially remember if they observe that more than one is hidden as has been shown for other species that regularly pilfer caches. For example, Pinyon Jays were able to remember, out of 17 possibilities, the general areas in which their partners had cached a week before in an experimental set-up (Bednekoff and Balda 1996b). As explained above, ravens remember 6 caches out of 10 possible cache locations. Mexican Jays can recover 1 cache out of 6 possible locations more accurately than expected by chance after a 1-day retention interval (chance level of errors: 2.5, mean error rate: 1.4, Bednekoff and Balda 1996a). Eurasian Jays had greater search success and greater search efficiency than expected by chance when pilfering 2 - 3 available caches out of 16 possible locations after they had the chance to observe a caching conspecific (Shaw and Clayton 2014).

Another interesting question when confronting animals with the opportunity to retrieve caches that a partner stored before is whether they use the optimal route to do so. Optimal Foraging Theory (OFT) predicts that through natural selection foragers should care for the highest net-intake of energy (Krebs 1977) to achieve maximum fitness (Pyke et al. 1977). Usually it is assumed that a predator has to move between different habitat patches with differing prey densities (Bartumeus and Catalan 2009). While a predator forages within one patch, prey density within this patch diminishes through the foraging activity, decreasing the benefit of staying in this patch over time (Krebs et al. 1981). According to the optimality approach, animals should make optimal decisions in order to maximize their foraging efficiency (Bartumeus and Catalan 2009). Predators should therefore optimize the following variables: (1) diet choice, (2) patch choice, (3) departure time from patches and (4) movements between patches (Pyke et al. 1977).

The patch model assumes that the forager has all the information required for a rational decision: the quality and location of each patch and traveling time between patches (Green 1987). This is often not the case in reality, but can be achieved in an experimental environment. The test for OSM provides a very simplistic model to test one component of OFT – the movement between patches. If animals have good OSM abilities, they have

perfect information about all the cache locations (= foraging patches). According to OFT, foragers should try to minimise the travel distance between patches in this set-up (Anderson 1983). This problem can be compared with the travelling salesman problem: A salesman needs to visit a previously defined number of cities, starting from one city and returning there at the end. The optimization task it to minimize the travel time (Lin 1965). In an experimental set-up for testing OSM abilities, animals do not have to return to the starting point, but in this simplified model the optimization problem would be as follows: Moving from the starting position to all cache locations in the shortest possible way.

The aim of this study is to find out if wolves have Observational Spatial Memory and if so, how well their abilities are developed. Therefore captive timber wolves were required to find hidden food items either, in the test condition, after watching a human experimenter caching food or in the control condition, where they did not see where the caches were made. If wolves possess good OSM abilities, they should perform better in the test condition than in the control condition. In order to test the limits of short-term OSM, the amount of caches hidden was alternated between 4, 6 and 8.

We expected (1) the success of finding the caches to be higher (2) the latency to find caches to be lower and (3) the distance walked between the caches to be lower in the test than control condition. If wolves have good OSM abilities, we expect them to (4) follow the optimal foraging path according to Optimal Foraging Theory.

METHODS

No special permission is required in Austria for using animals in such cognitive studies. The applicatory committee for research without special permission regarding animals is the 'Tierversuchskommission am Bundesministerium für Wissenschaft und Forschung (Austria)'.

Subjects

The study was conducted with 9 hand-raised timber wolves (*Canis lupus*) living at the Wolf Science Center in Ernsbrunn, Lower Austria, Austria. At the time of this study the wolves lived in 4 packs in separate enclosures (2x 8000 m^2, 1 x 4000 m^2 and 1 x 3000m^2) and were daily trained using positive reinforcement. They were used to participating in cognitive tests and to being separated from their pack regularly for tests, training and leash walks. They were fed two to three times a week with rabbits, chunks of meat, dry food, sausage or bones. Water was provided ad libitum.

Figure 2: Legs of a roe deer cached by a captive wolf in Ernstbrunn, Austria 2013 Foto: Martina Lazzaroni

Experiments for this study were conducted within two periods. Three wolves, aged 17 to 20 months at the time of the study, were tested between October and December 2009 and six wolves, aged 12 to 47 months, were tested between April and August 2013. A detailed summary of age, gender and genetic relationship of the test animals can be seen in table 1.

The wolves have been repeatedly observed making food caches after feeding events. Cached items consisted of parts of rabbit or chicken (oral communication, Rita Takács, February 2013), whole chicks (Lena Schaidl, August 2013) or parts of a deer (see figure 2).

Table 1: List of animals showing genetic relationship, sex (f=female, m=male), age, origin, pack structure and year of experiment.

Individual	Sex	Born	Origin	Sibling of	Pack	Experi-ment
Tala	f	2012	Minnesota Wildlife Connection	Amarok	1	2013
Chitto	m	2012	Minnesota Wildlife Connection	Una	1	2013
Una	f	2012	Minnesota Wildlife Connection	Chitto	2	2013
Kenai	m	2010	Parc Safari, Kanada	-	3	2013
Geronimo	m	2009	Triple D Farm, Montana, USA	Yukon	3	2013
Yukon	f	2009	Triple D Farm, Montana, USA	Geronimo	2	2013
Shima	f	2008	Zoo Herberstein, Austria	Aragorn	4	2009
Aragorn	m	2008	Zoo Herberstein, Austria	Shima	4	2009
Kaspar	m	2008	Zoo Herberstein, Austria	-	4	2009

