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Cooperative string-pulling in wolves (*Canis lupus*)

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Summary

The aim of this study was to investigate whether grey wolves (*Canis lupus*) cooperate in an instrumental string-pulling task when either two or only one piece of reward was offered, and whether the wolves recognized when a partner was needed to solve the task.

Two of three timber wolves learned quickly to pull a rope connected to one of two platforms in order to move the platform and to reach the food placed on it. After this initial individual training the wolves were tested in a cooperative version of the task when the two platforms were connected and both wolves had to pull, each on a rope, at the same time in order to move the platforms that were connected to each other, forward. The wolves were tested in different conditions when the two platforms were either connected or could be moved separately by one individual. In both conditions either both or only one platform was baited. Furthermore, the wolves were tested in means-end trials when only one platform was baited but the single rope presented was attached to the empty platform.

The wolves solved the cooperative trials irrespectively whether both or one platform was baited. They synchronized their behaviour, and solved the cooperative trials faster over time. Additionally each wolf started pulling later when the partner was not within 250 cm to the apparatus than when they were there together, showing that they might have recognized when a partner was needed. Furthermore, the subordinate wolf might have perceived when cooperation was needed and when the task was individually solvable. In the individual condition when only one food reward was presented this wolf did not pull on the unbaited side, but did so when cooperation was necessary to solve the task. However, in the means-end condition no clear conclusion could be drawn whether the wolves had an understanding of the connection between the food presented on the platform and the rope on it or whether they had not.

In general the high success of the two wolves in this pilot study was seemingly based on their behavioural flexibility and their quick adaptation to the different experimental conditions. Because of our low sample size not all of our results are

conclusive and alternative explanations are discussed. But the method is promising for studying cooperation in wolves.

Zusammenfassung (German Summary)

Das Ziel dieser Studie war es zu untersuchen, ob Wölfe (*Canis lupus*) in der Lage sind in einem instrumentellen Versuch zu kooperieren, wenn sowohl beide Tiere, oder nur eines eine Belohnung erhielt. Weiters untersuchten wir, ob die Wölfe verstanden, dass zum Lösen der Aufgabe ein Partner notwendig war.

Zwei von drei Timberwölfen lernten rasch an einem Seil zu ziehen, welche mit einer von zwei Platten verbunden war. Durch Ziehen an dem Seil bewegte sich die Platte nach vor und der Wolf konnte das darauf befindliche Futter nehmen. Nach der individuellen Trainingsphase wurden die zwei Platten mit einer Stange verbunden, wodurch ein Ziehen an einem Seil nicht mehr ausreichte um die Platten nach vor zu bewegen. Die Wölfe mussten kooperieren um an das Futter zu gelangen. Die Versuchsbedingungen wurden variiert, indem die Platten entweder verbunden oder unverbunden waren, sodass entweder beide Wölfe ziehen mussten um die Aufgabe zu lösen oder individuelles ziehen führte zum Erfolg. In beiden Situationen wurden entweder beide oder nur eine Platte mit Futter bestückt. Weiters wurden die Wölfe auf ein Verständnis für die Verbindung zwischen dem Seil und dem Futter auf der Platte getestet (means-end Versuch).

Die Wölfe kooperierten sowohl in dem Versuch wenn beide Platten bestückt waren als auch wenn nur eine Platte bestückt war. Sie synchronisierten ihr Verhalten und lösten den kooperativen Versuch schneller über die Zeit hinweg. Zusätzlich zogen beide Wölfe später das erste Mal am Seil, wenn der Partner mehr als 250 cm von der Apparatur entfernt war, als wenn sie gemeinsam innerhalb 250 cm zu der Apparatur waren. Das lässt vermuten, dass die Wölfe erkannt haben, dass der Partner benötigt wurde um die Aufgabe zu lösen. Weiters macht es den Anschein, dass der untergeordnete Wolf unterscheiden konnte, ob Kooperation erforderlich war oder nicht. In den Versuchen mit nur einer Platte bestückt zog dieser nicht an der unbestückten Seite wenn die Platten unverbunden waren, jedoch zog dieser an der unbestückten Seite im kooperativen Versuch. Mit dem „means-end“ Versuch hingegen konnte nicht gezeigt werden, ob die Wölfe ein Verständnis für die physikalische Verbindung zwischen der Platte mit Futter und dem Seil haben oder nicht.

Die hohe Erfolgsrate der zwei Wölfe in dieser Pilotstudie war vermutlich möglich, weil die Wölfe sehr flexible in ihrem Verhalten waren und sich sehr rasch an die neue Situation im Gehege anpassten. Auf Grund der kleinen Stichprobe von zwei Tieren sind die Ergebnisse nicht schlüssig und alternative Erklärungen wurden diskutiert. Jedoch konnte gezeigt werden, dass diese Methode an sich gut funktioniert und Kooperation bei Wölfen damit untersucht werden kann.

1 Foreword

Human societies are built on cooperation e.g. human life is organized on cooperation of individual people, groups, companies, states, and so on. Human cooperation seems to be exceptional is some ways but its evolutionary origins can be found in animal species. In humans, cooperation occurs between related and also between unrelated individuals (Boyd 2006). For example a mother can bring her child to a friend of hers for a few hours. This friend will take care of the child, will give him/her something to eat, to drink, will play with him/her and will protect him/her from danger. Similarly, it has been found that also in nonhuman primates, group members take care of the offspring of others (Dugatkin 1997).

Humans can remember the persons that cooperated with them in the past and are more likely to cooperate with them again. For example, at school it is common that one pupil helps another to prepare for a test on one subject, and for a different subject it is the other way around. Again, this is not uniquely human. For example, grooming in chimpanzees (*Pan troglodytes)* brings some future benefits for the actor e.g. by getting food from the individual groomed before (de Waal 1989). Also vampire bats (*Desmodus rotundus*) share food with others sometimes giving, sometimes receiving food from the same individual (Wilkinson 1984).

Moreover, humans are usually aware when they need a partner to solve a problem impossible or more difficult to solve alone. They understand the role of the other individual, and can also carry out different roles while knowing why the other one is needed. For example, big companies cooperate with other companies to complete a job. In a building company there are purchasing, producing and selling departments. It is important that each department does a good job, and for this they have to take each other into account. In experimental studies with chimpanzees (Melis et al. 2006a) and orang-utans (*Pongo pygmaeus*) (Chalmeau et al. 1997) it was shown that the animals may understand the need for a partner to get a reward because they recruit a partner to work with to complete a task. In another study the animals had to perform different roles (Werdenich and Huber 2002). One animal had to pull the rope while the second animal had to grab a receptacle with the food (Werdenich and Huber 2002).

Comparative studies may reveal the similarities and differences between different species, and help to discover the origins of the exceptional human cooperation.

2 Introduction

2.1 Defining and studying cooperation

Cooperation was often studied from the evolutionary point of view asking whether animals cooperate based on mutualism, reciprocity or kin-selection (Dugatkin 1997). Alternatively, one may approach the question from the point of view of proximate mechanisms underlying cooperation such as the behavioural, physiological and/or morphological strategies of individual participants (Noë 2006) as well as the cognitive abilities needed to cooperate with others (Brosnan and de Waal 2002). Based on criteria of both approaches cooperation has been defined in various ways. In my thesis I talk about cooperation in a more functional sense, and define cooperation as "… the voluntarily acting together of two or more individuals that brings about, or could potentially bring about, an end situation that benefits one, both or all of them in a way that could not have been brought about individually" (Brosnan and de Waal 2002). This definition tells nothing about the evolutionary and mechanistic origins of cooperation and leaves the question of underlying proximate processes open. In my study I focused on the latter questions.

2.2 Cooperation in social carnivores

The evolution of human cooperation is traditionally studied by comparisons with our closest relatives, the apes or other primates. However, it has been suggested that man was exposed to ecological pressures shared rather with social carnivores like wolves than with apes (Hall and Sharp 1978; Schaller and Lowther 1969). Social carnivores live in small groups in open areas, and, as it was presumed for the early hominids adapted to open areas, they hunt large prey together, defend it against scavengers, and defend their group against strangers (Schaller and Lowther 1969). Furthermore, Schleidt and Shalter (2003) postulated that human social organisation is more similar to a wolf pack than to a chimpanzee group, and drew an analogy between the wolf and human family (Schleidt and Shalter 2003). In wolves, like in humans, the basis of the group is the breeding pair and its offspring. They live in packs which consist of 2 to 36 individuals, and in which the alpha male mostly mates with the alpha female. Male wolves are generally larger than their mates, and the offspring stays in the group at least until they are mature (Mech

1970). The pack members cooperate with the mating pair in rearing, feeding and protecting their offspring (Mech 1970). The pack members hunt together, although the per capita outcome can be lower in a large pack than in a pair, but only when the pack hunts cooperatively large prey becomes accessible (Schmidt and Mech 1997). Wolves live up to 13 years or even more in the wild (Mech and Boitani 2003). Probably partly thanks to their social structure, wolves have been very flexible in adapting to their environment, to the changes in temperature and prey activity over time (Packard 2003).