Experimental Site

Experiments were conducted in a testing enclosure containing 131 stones. Every stone represented a possible cache location. The testing enclosure of the year 2009 measured approximately 41 x 26 m and the test enclosure of 2013 measured 28 x 25 m. The stones were set up in a 2 x 2 m grid. In both test enclosures the grids used for the set-up of the stones measured about 670 m^2, so that the conditions are comparable between 2009 and 2013. In a shifting system that runs along the test enclosure, wolves could watch the caching process (see figure 3).
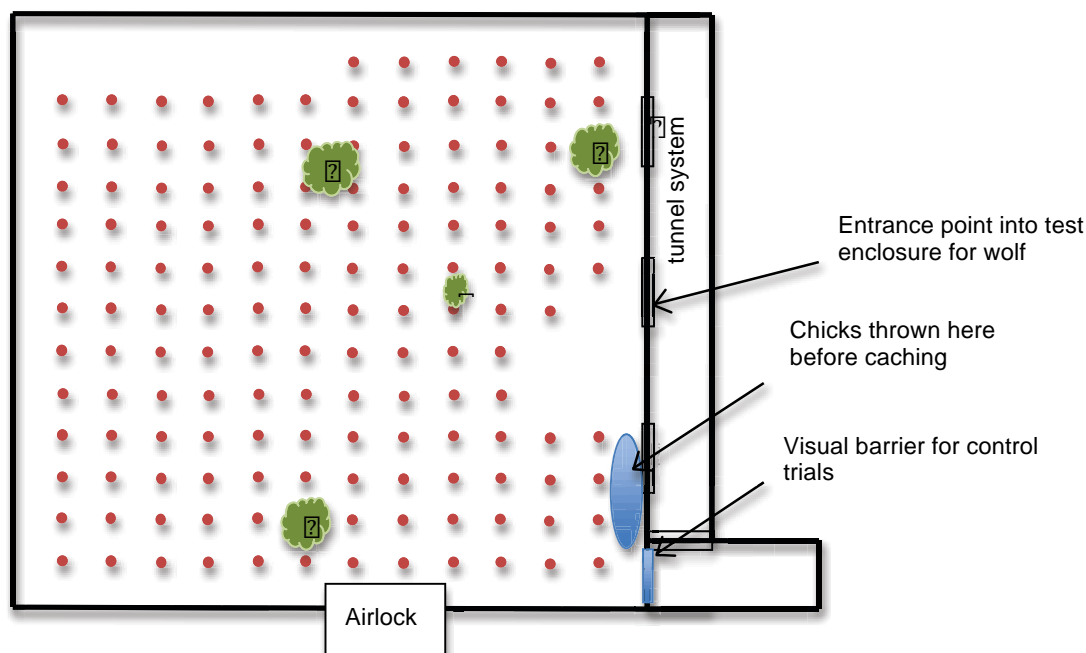
Figure 3: Outline of experimental site. Red dots represent possible cache locations.

Experimental Set Up

Plastic covers were fixed on the fences along the testing enclosure to ensure that the other wolves living around the test enclosure were not able to observe the caching process. This measure should prevent learning effects and distraction. Chicks were used as bait in this experiment, as wolves were highly motivated to find them and they were used to this food from other experiments.

Training Sessions

In 16 training sessions each wolf could learn that caches are always located next to a stone and they were trained to pay attention to the hiding process. In each session 2 chicks (dead, 1 day old) were hidden as bait. If a wolf did not find all caches during training trials, they were shown to the wolf after the trial.

Experimental Sessions

During test sessions the individuals had to retrieve caches either after they were able to observe the caching process (TEST) or after they were not able to observe the caching process (CONTROL). In order to investigate the limits of OSM in wolves, we provided differing amounts of caches: 4, 6 or 8. Each focal animal was tested 6 times in each of the 6 possible experimental situations (test or control trial with 4, 6 or 8 caches), resulting in a total of 36 tests per animal. All trials were randomised within and between individuals to control for learning effects.

A program written in R 3.0.1 calculated cache locations randomly. It allowed for setting the optimal retrieval distance as well as a minimal distance between caches. For cache locations in experimental tests the optimal retrieval distance was set to the number of caches times 10 (4 caches = 40 m, 6 caches = 60 m, 8 caches = 80 m). The average distance between the caches was therefore the same in all cache conditions. Minimal distance between two caches was set to 4 m, so that two caches were never located at two stones next to each other.

The hiding order of caches was fixed and makes it possible to see if the wolf follows the experimenter's tracks. Assuming that caches are numbered according to their optimal retrieval order from 1 to 8, caching order was: 3-1-4-2 for 4 caches, 4-1-5-2-6-3 for 6 caches and 5-1-6-2-7-3-8-4 for 8 caches. In training sessions, caches were made in the orders 1-2 or 2-1, alternating on a random basis.

Test Procedure

In all experiments the focal animal was called into the shifting system. In order to increase the animal's motivation to follow the hiding process, the experimenter (2009: Sebastian Vetter (SV), 2013: Lena Schaidl (LS)) threw the amount of chicks to be cached one by one in front of the animal on the other side of the fence (see figure 3). The experimenter then entered the test enclosure and picked up the chicks one by one, while the wolf was watching. In test sessions the experimenter then made the caches while the wolf could observe the caching process.

In control sessions the wolf was led into a part of the tunnel, where it could not watch the caching process due to a visual barrier. Because the wolf would still hear the experimenter walking around in the test enclosure while making caches, the caches were already made before the beginning of the test procedure. The experimenter sat still for 2 minutes and hid the chicks in a bag while the wolf was in the confined part of the tunnel system. The experimenter then exited the test enclosure while the wolf was released back into the part of the tunnel system without a visual barrier.

The similar procedure for test and control trials before the caching process starts (throwing chicks, picking them up one by one) should ensure that the wolf expects in both situations to find caches in the test enclosure. After the caching process was finished, the wolf could enter the test enclosure and search for the caches. The wolves had 3 minutes to find a cache. Every time a wolf found a cache, the timer was again set to 3 minutes. The experiments ended, if a wolf did not find another cache for 3 minutes or 3 minutes after the last cache was found. 3 minutes after the last found cache were added to the experiment to see if wolves change their behaviour when all the caches are found, which could indicate that they know how many caches were made and how many they have already retrieved. In experimental

sessions unrecovered caches were not shown to the wolf but removed after the experiment to prevent further learning effects. Cache retrieval was recorded with a Sony HD R-C320E.

Data analysis

From the videos, we extracted which cache locations were found in which order, the distance wolves walked to recover the caches and the latency to find each cache. Furthermore we coded if a wolf was searching or obviously not looking for caches (e.g. urinating, lying down,…) (see Appendix 1 for a detailed coding scheme). The start of the trial was defined as the moment, when the wolf entered the test enclosure. It was furthermore determined how often a wolf followed the optimal foraging path. For further investigation of short term memory (recency and primacy effects) it was also noted how often the first cache recovered by the wolves was the last or the first cache that was hidden.

The videos of the year 2009 were coded by SV and the videos of 2013 were coded by LS. In order to ensure consistent analysis 20% of all videos were coded by both analysers. Spearmann's rank correlation (rho) was high in general: search duration: 0.91; handle duration: 0.94; duration nic: 0.89, duration eat: 0.84.

When comparing the test condition with the control condition we used linear mixed-effect models with the individual and the experimenter included as random factor.

We analysed whether the success of finding caches (how often all caches were found and the number of unrecovered caches), the latency to find caches (latency to find all caches and latency to find each single cache) and the distance walked to find caches were influenced by the number of caches hidden, the condition, the time since the last feeding or the trial number (how often the wolf has already been tested in that specific test situation). In a pre-test the following independent variables were excluded from the final models, as they did not show any effect in any of the models: time of day, temperature that day, testing order, soil condition and weather condition. How often all caches were found was analysed with a generalized linear mixed effect model with a binomial distribution, whereas the number of caches not found was analysed with a generalized linear mixed effect model with a poisson distribution. A general linear mixed effect model with a log-transformation was used for the latency to find caches, the latency to find all caches as well as for the distance walked. We used Fisher's Exact Test regarding the order of cache retrieval to test for the optimal foraging path and memory effects. The analyses were performed using the program R 3.0.1.

RESULTS

Success of finding caches

In total, 321 experiments (test: 159, control 162) were conducted. When analysing the number of trials in which wolves found all caches, we found that the wolves recovered all caches hidden by the experimenter in 60% and 45% of test and control trials respectively. This difference was significant (glmm: $z = 2.809$, $p = 0.005$, Figure 4) suggesting that observation of the hiding process increased the wolves' ability to find all hidden caches. While the number of caches hidden did not significantly influence the wolve's ability to find all caches made (glmm: $z = -1.300$, $p = 0.19$), they were more successful at finding all caches over tested trials (glmm: $z = 2.162$, $p = 0.03$, Figure 5), suggesting a learning effect.

We also analysed all trials that were conducted, including trials in which the wolves did not find all available caches but only a subset. We found that the number of unrecovered caches was significantly lower in test conditions than in control conditions (glmm: $z = -2.856$, $p = 0.004$, Figure 6) with a mean of 0.60 (± 0.07, n= 139) in test and 0.82 (± 0.08, n= 119) in control. This further supports that observation improved the animals' ability to find caches. The days since the last feeding event did not influence the number of unrecovered caches significantly (glmm: $z = 0.016$, $p = 0.99$).
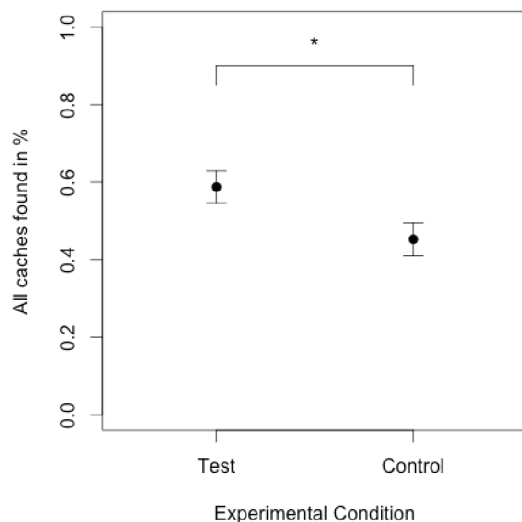

Figure 4: Percentage of how often all caches hidden were found in the test and in the control condition. Filled circles represent the mean and whiskers indicate the SEM.
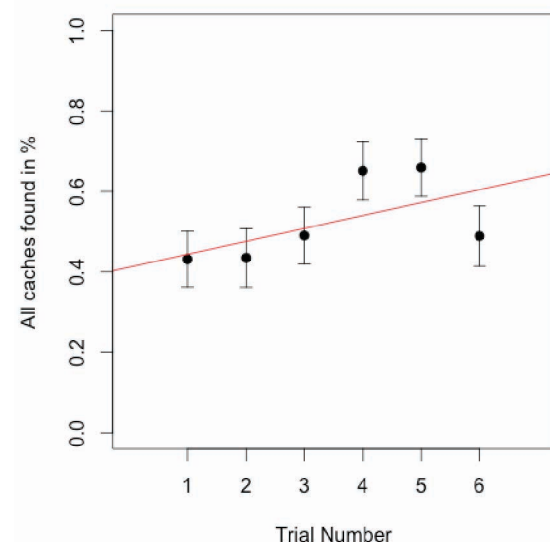
Figure 5: Percentage of how often all caches hidden were found for every trial number. Filled circles represent the mean and whiskers indicate the SEM. The red line is the regression line.
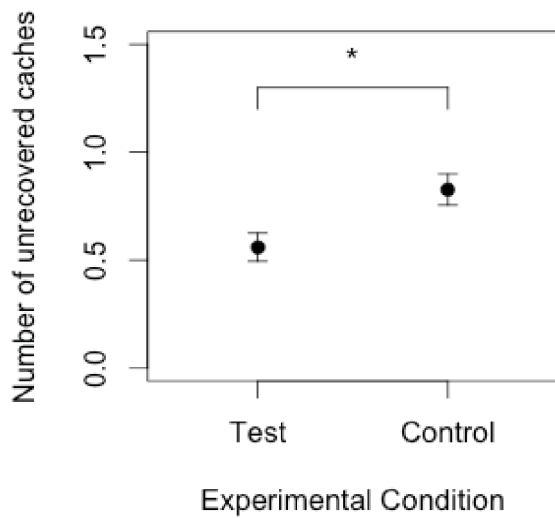
Figure 6: Number of unrecovered caches in test and control condition. Filled circles represent the mean and whiskers indicate the SEM.
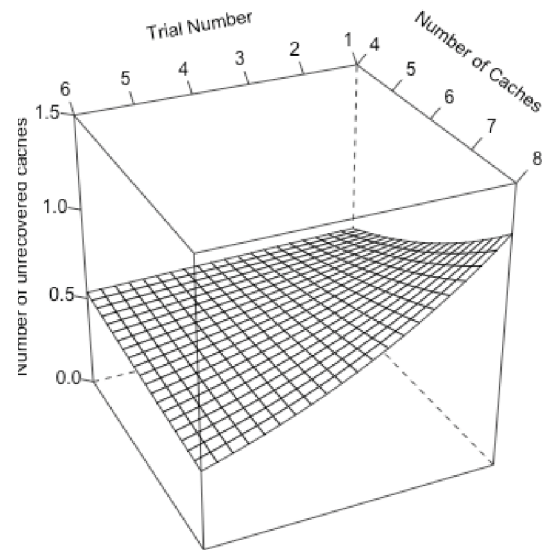
Figure 7: Number of unrecovered caches plotted against the number of caches made (4, 6 or 8) and the trial number ranging from 1 to 6.

Finally we found an interaction between the number of caches made and the trial number (glmm: z = -2.050, *p* = 0.040, Figure 7). Figure 7 illustrates that the number of unrecovered caches is significantly higher in the first trials in the 6 and 8 cache conditions (6 caches: glmm: z = -2.316, *p* = 0.021, 8 caches: glmm: z= -3, *p* = 0.003). With a rising number of trial repetitions this influence fades until the number of unrecovered caches is the same for 4, 6 and 8 caches in the 6th trial repetition. This interaction suggests that they learn over trials in the more difficult conditions. In the test trials, were only 4 caches were hidden, the number of unrecovered caches is not affected by the trial number (glmm: z = 0,16, *p* = 0.87).
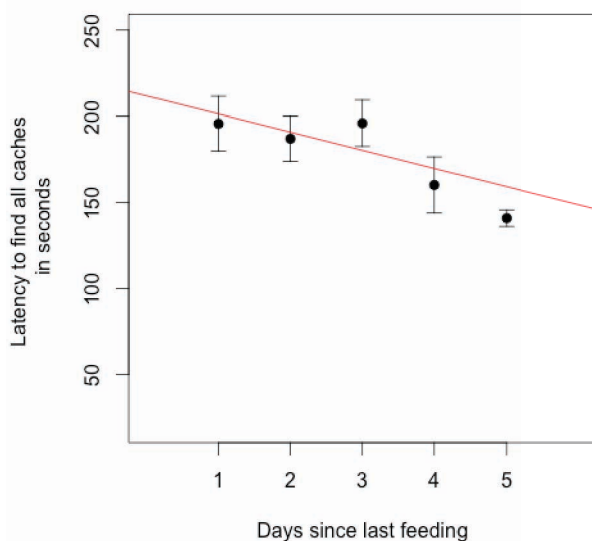
Latency to find caches