2.2.1 Group hunting as cooperative activity

Group hunting may be a good example to describe cooperation since it is widely distributed in animal species and it may be important for the evolution of sociality (Packer and Ruttan 1988). As mentioned above, early hominids lived as hunter-gatherers, and even today living hunter-gatherer human societies cooperate during a hunt (Nowak 2006; Schaller and Lowther 1969). During cooperative hunting it is important for the participants to pay attention to each other and to adjust to the others' behaviour. For example if one starts running after a prey another individual should join in to increase the chance for success. Creel and Creel (1995) mentioned that in a communal hunt it is possible to hunt larger prey with shorter individual chases, and the success of the hunt can be improved. Furthermore, there is some evidence that already early hominids had different roles in hunting, e.g. one individual drove the prey forward, others blocked it, and others hid until the prey was close to them and then caught it (Schaller and Lowther 1969). Similar cooperative hunting has been observed in wild living chimpanzees in the Tai National Park in which the hunters performed different complementary actions which were all directed toward the same prey e.g. driving, blocking the prey to escape and chasing the prey (Boesch 2002; Boesch and Boesch 1989).

Cooperative hunting, in which the individuals take complementary roles when hunting for the same prey, occurs also in non-primate species like wild dogs (*Lycaon pictus*), hyenas (*Crocuta crocuta*), lions (*Panthera leo*), and wolves (Creel and Creel 1995; Mech 1970; Stander 1992). A study by Stander (1992) showed that female lions from Etosha National Park performed different stalking roles during hunts. In most cases the individuals occupied a specific role, but some animals

also compensated if one animal switched her role. Also wolves have several times been reported to hunt together and to chase the same animal (Mech and Boitani 2003; Trokowicz 1980).

Very little is known, however, how much the animals understand the role of each other to bring down the prey together. Some observations of wolves taking different roles during a hunt seem to support that the individuals may understand the role of the others. Trokowicz (1980) reported group hunting in wolves in the Biebrza valley in Poland, where four wolves drove a deer towards two other wolves, which were hiding behind bushes. Another hunt took place near to a house standing in the forest. One wolf was waiting hidden behind the house, and the other two wolves drove the deer in its direction. The deer was attacked near the house (Trokowicz 1980). In another documented hunt, parent wolves positioned themselves in ambush along a rock while the pack members chased an arctic hare towards them (Mech 1995). These examples give some evidence that wolves may understand the need for partners and behave according to their behaviour.

2.3 Investigating cooperation experimentally

Based on field observations it is hardly possible to figure out the precise mechanisms of such hunts due to poor visibility and the lack of control conditions. Laboratory experiments under controlled circumstances are needed to test, for example, whether animals pay attention to each other or not. Cooperation has been tested in captivity in several primate species in problem-solving-tasks (e.g. chimpanzees, Chalmeau 1994, Hirata and Fuwa 2007; capuchins (*Cebus paella*) Mendres and De Waal 2000; cotton top tamarins (*Saguinus oedipus*) Cronin and Snowdon 2008). In general, in these tasks food was out of reach of the subject and had to be pulled closer in a certain way. For example, the animals could reach the food by pulling a string fixed to the food reward (Hirata and Fuwa 2007; Melis et al. 2006a; Melis et al. 2006b). In some studies, the animals had to learn to pull together (Hirata and Fuwa 2007) while in others they pulled together spontaneously (Cronin et al. 2005; Melis et al. 2006b). Mostly the animals were able to synchronize their behaviour to complete the task and to get the reward (Cronin et al. 2005; Melis et al. 2006a; Melis et al. 2006b; Mendres and De Waal 2000).

2.3.1 Recognizing the need for a partner

Whether the animals in these studies took the other animal's behaviour into account or whether they just performed similar actions on the same goal was not clear. Mendres and De Waal (2000) mentioned that the need for synchronisation could also be learned. Therefore, the animals were tested without a partner present. In some studies it was shown that the animals pulled less often when being alone at the apparatus compared to having a partner present (e.g. Menders and De Waal 2000, Cronin et al. 2005, Melis et al. 2006a), or the animals waited to start pulling until the partner was present (Chalmeau 1994; Chalmeau and Gallo 1996). Even more convincing are occasions in which the animals recruited others to cooperate (Chalmeau 1994; Chalmeau et al. 1997; Hirata and Fuwa 2007; Melis et al. 2006a).

Furthermore, it was tested whether the animals recognized in which condition the partner was needed to solve the task and when it was not. To check for it, the animals were tested in trials when they could solve the task on their own and when they needed help to solve the task. Chimpanzees recruited more often a partner if they needed them to solve the task then when they could have solved it on their own to obtain the food (Melis et al. 2006a).

A further indication that the animals perceived that cooperation was necessary would be if they continued cooperation when only one animal got rewarded while the other one got nothing. Monkeys in several studies continued cooperation but at a lower success rate (Cronin and Snowdon 2008; de Waal and Berger 2000).

2.3.2 Cooperating and sharing the reward

The condition with a single, monopolizable reward causes further questions: Which animal would get the food? Was the food shared by the animals or was it monopolized? The food could be shared by offering it to the cooperator as it was the case in cotton-top tamarins (Cronin et al. 2005) and capuchins (de Waal and Berger 2000). They offered the food to their partner and did so more often when they needed a partner to solve the task compared to situations when they could perform solitarily (Cronin et al. 2005; de Waal and Berger 2000). Or it occurred that the animals cooperated with each other although the food resource was mo-

nopolized by one individual (Chalmeau 1994; Cronin and Snowdon 2008; de Waal and Davis 2003). In these cases mostly the dominant animal got the rewards (Chalmeau 1994; de Waal and Davis 2003).

2.3.3 Understanding means-end connections

If cooperation is about pulling strings together in order to reach the reward, it is beneficial for the animals if they understand the physical connection between the rope and the food (Visalberghi et al. 2000). Such means-end understanding mostly was tested by offering a physical connection to an out of reach object (Hauser et al. 1999; Osthaus et al. 2005; Stephen et al. 2006). Chimpanzees pull more often a rope that is clearly fixed to the banana than another one that is lying in front of a banana (Povinelli 2003). Osthaus and colleges (2005) tested dogs (*Canis familiaris*) with different string arrangements, but the dogs were successful only with the simplest arrangement. If the strings crossed each other, or the food was actually physically closer to the accessible end of the empty rope the dogs failed, and chose the empty rope based on proximity to the food. Other canines have not been tested with this method.

2.4 Cooperative string-pulling in non-primate species

Cooperative string-pulling tasks can be used not only with primates who have hands, but also for species that can use their peak or mouth for pulling (rooks (*Corvus frugilegus*): Seed et al. 2008, hyenas (*Crocuta crocuta*): Drea and Frank 2003, rats (*Ratus norvegicus*): Rutte and Taborsky 2007). Spotted hyenas (*Crocuta crocuta*) were tested in a cooperative string-pulling task while having free access to the apparatus. They needed no specific training to complete the task, coordinated their behaviour and showed behavioural flexibility during cooperation by switching positions when necessary (Drea and Frank 2003). Wolves have a rather similar body schema to hyenas, so we can expect them to be physically able to perform in a similar task. Wolves have been shown to pull on a string connected to a piece of food in order to get the reward (Miklósi et al. 2003), but the paradigm has not been used to test cooperation or means-end understanding in wolves.

2.5 Research Questions and Hypothesis

In the present study three wolves were tested in an instrumental cooperative string-pulling task to investigate under which conditions they would cooperate with each other. The wolves were tested with an apparatus consisting of two platforms each connected to a rope that could be pulled in order to move the platform, baited with food, forward. The platforms could be connected, so that two wolves had to pull simultaneously in order to move the platforms (Fig.1).

Figure 1. Two wolves pulling simultaneously, each on a rope, in order to move the baited platforms forward to reach the meat pieces.

I tested the wolves in different conditions when either pulling together was necessary to solve the task or pulling on its own led to success. For both conditions the amount of food was varied by offering food either on both or only one platform. Additionally, I tested them in a means-end condition in which the platforms were not connected, one platform was connected to a rope but the other one, with no rope, offered the reward.

3 Methods

3.1 Animals

Experiments were conducted with three adult timber wolves (*Canis lupus occidentalis*) at the Zoo Schönbrunn, Vienna. They were siblings from different litters. The male alpha wolf was born in Schönbrunn in 1993, the female (sterilized) in 1992 and the male beta wolf in 1996 (Fig.2). The enclosure had an area of 2500 m² and contained natural vegetation, trees, tree trunks and rocks. The wolves were fed with horse meat, beef or rabbit (approximately 1 kg per wolf) at 11 a.m. every day except on Wednesdays and Saturdays. Water was freely available. None of the wolves had ever participated in behavioural experiments before.

White Grey Black

Figure 2. The three wolves. White and Black were males and Grey was a female. They were between 11 and 14 years old.

Before the experiments started, the behaviour of wolves was observed in order to describe their social interactions like affiliation and dominance. The experiments took place on two to four days per week and were conducted between November 2007 and May 2008.

3.2 Behavioural Observation

The behaviour of the wolves was recorded before the apparatus was set up (23 days), while they were habituated to the apparatus (4 days) and during the experiments (65 days). Before starting the experiments the observations were aimed at getting to know the wolves and their social relationships as well as to habituate the wolves to the experimenter. The observed behavioural interactions were further used for analysis of the behaviour during the experiment.

The ethogram was adjusted to the one from Wolfpark (Goodmann et al. 2002). The three wolves were observed on 23 days in the mornings including the feeding time or in the afternoon via focal sampling (from day 19 on when the foundation was put into the enclosure, via instantaneous sampling because observing all three wolves at the same time was possible and therefore the first reaction of each wolf to the foundation and later on to the apparatus could be recorded) and during the experiments via instantaneous sampling. For focal sampling the behaviour of one individual was recorded for 15 minutes, and its behaviour in interactions with other wolves and also the distance to the other wolves were noted. For instantaneous sampling all three wolves were observed at the same time and their behaviour was noted every minute. In addition to the focal and instantaneous sampling I used ad libitum sampling to note all interactive behaviours which were important for this study.

3.3 Experimental apparatus

For testing the wolves in the cooperative-string-pulling-task an experimental enclosure (350 cm x 350 cm) was built of 180 cm high wire mesh fence in the enclosure, next to the visitor's house, at the place where the wolves were usually fed by their caregiver. Therefore, the wolves already associated this place with food (Fig.3). The fence of the enclosure formed the back side of the experimental enclosure. On the front side, toward the centre of the enclosure, 190 cm apart two holes (23 cm x 25 cm high, 30 cm diagonal) were cut into the fence of the experimental enclosure through which the wolves could reach the experimental apparatus.

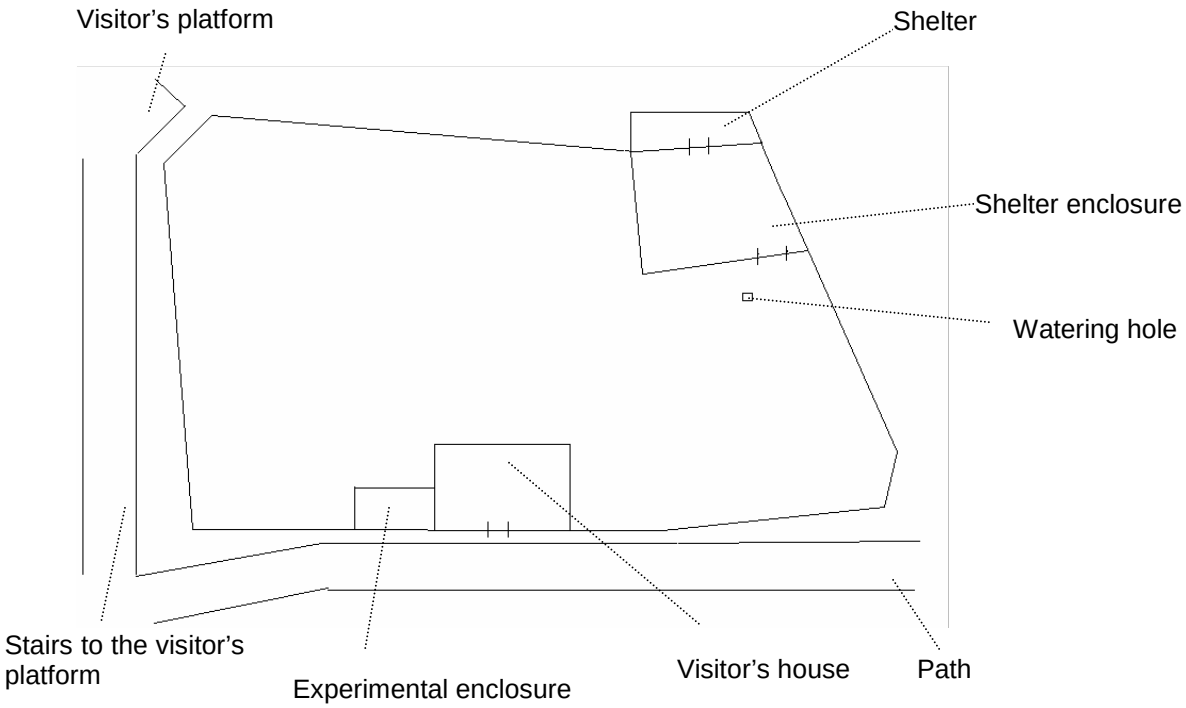


Figure 3. Sketch of the wolf enclosure in the Zoo Schönbrunn with the position of the experimental apparatus.

Inside the experimental area the experimental setup was built. As foundation for the apparatus, four iron stakes (10x10 cm) were hammered into the ground (246 cm and 155 cm apart from each other). On these stakes two transverse rails (300 cm) were fixed, parallel to the front of the experimental fence. At right angles to these rails two other iron rails (250 cm long) were fixed 186 cm apart on which an aluminium food platform (30 cm x 30 cm) on iron wheels could be moved forward and backward along the rail. Each platform was connected to a rope which the wolves could pull in order to move the platform forward and to reach the reward. Each rope (2 cm in diameter) was 150 cm long and was extended through a hole on the fence into the wolves' enclosure so that the wolves could reach and pull it. The reward was either a 40g piece of meat or a dead chick, provided by the care-giver.

On the other side of the platform a cord (diameter 0.5 cm) was stretched over a roll on a post at the back of the rail. On these ropes, weights were fixed to make the platform harder to move forwards. Two iron rods (the blockers) fixed on the bottom of each platform reached the ground and prevented the platforms from be-

ing pulled back by the weights. To move the platforms back to the starting position after each trial the experimenter had to lift the blockers up from the ground.

For the cooperation experiments the two food platforms could be connected (Fig.4). If connected the platforms could only be moved simultaneously by pulling both ropes at the same time (Fig.5). If a wolf pulled only on one side, the platforms would get stuck. During the experiment the experimenter stood in the back of the experimental enclosure and after each successful trial, the platform was retrieved and a new piece of meat was placed so that the next trial could start.