In an analysis of those trials, where wolves found all hidden caches, it took them significantly longer to do so in the control than in the test condition (lme: $F_{1,137} = 5.735$, $p = 0.018$, Figure 8) with a mean of 178 seconds in test (± 8.43, n = 84) and 200 seconds in control trials (± 12.46, n = 62). It also took them longer to find all caches, the more caches were hidden (lme: $F_{1,139} = 47.715$, $p < 0.001$, Figure 9). The more days had passed since the last feeding, the faster wolves recovered all hidden caches (lme: $F_{1,137}=5.334$, $p = 0.022$, Figure 10), suggesting more motivation when the wolves were hungry.
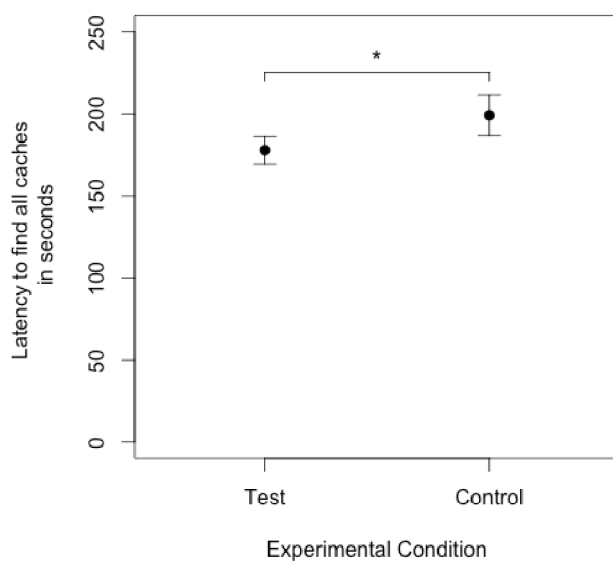
Figure 8: Latency to find all caches in seconds in test and in control condition. Filled circles represent the mean and whiskers indicate the SEM.
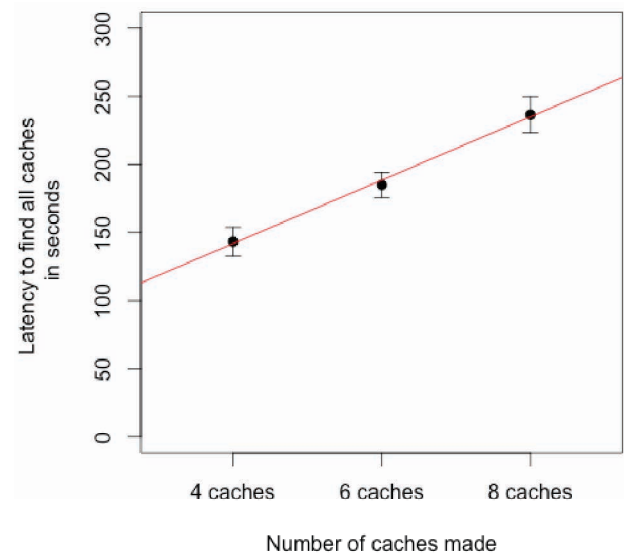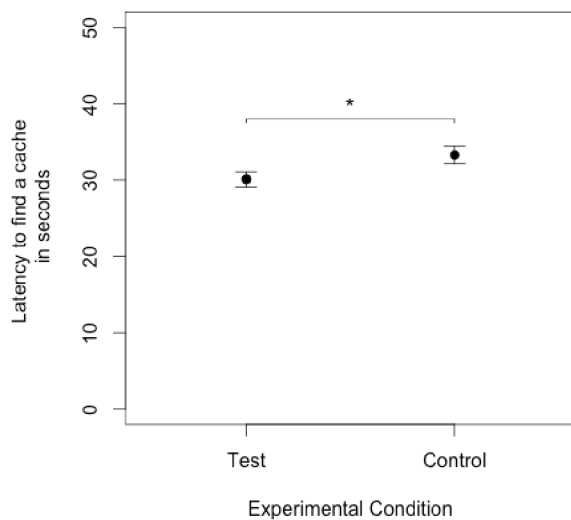

Figure 9: Latency to find all caches in seconds with 4, 6 or 8 caches made. Filled circles represent the mean, whiskers indicate the SEM and the red line is the regression line.
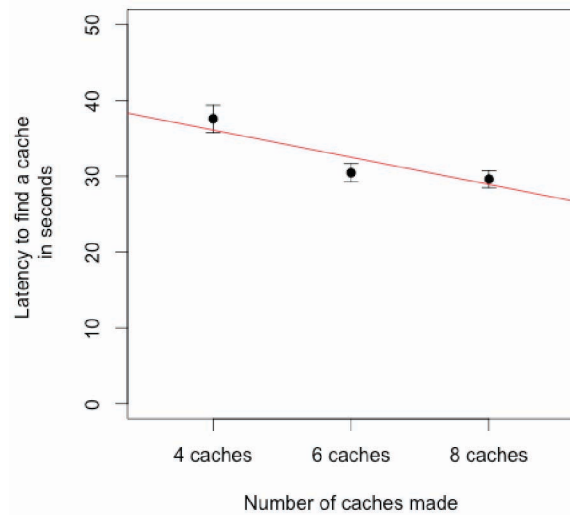

Figure 10: Latency to find all caches in seconds after 1 to 5 days since the last feeding. Filled circles represent the mean, whiskers indicate the SEM and the red line is the regression line.

When analysing all trials conducted, including those were wolves did not find all caches, the experimental condition also had a significant influence on the latency to find each single cache (lme: $F_{1,1610}$ = 5.765, p = 0.008, Figure 11) with wolves needing more time to find caches in the control condition (mean: 34 seconds ±1.14, n = 783) than in the test condition (mean: 30 seconds ±1.01, n = 838). The time wolves needed to find a cache was also significantly influenced by the number of caches made (lme: $F_{1,1608}$ = 18.844, p < 0.001, Figure 12). The more caches were hidden, the less time wolves needed to find a cache. The more days since the last feeding had passed, the faster wolves were at recovering caches (lme: $F_{1,1615}$ = 5.647, p = 0.018, Figure 13) and the latency to find caches decreased with rising trial numbers (lme: $F_{1,1610}$ = 9.563, p < 0.001, Figure 14), again suggesting a learning effect.