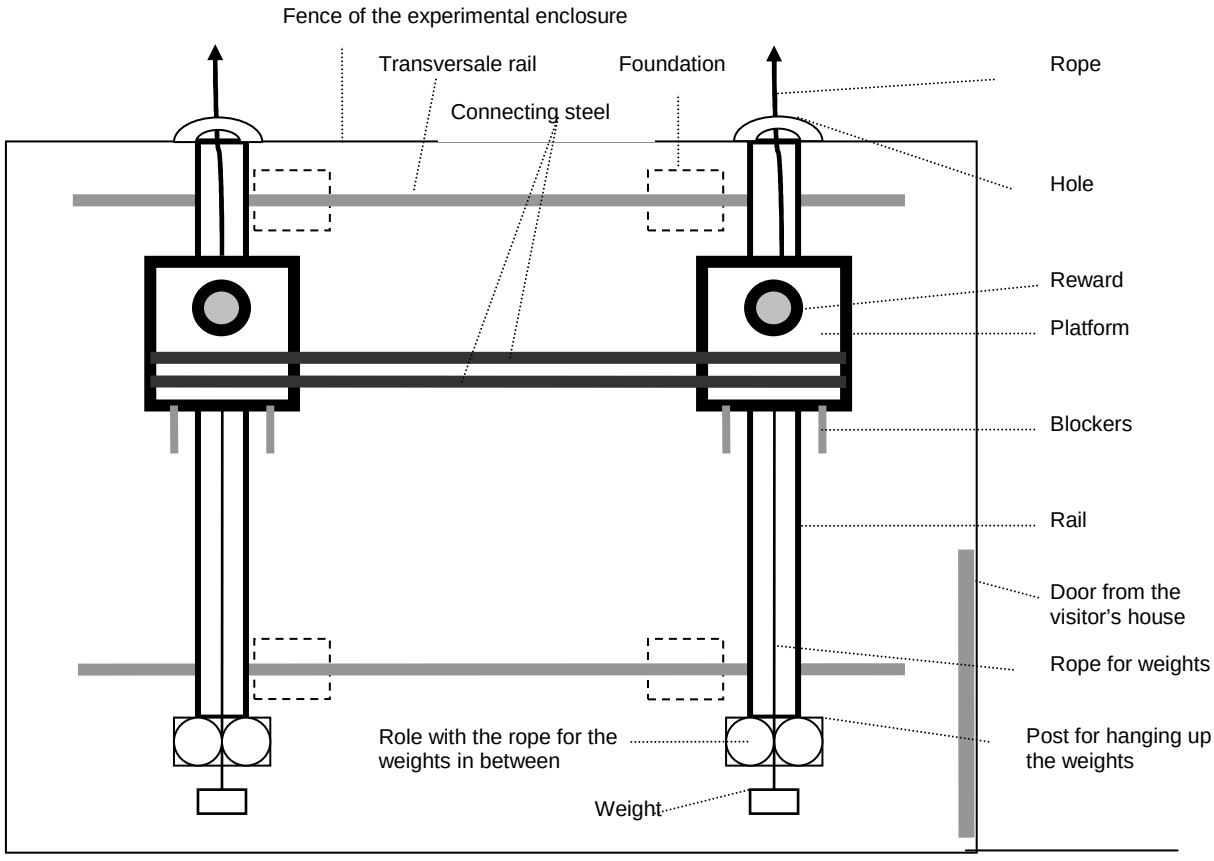


Figure 4. Sketch of the apparatus in the experimental enclosure next to the visitor's house in which the wolves were tested. The wolves had to pull the rope forward in order to move the platforms with the reward on it. The connecting rail could be removed for the individual tasks.

Figure 5. Both wolves pulling each on a rope in the connected both sides baited task. On each platform was a small piece of food presented.

3.3.1 Experimental procedure

The wolves always had free access to the experimental setup but only during the testing phases the rope was connected to the platforms and its end made accessible from the enclosure. Furthermore, participation by the wolves was voluntary - they could move freely in their enclosure, approach or leave the setup and could change from one side to the other of the apparatus as they liked.

The tests started in the mornings and lasted one to two hours depending on the motivation of the wolves. Depending on the experimental condition, the experimenter placed meat either on both or on one platform and one or two ropes were put into the enclosure. A trial started as soon as meat was offered on one or two platforms, and ended when all reward was taken by a wolf or after 10 min if no wolf had manipulated the apparatus during this time. In the latter case the experimenter removed the meat and restarted the test a few minutes later, independently whether a wolf was close (250 cm) to the apparatus or not since the wolves

watched the setup and the experimenter independent of distance to it. Placing the meat on the platforms often led the wolves to come down to the apparatus and to participate again. A trial was successful if the platforms were pulled forward and a wolf got the reward. It was scored not successful if they did not get the reward.

For the cooperative tasks, both platforms were connected so it was impossible to move both platforms by pulling only one of the two ropes. Thus, two wolves had to pull their ropes simultaneously. Each rope reached just 20 - 30 cm into the wolves' enclosure, making it impossible for one wolf to pull both ropes simultaneously.

3.4 Training sessions

3.4.1 Familiarization

After setting up the apparatus on the 12 November 2007 (Fig.6), the wolves were familiarized with this structure and with the presence of the platforms. Firstly the platforms were presented close to the holes in the fence but no ropes were connected to the platforms and the experimenter was not in the enclosure. As usual, they received their daily food by the caregiver at the usual place, now close to the apparatus. Thus, to feed they had to approach the experimental setup. The behaviour of the wolves towards the apparatus was recorded from the visitor's platform or in front of the enclosure next to the visitor's house. One week and three feeding days later the training started. Already on the first day after putting the apparatus in place all three wolves came close to the apparatus and took the food from their caregiver.

a) b) c)

Figure 6. Setting up the apparatus on 12 November 2007. First we carried the components next to the vistors's house (a), built up the apparatus (b) and finally we put up the experimental fence (c).

3.4.2 Training

3.4.2.1 Without a rope

The training started on 19 November 2007 first by throwing small pieces of meat through the holes towards the animals. Later, food was placed on one of the platforms placed close to the fence. In order to reach the reward, the animals had to stretch their head through the hole (Fig.7). The meat was randomly placed on either of the two platforms, so that no side preference would develop. Following this phase, the platforms were moved by the experimenter to make the wolves acquainted with the noise of the apparatus. Already after 6 days the individual training with the rope started.

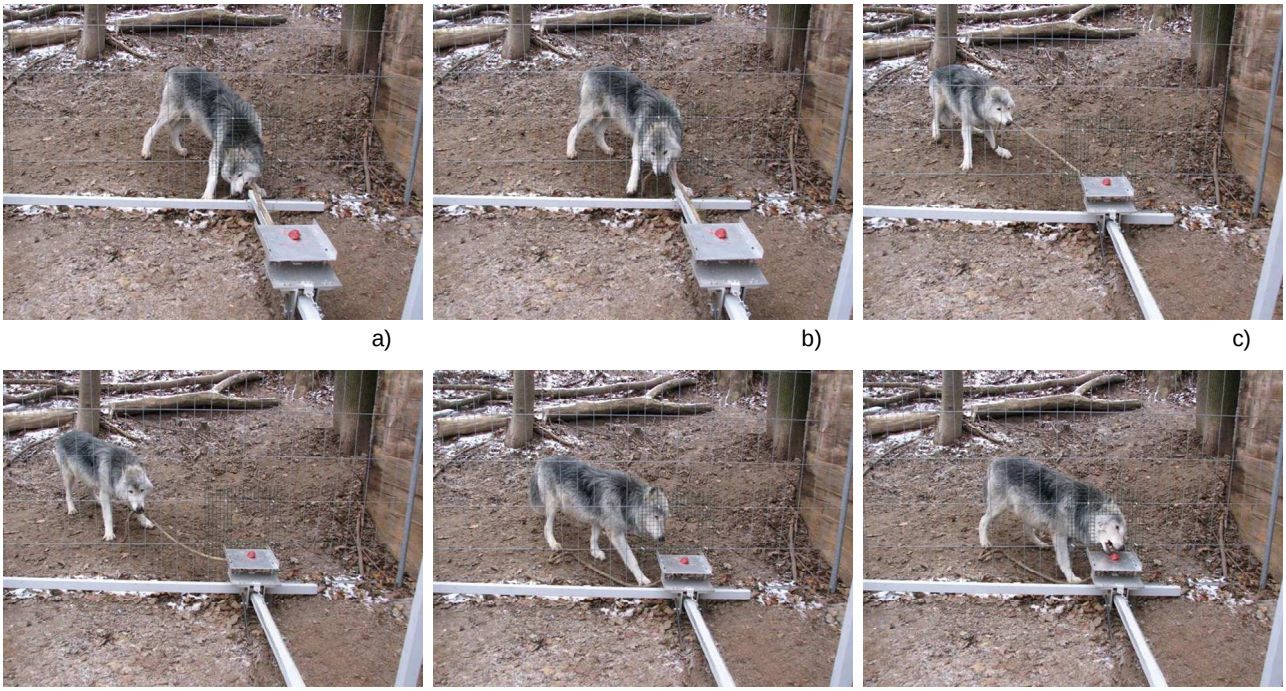
a) b) c)

Figure 7. Grey the female in the training without the rope. Food was placed on the platform placed close to the fence (a). The wolf had to stretch their head through the hole (b) to get the piece of food (c).