Figure 11: Latency to find a cache in test and control conditions. Filled circles represent the mean, whiskers indicate the SEM.

Figure 12: Latency to find a cache with 4, 6 and 8 caches hidden. Filled circles represent the mean, whiskers indicate the SEM and the red line is the regression line.
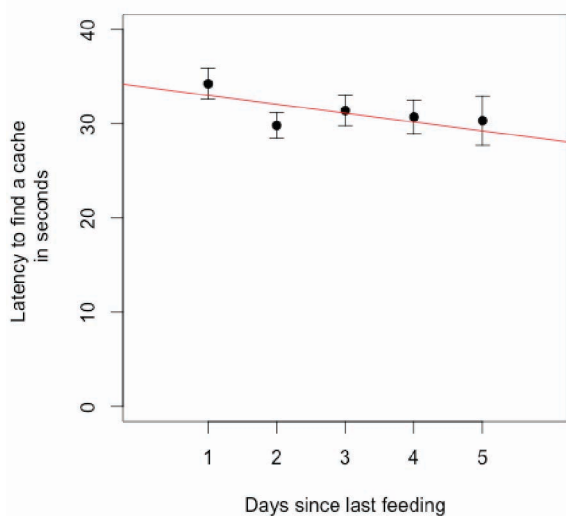
Figure 13: Latency to find a cache after 1 to 5 days since the last feeding. Filled circles represent the mean, whiskers indicate the SEM and the red line is the regression line.

Figure 14: Latency to find a cache plotted against the trial number.. Filled circles represent the mean, whiskers indicate the SEM and the red line is the regression line.

Distance walked

The distance walked to recover a cache was not influenced by the experimental condition (lme: $F_{1,1659}$=1.863, p = 0.17, Figure 15). However, the more caches had been recovered already in a trial, the longer was the distance walked to recover the next cache (lme: $F_{1,1664}$=114.948, p < 0.001, Figure 16). In other words, the distance walked to find a cache increased with the number of caches already found.

Furthermore, the distance walked decreased with rising trial numbers (lme: $F_{1,1660}$=8.832, p = 0.003, Figure 17) and it decreased, the more caches were hidden (lme: $F_{1,1661}$=135.638, p < 0.001, Figure 18).
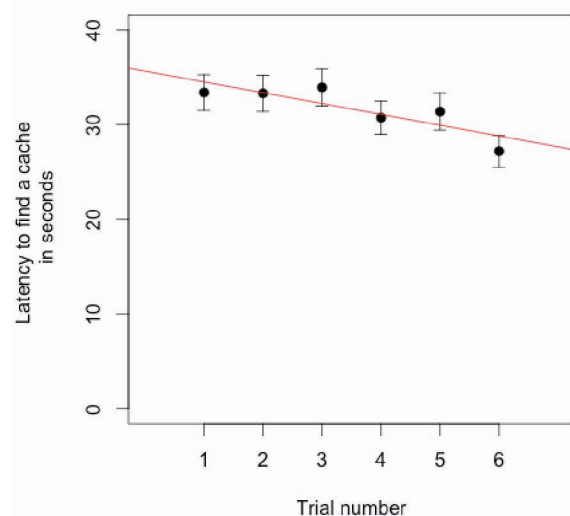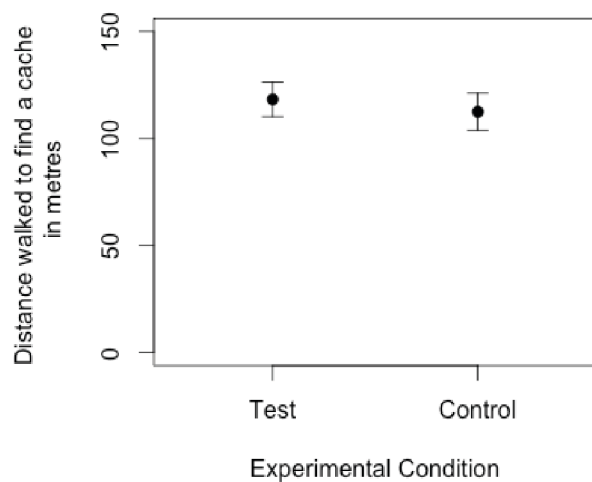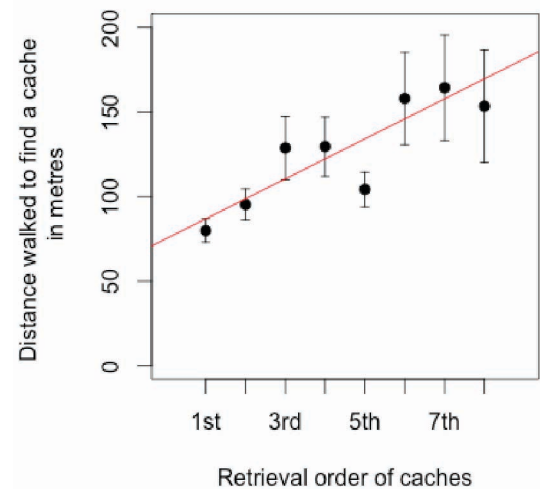

Figure 15: Distance walked to find a cache in test and control condition. Filled circles represent the mean and whiskers indicate the SEM.

Figure 16: Distance walked to find a cache plotted against the retrieval order of caches. Filled circles represent the mean, whiskers indicate the SEM and the red line is the regression line.
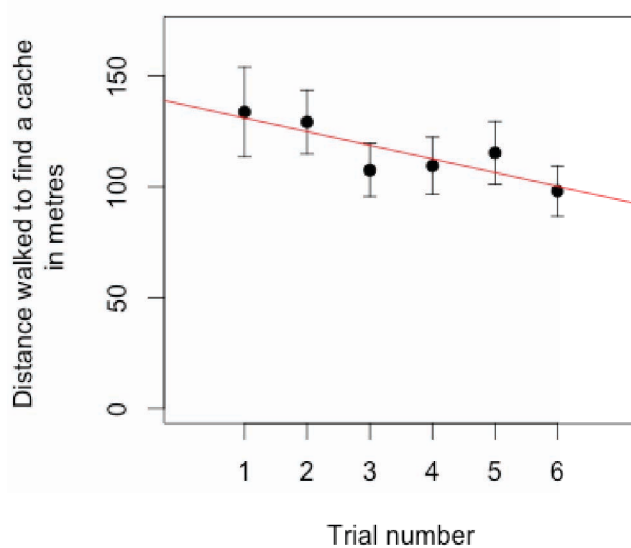
Figure 17: Distance walked to find a cache after 1 to 6 trial repetitions. Filled circles represent the mean, whiskers indicate the SEM and the red line is the regression line.
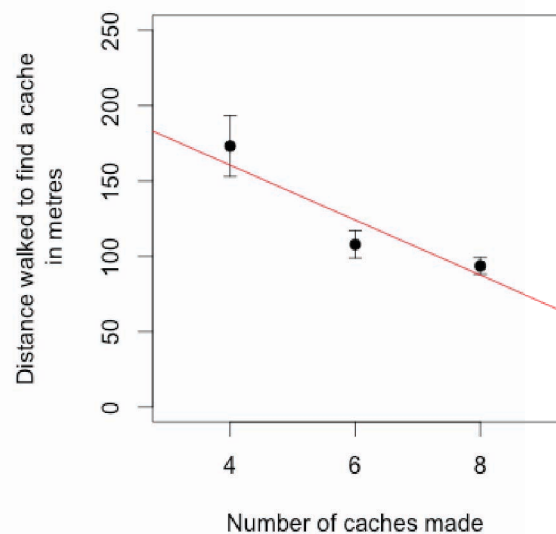
Figure 18: Distance walked to find a cache with 4, 6 and 8 caches hidden. Filled circles represent the mean, whiskers indicate the SEM and the red line is the regression line.