3.4.3 Individual training

First, the wolves learned individually to reach the food by pulling a rope in order to move the baited platform towards them. In random order one of the two platforms was baited. The platform was placed 1 m from the fence so that a wolf had to pull the rope in order to move the platform to receive the reward. A trial was scored successful when a wolf got the reward by pulling on the rope (Fig.8). On the first training day, White and Black pulled the rope immediately when the rope was put into the wolves' enclosure. White pulled in 9 of 13 trials and took the food afterwards, Black pulled 2 times and Grey pulled once but she did not take the food and once none of the wolves pulled. Training was terminated when Black had pulled 295 times and White had pulled 283 times on either the left or the right side. Grey, the female, took the food out of the hole but was scared of the apparatus

during the entire experiment. She only pulled once and was therefore excluded from further analysis. Therefore two of the three wolves solved this task.



a) b) c)

d) e) f)

Figure 8. Individual training. Black grabbed the rope (a) and pulled the platform forward (b, c). Then he released the rope (d) went forward to the baited platform (e) and took the food from the platform (f).

3.5 Experiment

Following the training, the experiment started on 15 January 2008. It had five different conditions. Two cooperative conditions, two individual conditions, and one means-end control condition (Fig.9). In the cooperative and individual conditions a rope was attached to each of the two platforms allowing both wolves to pull at the same time. In the means-end condition rope was attached only to one platform. In all conditions both platforms were always presented one meter away from the hole.

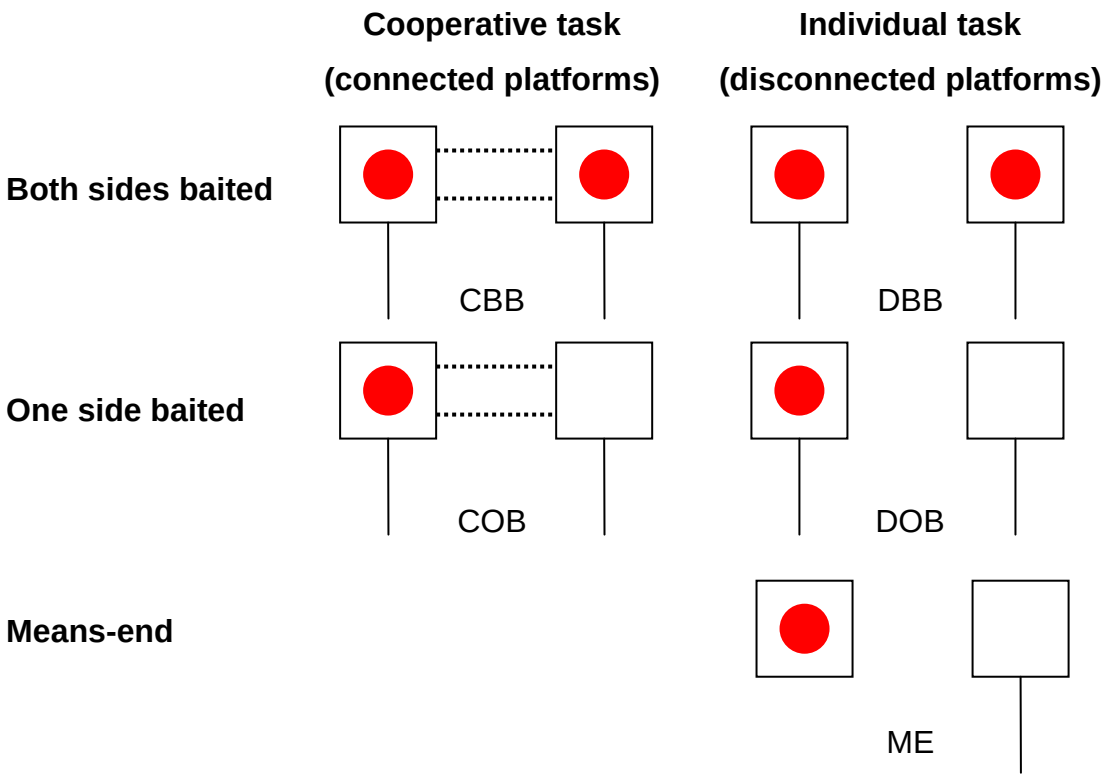


Figure 9. In the cooperative tasks the platforms were connected and either both or only one platform was baited with meat (red circle). In the individual tasks, the platforms were disconnected and could be moved by one wolf - again either both or one platform was baited with food. In the means-end condition one platform was baited with food but the rope was attached to the other platform.

3.5.1 Cooperative tests

The platforms were connected and both wolves had to pull at the same time each on different rope to move them forward (Fig.10a). If only one wolf pulled on one side the apparatus would get stuck until the second wolf started pulling on the other side too. The experimenter had to ensure by holding a rope fixed in the middle of the connecting rails that one wolf could not solve the problem on its own by pulling alternately on the two sides to move the platforms forward.

3.5.1.1 Connected and both sides baited trials (CBB)

Both platforms were baited with one piece of food and after the wolves pulled the platforms simultaneously each of them could get a reward.

3.5.1.2 Connected and one side baited trials (COB)

One piece of food was offered either on the left or on the right platform. The wolves had to pull together but only one of them got the reward. The side on which the piece was placed was randomized. This condition was done to examine the

conditions under which wolves would still cooperate, and whether each wolf got the same amount of food over time if only one piece of food was offered.

3.5.2 Individual tests

The platforms were disconnected as in the individual training but now a rope was attached to both platforms. Both wolves had the opportunity to pull a rope but pulling simultaneously was not necessary because the platform moved immediately forward when a wolf pulled the rope (Fig.10b). The connecter between the platforms was leaning visible for the wolves against the visitor's house.

3.5.2.1 Disconnected and both sides baited trials (DBB)

Both platforms were baited with a food and after the wolves pulled the platforms forward each of them could get a reward.

3.5.2.2 Disconnected and one side baited trials (DOB)

In this condition, food was offered on either the left or the right platform. Hence, only one of the wolves hat to pull the baited side for a successful trial. If a wolf pulled on the unbaited side the platform moved forward but the wolf got no reward. The side on which the piece of meat was placed was randomized.

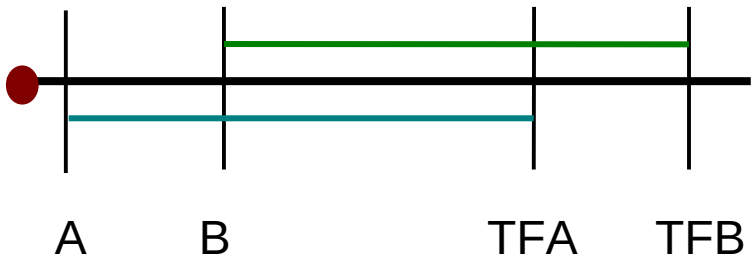


Figure 10a. Sketch of a time scale of a DBB trial. Red dot shows the start of the trial when the food was placed on the platforms. Then the first wolf starts pulling (A), followed by the second wolf (B). Blue line showed the pulling time of Wolf A from its first pull (A) until it took the food (TFA) and the green line showed the pulling time of Wolf B from its first pull (B) until it took the food (TFB).

Figure 10b. Sketch of a time scale of a CBB trial. Red dot shows the start of the trial when the food was placed on the platforms. Then the first wolf starts pulling (A), followed by the second wolf (B). Wolves pulled together (orange line) until the food got in reach and a wolf took the food (TF).

3.5.3 Means-end understanding

The platforms were disconnected and the connector was leaning against the visitor's house visible for the wolves, as in the individual tests. However, only one rope was presented in the wolves' enclosure attached to one of the platforms, which, however, did not carry food. The second platform offered food but had no rope attached to it. If a wolf pulled the rope the empty platform moved forward. As it was not possible to reach the reward therefore it was expected that the wolves would not pull at all in this condition.

3.6 Time table

Starting with November 19, 2007 the wolves were trained to approach the apparatus and to take the food from the platform on six days and then, were trained to pull the rope to get the reward on the following16 days. The experiment proper started on January 15, 2008 with a CBB trial. From the third testing day on, for 35 days, the CBB trials were interspersed with DBB trials. On experimental day 9 the connected one side baited (COB) trials started. On experimental day 11 the means-end (ME) condition was added, and one day later disconnected one side baited (DOB) trials were given too. On the last 26 experimental days the conditions were randomly varied (Fig.11). In total the CBB trials were conducted on 38 days, the COB trials on 29 days, the DBB trials on 22 days and the DOB trials on 13 days. The means-end trials were conducted on 14 days.