Optimal Foraging Path and Possible Effects on Memory

Wolves followed the optimal foraging path during cache retrieval rarely (10 times out of 159 test trials and 6 times out of 162 control trials, Table 2). Fisher's Exact Test revealed no significant difference between test and control trials ($p = 0.32$). In order to visualize the retrieval order of caches, figure 19 shows the actual retrieval order of caches plotted against the optimal retrieval order for each individual.

Table 2: Table showing how often wolves followed the Optimal Foraging Path in test and control condition in comparison to the total number of trials.

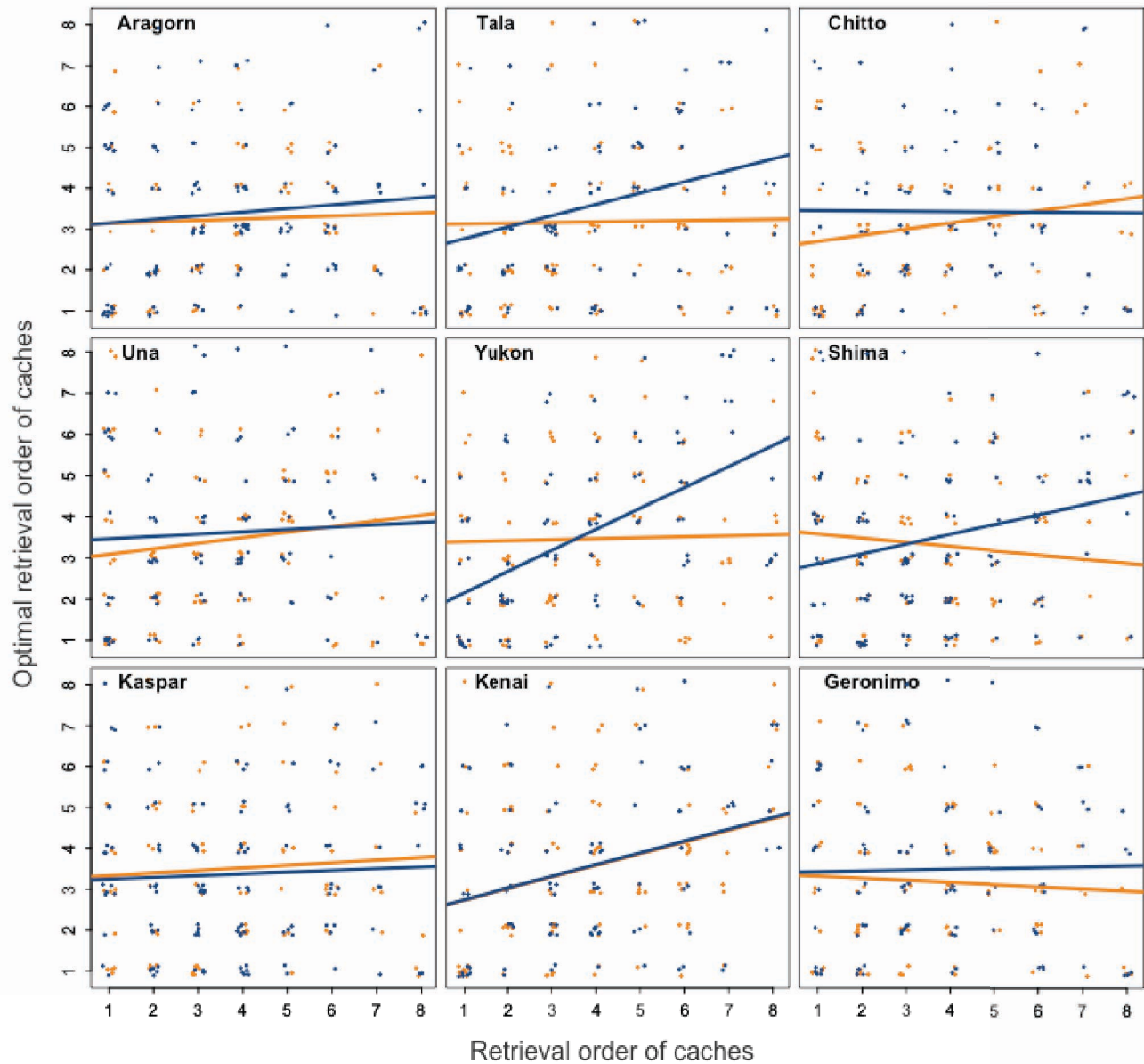|	Test		Control	
	OF (whole path)	Total Number of Trials	OF (whole path)	Total Number of Trials
4 caches	6	52	3	54
6 caches	2	53	3	54
8 caches	2	54	0	54
Total	**10**	**159**	**6**	**162**

As wolves followed the whole optimal foraging path very rarely, we wanted to see, whether the wolves followed only part of the optimal foraging path. Therefore we analysed how often the first cache retrieved by the wolves was the first on the optimal foraging path (OF). However, there was also no significant difference between test and control trials regarding this variable (Fisher's Exact Test, $p = 0.71$).

To further understand if the wolves followed certain rules to retrieve caches, we tested for primacy effects e.g. if wolves recovered first the cache that was hidden first and recency effects e.g. if wolves recovered first the cache that was hidden last. We found no indication for recency effects (Fisher's Exact Test, $p = 0.88$) and also no significant difference between test and control trials regarding primacy effects (Fisher's Exact Test, $p = 0.55$).

Table 3: Table showing how often wolves first recovered the last cache hidden (recency), the first cache hidden (primacy) or the cache that was the first on the optimal foraging route (Optimal Foraging) in comparison to the total number of trials.

	Recency		Primacy		Optimal Foraging (first cache)	
	Test	Control	Test	Control	Test	Control
4 caches	14 (52)	13 (54)	10 (52)	10 (54)	17 (52)	18 (54)
6 caches	5 (53)	8 (54)	5 (53)	2 (54)	19 (53)	17 (54)
8 caches	5 (54)	5 (54)	0 (54)	0 (54)	12 (54)	10 (54)
Total	**24 (159)**	**26 (162)**	**15 (159)**	**12 (162)**	**48 (159)**	**45 (162)**

Figure 19: Retrieval order of caches plotted against the optimal retrieval order for each individual. Blue dots = test condition, orange dots = control condition. Blue and orange lines indicate the regression lines for test and control conditions respectively. If wolves followed the optimal foraging path, the blue line should go from the bottom left to the top right.

DISCUSSION

Overall, this study suggests that wolves benefitted from observing the caching process as shown in a higher success in finding all caches, fewer unrecovered caches and a lower latency of finding caches in test compared to control trials. We therefore suggest that wolves have an Observational Spatial Memory. This is the first experimental study that provides evidence for OSM in a canid.

However, the difference in performance between test and control trials was small, which suggests that wolves often use their sense of smell for cache recovery. This has also been shown for other species. Rodents are very successful pilferers due to the combination of their spatial memory abilities and their sense of smell (Vander Wall 2000). For example, in a comparative study of Yellow pine chipmunks and Steller's jays, chipmunks even outcompeted the jays with their excellent OSM skills in finding food caches of others (Thayer and Vander Wall 2005). Especially, under wet conditions, seeds emit strong odours which helps Chipmunks to detect caches with olfaction leading to the fact that they successfully recovered caches made by Steller's jay under wet conditions (67.9% ± 29,7%, n = 354), whereas Steller's jays were not able to recover caches made by chipmunks under wet conditions, recovering only 1 of 79 caches available during the first four trials. Under dry conditions, however, when seeds did not smell strongly, Chipmunks recovered only 5.3% (± 7.7%, n = 354) of available caches, suggesting that Chipmunks use their sense of smell for cache recovery. Steller's jays on the other hand found the same number of seed caches under both conditions. These findings match our study results and the use of olfaction would give an explanation to why wolves were so successful at cache recovery even in control trials. It is well known that next to visual information, olfactory cues are important in hunting for red foxes (Österholm 1964) and coyotes (Wells 1978) and wolves use olfaction to acquire information about food sources in the wild (Harrington and Asa 2003). Dogs, closely related to wolves (Vilà et al. 1997), have a very good sense of smell which has been shown to be at least 100 times greater than the human sense of smell in behavioural experiments (e.g. Moulton et al. 1960) and it seems that olfactory information is more important than visual cues at least for the discovery of explosives (Gazit and Terkel 2003).

To test the limits of wolves' OSM, we provided trials with different numbers of caches. Interestingly, the number of caches had no significant influence on the success of finding all caches suggesting that if the wolves paid sufficient attention they as easily remembered 8 as 4 locations. However, when analysing the latency to find each single cache for all trials, we found a significant interaction between trial number and the number of caches hidden suggesting a learning effect across trials, at least under more difficult conditions where more caches were made (8 and 6 vs. 4 caches). There are two possible explanations for this

effect: (1) During training trials, wolves learned to recover 2 caches, whereas experimental trials were performed with 4, 6 or 8 caches. Accordingly, wolves might have needed some trials to get used to higher numbers of caches being hidden. But as no learning effect could be shown for the 4-cache situation, this is rather unlikely. (2) Another possible explanation for this phenomenon is that this interaction shows limits of short-term OSM in the wolf. While they can remember the location of 4 food caches quite well, they need repeated trials to learn to pay enough attention to recover more caches. Learning to pay sufficient attention within only 6 trial repetitions would signify a fast learning ability. Wolves live in a very stochastic environment and need to be able to adapt quickly to changing environmental conditions (Packard 2003), which could explain these results. Learning effects in wolves, indicated by an improved performance with every trial repetition, could also be shown for the success of finding all caches, the latency to find caches and the distance walked to recover caches. Also other species, such as cats *(Felis silvestris f. catus)* (Warren and Baron 1956), racoons *(Procyon lotor)* (Michels and Pustek 1961), chimpanzees (*Pan troglodytes*) (Hayes et al. 1953) and rats *(Rattus norvegicus)* (Slotnick and Katz 1974) showed a learning effect after a few trials in discrimination tasks. As Michels and Pustek (1961) state, this demonstrates behavioural plasticity, which is advantageous in changing, new or artificial environments.

Limits of OSM are further suggested by the analysis of the distance walked. Although wolves found more caches in less time in test trials compared to control trials, the distance wolves walked to recover caches did not differ significantly between test and control trials. This could be due to the fact that wolves remember the general area where food caches were made but not the precise location. If they do not walk directly from one cache location to the next one, the searching process causes a lot of walking forwards and backwards to find the actual cache and could be an explanation for the higher success rates in test trials whereas the distance walked to recover caches was as high as in control trials.

Furthermore, the distance walked during cache recovery increased with every cache found (e.g.: the mean distance walked to recover the first cache was lower than the mean distance walked to recover the second cache). If wolves had remembered the exact cache locations during test trials, the distances walked to recover them would have been stable and there would have been a significant difference in the distance walked between test and control trials. Shorter retrieval distances for the caches recovered first could have been caused by chance, as cache densities are highest at the beginning of each trial and wolves could have discovered the closest caches coincidental, since they have to pass them to get to the back of the enclosure.

If wolves cannot remember 4 to 8 caches accurately, it could have been due to serial-position effects, such as recency or primacy effects. Rats *(Rattus norvegicus)*, for example,

have shown clear primacy and recency effects in a spatial memory recall test in an 8-arm radial maze, depending on the retention interval (Bolhuis and van Kampen, 1988). After short retention intervals of 30 sec, rats showed recency effects, whereas primacy effects could be observed afters delays of 16-min. Seed-caching birds have also shown serial-position effects: black-capped chickadees (*Poecile atricapillus*) clearly showed primacy and recency effects in a spatial list learning task (Crystal and Shettleworth 1994) and Clark's nutcrackers demonstrated strong primacy and week recency effects in a spatial operant task (Basil 1992). North American Badgers (*Taxidea taxus*) have been shown to recover their own food caches in the order they were made (Michener 2000), indicating a primacy effect. However, in our wolf study, we did not find any significant differences in which caches were found first or last between test and control trials, indicating that they occurred by coincidence and not because of limited memory skills.