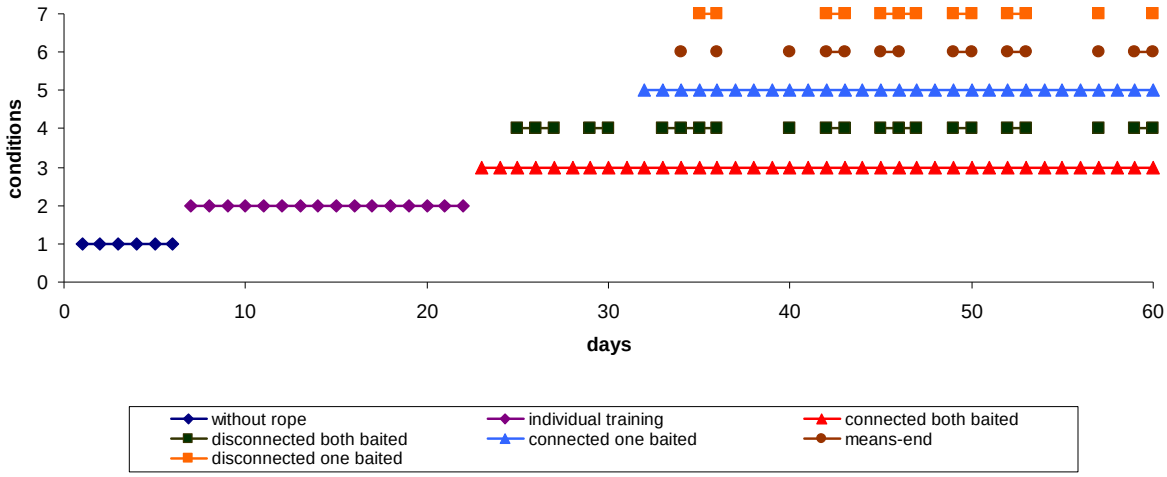


Figure 11. The time table shows the number of days the wolves were tested in each condition. The connected trials were interspersed with disconnected (individual) trials.

3.7 Data analysis

All experiments were recorded with two digital video cameras. The JVC Hard Disk Drive Camcorder (25 x Optical zoom) was positioned out of the enclosure to record both platforms as well as the area behind the experimental set-up. The second camera (Sony Handycam (20 x Optical zoom, Carl Zeiss Vario-Tassar) was placed at the left corner of the visitor's house so that the behaviour of wolves away from the experimental setup could also be taped. The video cameras recorded the entire time so the behaviour of the wolves was recorded before and after each trial. In addition to the video recording some behaviour parameters were noted. The parameters were recorded according to the ethogram (see supplement).

The videos from the JVC Hard Disk Drive Camcorder were analyzed with the Observer Version 5 Video Pro (Noldus Information Technology). Position and behaviours of the wolves during the tests were determined according to the following relevant variables for this study.

Position:

1) area 1: the wolf is within 250 cm (area one) to the apparatus

2) close left, close right: the wolf is 20 cm around the left or right hole

3) body length: the wolf is a body length or closer to the fence of the apparatus

4) area 2: the wolf is more than 250 cm apart from the apparatus

5) out of sight: the wolf is not visible

For analysis area 1 or the wolf was more than 250 cm apart (included area 2 and out of sight) from the apparatus was used.

Latency to pull: time from offering the rope to pulling for the first time (first pull) and to taking the food from the platform (take food) both either on the left or right side.

Dominant approach: a wolf moved forward directly to another one with its tail perpendicularly or above the plane of the back and its head held high.

Due to the free access of the wolves to the apparatus, in some experimental trials both wolves were standing within 250 cm (area 1) of the apparatus when the food was placed on the platforms, in others only one did or none of the wolves. In the last two cases the wolves were anywhere in the enclosure at least more than 250 cm apart from the apparatus. For further analysis, only trials were considered when both wolves were in area 1 at the beginning of the experiment (Tab.1). Thus, the wolves had the same opportunity to see the food placed on the platforms and to start pulling the ropes approximately the same time.

Table 1. Number of trials in the different conditions. Total trials showed the numbers of performed trials irrespectively whether both, one or none of the wolves were at the apparatus (within area 1) at the beginning of a trial. Analysed trials showed the number of trials both wolves were within area 1 at the beginning of the trial and which were used for further analysis.

Condition	Total trials	Analysed trials
Connected both sides baited (CBB)	691	487
Connected one side baited (COB)	132	127
Disconnected both sides baited (DBB)	221	84
Disconnected one side baited (DOB)	70	24
Means-end condition (ME)	20	8

SPSS (version 11.0) was used for statistical analysis. Based on the Observer data the median and the first and third quartile of the latency to pull and the time they needed from the first pull until they took the food were calculated and presented in the results (median (first quartile; third quartile). Because of the low sample size and the not normally distributed data the Wilcoxon Signed Ranks Test was used to

compare the first and second half of the trials of each wolf and the Mann-Whitney U-Test was used for comparison between two wolves.

4 Results

4.1 Behavioural observations

The behavioural observations before the apparatus was installed showed that the white wolf was dominant over the black. In total, 66 focal animal samples for White, 67 focal animal samples for Black and 65 focal animal samples for Grey were collected. Additionally 51 instantaneous samples were collected of each wolf, amounting to a total of 65 hours of observation.

All 15 dominant approaches observed were from the white towards the black wolf. Black reacted in 8 cases with a crouched position (the wolf lowered its head and body, often tucking its tail between the legs) in 6 cases with a passive submission (the wolf laid on its back showing its belly with its tail between its legs and the ears were directing backwards, close to the head) and once did not show any change in his body posture.

4.2 Experiments

4.2.1 Cooperative and individual tasks with both platforms baited (CBB)

In 90.7% of the CBB trials, White pulled first on the right side e.g. showing a strong side preference. Accordingly, Black pulled the first time on the left side in 91.32% of these trials. In the disconnected both sides baited (DBB) trials, the same side preference was found with White pulling firstly on the right side in 96.43% of the trials and Black in 92.86% on the left side.

In the disconnected condition, a wolf could solve the problem by pulling the rope without assistance. Thus all trials were successful. In the CBB condition, however, the wolves needed to pull together (Fig.12). They did so from the first trial on, and succeeded in almost all CBB trials 99.38%.

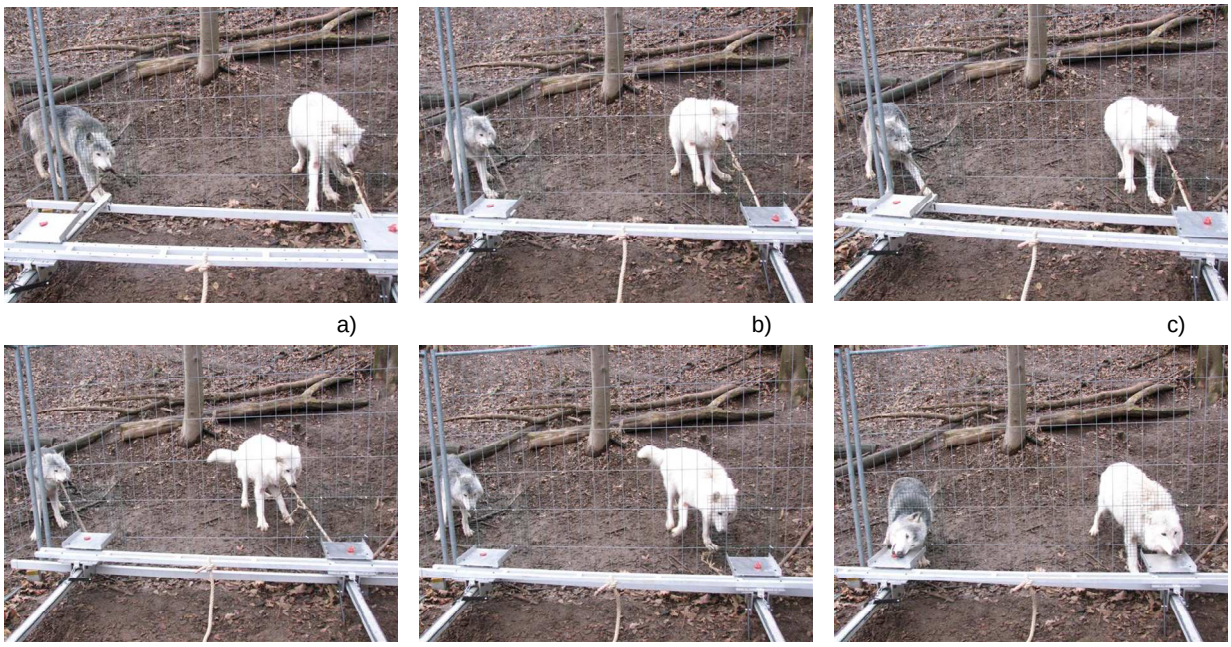


Figure 12. Black and White pulling together in the connected both sides baited task to move the platforms forward (a - d). Then the wolves released the rope (e) and took the food from the platforms (f).

In 70.87% of the CBB trials, the dominant White started pulling and then Black joined in, in 21.90% Black started and White joined and in 7.23% White and Black started pulling at the same time. The time difference between the first pull of the white and the first pull of the black wolf (see points A and B on Fig.10b) decreased over time from 1.7 (0.7; 3.3) seconds in the first half of the CBB trials (N=242) to 0.8 (0.4; 1.6) seconds in the second half of the CBB trials (N=242) (Wilcoxon Signed Ranks Test, N=242, z=-5.851, p<0.001; Fig.13).

In the DBB condition the wolves could retrieve the platform on their own and did not need to synchronize their behaviour in order to get the reward (Fig.10a). Accordingly, the time lags between the white and the black first pulls did not change significantly from the first (N=38) and to the second half (N=38) of these trials (Wilcoxon Signed Ranks Test, N=38, z=-1.509, p=0.131). The median time difference in the DBB trials was 1 (0.5; 1.8) second.

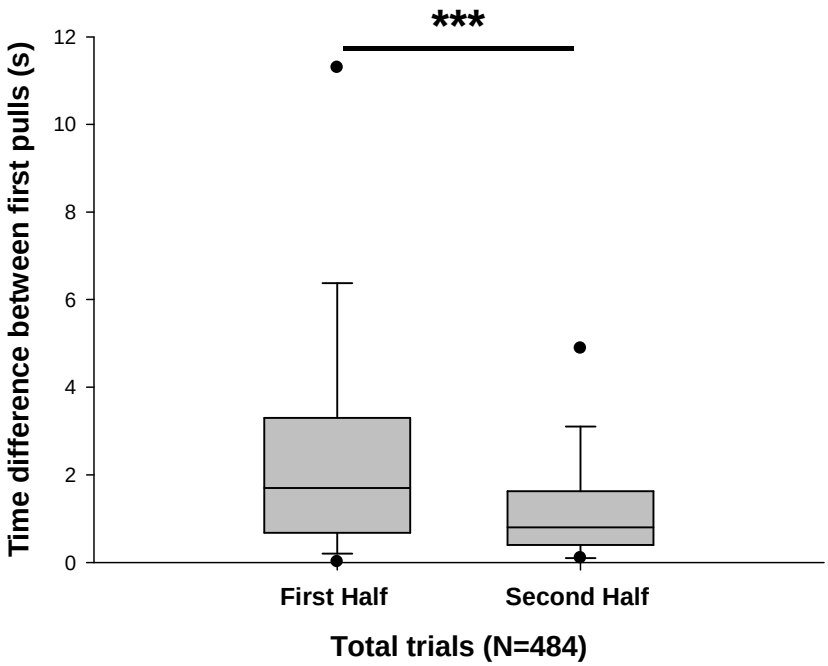


Figure 13. Time difference between the first pull of the white and the first pull of the black wolf in the first and second half of the CBB trials. Wilcoxon Signed Ranks Test *** P<0.001

Furthermore, the time the wolves needed to solve the task from their first pull until they reached the reward was calculated and compared between the first and second half of all trials. In the DBB condition (Fig.10a), there was no difference for either of the wolves between the first and second half of the trials (Black: Wilcoxon Signed Ranks Test, N=27, z=-1.423, p=0.155; White: Wilcoxon Signed Ranks Test, N=27, z=-1.803, p=0.071), suggesting that they did not refine their pulling over time. Furthermore, there was no significant difference between the two wolves. Across all trials (N=55) White needed a median of 2.96 (2.52; 3.8) seconds and Black needed a median of 3.24 (2.92; 3.56) seconds to solve the task individually (Mann-Whitney U Test, N=55, z=-1.669, p=0.095).

To describe the wolves' efficiency in the CBB condition, we calculated the time when the second wolf joined the first one in pulling until the food was reached (Fig.10b). The first and second half of the CBB trials (N=435) were compared, finding that in the second half of these trials they needed less time (3.8 (3.2; 4.73) seconds) than in the first half of the trials (4 (3.4; 5.4) seconds; Wilcoxon Signed Ranks Test, N=217, z=-2.346, p=0.019) suggesting that the wolves became faster in solving the task together (Fig.14).

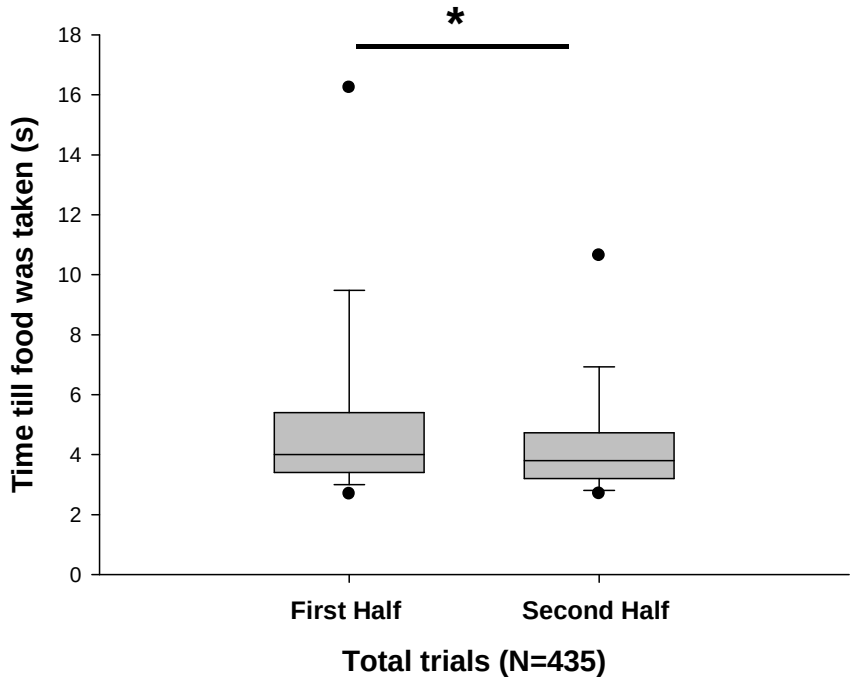


Figure 14. Time the two wolves needed in the CBB trials to reach the reward after they started to pull together. Wilcoxon Signed Ranks Test * P<0.05.

4.2.2 Cooperative and individual task with one platform baited

If food was placed on both platforms, the wolves pulled at least once in 97.76 ± 1.33 (mean + SEM) % of the trials, irrespectively whether the platforms were connected or disconnected. If only one platform was baited, White's performance remained similar. He pulled in all one-side baited trials (COB: N=127, DOB: N=24) at least once, independent of whether the platforms were connected or disconnected. Furthermore, White pulled more often on the right side in the COB (83.46%) as well as in the DOB (83.34%) condition than on the left side (COB: 16.53%, DOB: 16.67%). Black, however, pulled less often if only one platform was baited compared to the both sides baited conditions. He pulled in only 77.95% (72.44% on the left side, 5.52% on the right side) of the connected trials, and even less often (45.83%, all of them on the left side) in the disconnected trials.

COB trials in which a wolf stood and pulled on the baited side were compared to COB trials in which the wolf stood and pulled on the unbaited side. Both wolves started pulling later when being on the unbaited side: Black: unbaited side: 4.24 (3.36; 14.60) seconds; baited side: 2.52 (1.96; 3.20) seconds (Wilcoxon Signed Ranks Test N=31, z=-3.919, p<0.001); White: unbaited side: 2.92 (2.12; 4.12)

seconds; baited side: 1.52 (1.28; 1.80) seconds (Wilcoxon Signed Ranks Test N=35, z=- 4.357, p<0.001); These data suggest that the wolves noticed before pulling whether or not a particular platform was baited or not.

Furthermore, compared to the high success rate in the CBB trials (99.38%), success rate of the wolves decreased when only one platform was baited (64.57% of the COB trials). To investigate, whether the number of successful trials in the COB condition remained stable over time, the COB trials were divided in four parts and calculated the percentage of successful trials for each quarter. In the first 31 COB trials, the wolves solved 87% of the trials, but there was a sharp drop in the success rate from the second to the third quarter of the COB trials (from 75% to 47%). In the final quarter of the experiment the success rate remained similarly low (50% of the last 32 trials; Fig.15). This suggests that something might have influenced their cooperative behaviour. Because of the fact that only one wolf could get the reward the amount of food each wolf got over this part of the experiment was calculated as a possible factor of their decrease in success rate.