Limited OSM-skills could be inferred by the results regarding optimal foraging theory (OFT). According to OFT, wolves should have chosen the shortest route between the available caches to maximize their energy gain. However, wolves followed the optimal foraging path only very rarely and again there was no difference between test and control trials suggesting that the retrieval order of caches was based on chance and not on their memory of cache locations. Although some individuals (n=3) seemed to approximate the optimal retrieval order during test trials in a graphical analysis (see figure 19), most animals did not demonstrate a visually apparent difference in their retrieval order between test and control trials. Finding the shortest route for a set of predefined goals is a simple version of the Traveling Salesman Problem (TSP). TSP-like problem-solving skills have for example been investigated in primates who demonstrated OSM (MacDonald & Wilkie 1990, Lührs et al. 2009, Janson 2007, MacDonald et al. 1994, Menzel 1973, Gallister and Cramer 1996). In Menzel's experiment (1973), 4 chimpanzees (*Pan troglodytes*) could retrieve up to 18 caches, which were previously hidden by a human experimenter in an arbitrary order. All animals did choose shorter routes than could have been expected by chance and did not follow the route the human cacher had taken. The objective to minimize the travel distance could also be noted for Yellow-nosed monkeys (*Cercopithecus ascanius whitesidei*) in retrieving 2 to 4 caches (MacDonald and Wilkie 1990) and vervet monkeys (*Chlorocebus pygerythrus*) in retrieving 6 caches (Gallistel and Cramer 1996). Among other organisms, birds have demonstrated this ability as well. Recently, Baron et al. (2015) demonstrated that pigeons (*Columba livia*) can learn to choose efficient routes over repeated trials. Travel routes to 3 - 6 goals became shorter over trials for known cache locations and also when confronted with new configurations, routes were shorter than expected by chance. However, it is currently debated, whether these results can be explained by the animal's ability of multi-step route planning (e.g. Janson 2014, Howard and Fragaszy 2014). The TSP has not yet been solved

efficiently with a mathematical model (Janson 2007) and requires exponentially more computing capacity with every additional location involved. Howard and Fragaszy (2014) state that the costs to cognitively solve a TSP are so high that the payoff would be comparably small, especially if resources are available in moderate or high densities, which was the case in our experiment. Short - but not optimal - travel distances can also be reached by easier strategies, such as the "nearest-neighbour" technique (NN), where the individual always chooses the closest cache site which has not been visited yet or the "crossing avoidance" strategy (CC) in which subjects choose routes to visit all goals without crossing their paths. Janson (2014) proposes a "gravity rule" in which animals choose their path based on the mentally summed up spatial information they have about unused resources, including distance, value and distribution. He also mentions that some of the study results among primates clearly show that the lack of optimal route choice was not caused by limited spatial memory abilities but by decision making that was not uniquely focused on minimizing the travel distance, which could have similarly been the case in our experiment. It is questionable if our wolves needed to be cost efficient due to their living in captivity. For example, motivation has been proven to be important for efficient cache recovery. In an experiment with Clark's nutcracker, Bednekoff et al. (1997) suggested that not limited memory skills but rather a lack of search motivation and the will to explore the testing enclosure could have caused errors during cache recovery. In our experiment, the latency to find caches was influenced by the days since the last feeding, suggesting that motivation played a role. However, since appetite only increased the latency of cache recovery and not search success, it suggests that higher motivation did not increase their attention but rather their speed of walking.

Furthermore, travel distances to retrieve caches are likely much longer in the wild, resulting in a larger difference in energy expenditure for locomotion if the retrieval sequence is not optimal (Sayers and Menzel 2012). Given the smaller scale of the optimization problem for the captive wolves in our experiment, non-optimal retrieval orders could be of less costs and therefore solving the task in the most optimal way less important.

As mentioned, the density of available caches is important for cache recovery in the wild. Squirrels attempt to recover scatter-hoarded nuts preferentially where they are denser instead of using spatial memory (Stapanian and Smith 1984). In our experiment, the density of caches was highest in the 8-cache situation and this could explain the decreasing latency to find caches with an increasing number of caches made.

In this study, humans were used as demonstrator of cache locations, which was not done in most of the studies testing for OSM in corvids where conspecifics acted as cachers. Range and Viranyi (2013) however, could show that wolves at the Wolf Science Center do pay close

attention to a human demonstrator and this was also the impression gained from this study. During the caching process, wolves readily observed every movement of the human cacher.

Taken together, this study suggests that wolves do have OSM, but their memory abilities are limited especially in comparison to corvid species. Due to different study designs a direct comparison of the OSM abilities of corvids and wolves is not possible, but as the research about OSM in corvids suggests (e.g.: Bednekoff and Balda 1996a, Bednekoff and Balda 1996b, Watanabe and Clayton 2007), most corvid species probably would not have problems at remembering 4 to 8 caches out of 131 possible cache locations.

Considering the evolution of observational spatial memory in the context of social structure and the reliance on cached food, these results match well with what could have been expected. Food caches probably do not play a crucial role for wolves' survival and moreover, due to their very accurate sense of smell they need not necessarily rely on OSM to relocate caches. Due to their social life, however, they might be able to observe other caching individuals frequently, which could have driven the evolution of basic OSM abilities, which is also suggested by our test results. This would allow them to relocate the general area where a conspecific hid the cache via local enhancement (Range and Virányi, 2013) and then they could use their sense of smell to find the actual location.

For future research we suggest an in-depth study of OSM capabilities in wolves. A cluster design would help to find out if wolves remember exact cache locations or the general area in which caches are made. Additionally, the probabilities of finding a cache by chance with differing amounts of caches being made could be kept at the same level, if the amount of possible cache locations would be adapted accordingly. For a comparison of OSM in canids and for further investigation of the hypothesis of a relationship between the social life, the dependency on food caches and OSM abilities, more canids should be tested for their OSM abilities. The fox, for example, as a solitary living animal that caches a lot, could provide more insights into the importance of social living for OSM. The dog as the domesticated descendant of the wolf could give important insights as to how its social and cognitive abilities have changed through domestication.

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APPENDIX 1: Coding scheme with behaviours and modifiers

Behaviour	Description	Modifier
Behavioural Class 1		
number of caches found	how many caches are searched for until now	none
Behavioural Class 2		
search	searching for caches	none
handle	being at one of the caches and manipulating it in any way	none
nic	neither eating nor looking for caches (e.g. looking after people passing by, sniffing at urine marks, sitting in the shade)	
Behavioural Class 3		
stand	not moving (hind legs do not move more than two steps)	nose position distance
walk	walking	nose position distance
trot	trotting	nose position distance
eat	eating the cached food	cache number
Behavioural Class 4		
locs	locations passed by within a distance of 20 centimeters	none

Modifier	Description
cache number	the number of the cache in the hiding order
distance	close (< 20 m) middle (20-100 cm) far (100-200 m)
nose position	ground low normal high