Overall, White obtained most of the food. At the beginning (1. quarter), the difference in food acquisition between Black and White was 10%, but already in the second quarter White got the reward in most of the trials (71.88%). Thereafter, in the third quarter, the success rate dropped altogether and Black again got the reward more often (9.38%) than in the second quarter (3.13%). In the last quarter, the general success rate remained at 50% and Black got the rewards in 18.75% of the trials. Hence, there was some balance with respect which wolf obtained the reward at the beginning and at the end, but not in between, pointing at some dynamics of the interactions and motivational states of the wolves.

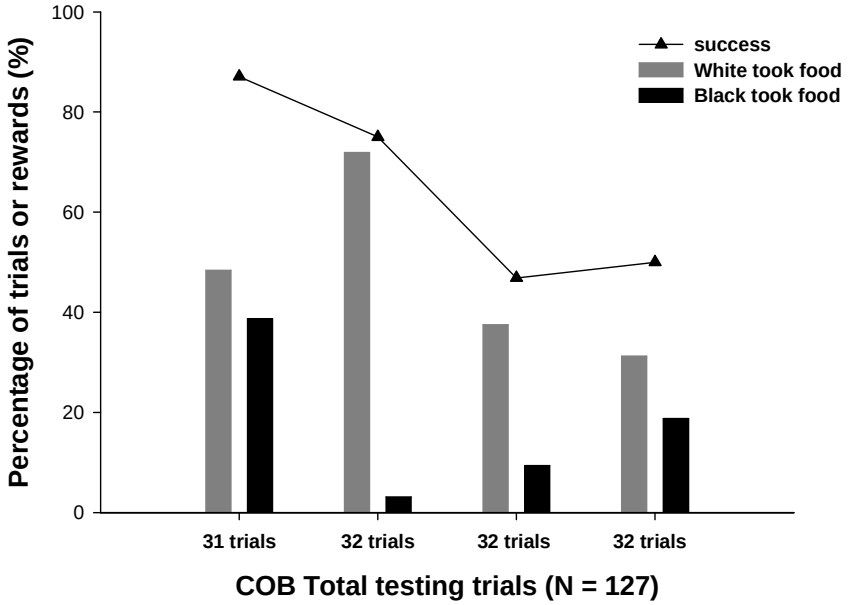


Figure 15. Percentage of trials solved and percentage of rewards received per individual in the COB condition over time. The bars show the percentage of trials either the white wolf (grey bars) or the black wolf (black bars) got the single piece of reward. The line shows the percentage of the solved trials.

As mentioned above, in comparison to the connected condition Black pulled less often in the disconnected condition. This difference already appeared in the first five trials: in the COB condition both wolves pulled together and solved the task successfully, while in the DOB condition in which only one wolf had to pull to reach the reward, they pulled together three times and twice Black stopped pulling together with White. If Black did not pull the unbaited side in the DOB condition but pulled on the unbaited side in the COB condition it would have shown that Black might have understood when he was needed to solve the task and when he was not.

To investigate whether the wolves or at least Black perceived that in the COB task, but not in the DOB task cooperation was necessary following analysis was done.
The percentage of trials was calculated a wolf pulled on the baited side in the COB and DOB condition (Fig.16). In addition, the percentage of trials the second wolf pulled on the unbaited side was calculated. Black pulled in 33.07% of the COB trials (N=127) on the unbaited side when White pulled on the baited side. However, in the disconnected one side baited condition (N=24), Black pulled only once (4.17%) on the unbaited side when White pulled on the baited side. White pulled in

36.22% of the trials on the unbaited side when Black pulled on the baited side in the connected condition (N=127). In the disconnected condition, White always pulled the unbaited side when Black pulled the baited side (Fig.16). This analysis showed that Black did not pull on the empty side when White pulled the baited side in the disconnected condition but showed more readiness to pull on the unbaited side when White could not solve the problem on his own in the connected trials. The behaviour of Black suggests that he understood the necessity of cooperation in the connected task or even the function of the apparatus. White, on the other hand, did not seem to understand the difference between the two experimental conditions – he also pulled in the disconnected condition when it was not necessary to solve the problem. Or he understood and pulled anyway because he had formed a powerful routine.

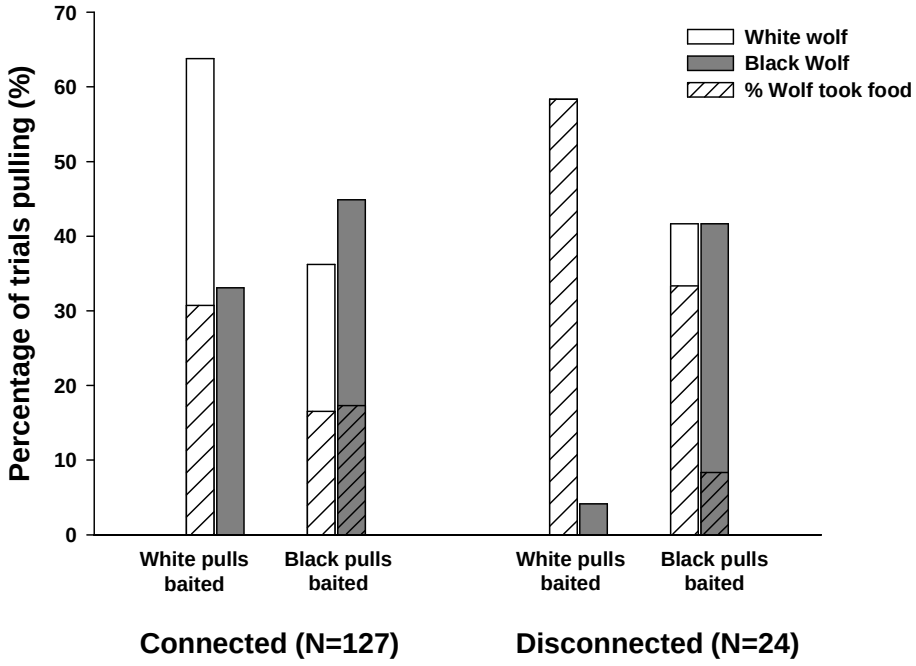


Figure 16. Percentage of the trials the wolves pulled on either the baited or unbaited side in the connected and disconnected condition when one side was baited with food. When White pulled the baited side the percentage of trials Black pulled on the unbaited side was shown by the second bar. White bars stand for the white wolf and the grey bars for the black wolf. The striped area marked the percentage of the trials in which the wolf got the reward.

Alternatively, one could argue that the food was longer present in the connected than in the disconnected condition since in the disconnected trials the platform moved immediately forward as soon as White pulled the rope in contrast to the

connected trials where White could not reach the food alone and thus the food stayed in place. That is, in the disconnected trials, Black might not have pulled simply because the food, and with this his motivation, had disappeared before he started to pull. To check whether this could explain the observed behaviour, we examined whether the time White needed in the DOB trials to get the food was shorter than the time Black needed in the COB trials to start pulling after White's first pull. For this analysis we used only the trials in which Black stood at, and pulled the rope on the unbaited side. The results showed that Black started pulling earlier (1.92 (1.44; 3.36) seconds) in the COB trials than White managed to reach the food (3.00 (2.60; 3.08) seconds) in the DOB trials (Mann-Whitney U- Test, N=15, z=-2.386, p=0.016) suggesting that this alternative that the food was longer present in the connected condition could not explain the behaviour of the black wolf.

4.2.3 Amount of food per wolf in the one side baited conditions

The wolves had a side preference with White preferring the right side and Black the left side. If White and Black would have always performed the task on their preferred side, the number of trials each wolf pulled the baited side should have been the same and accordingly the amount of food each wolf got should have been equal. However, as mentioned above White got most of the rewards even though in the successful COB trials the percentage of trials either White or Black pulled on the baited side was similar (Black: 33.86%; White: 30.71%). If White pulled on the baited side (63.78%) in the COB condition, he got the food in all successful trials (Fig.16). However, in the successful trials in which Black pulled on the baited side (33.86%) Black did not necessarily get the food (only in 17.32%). In 16.54%, White replaced him and took the food (Fig.17). In the disconnected condition it was similar. Black never got the food when White pulled the baited side but when Black pulled the baited side White got the food in 33.33% of trials and Black got the food only in 8.33% of the trials. These findings showed that food sharing in the sense that over time both partners receive the same amount of food did not occur. White always took the food when it pulled on the baited side.

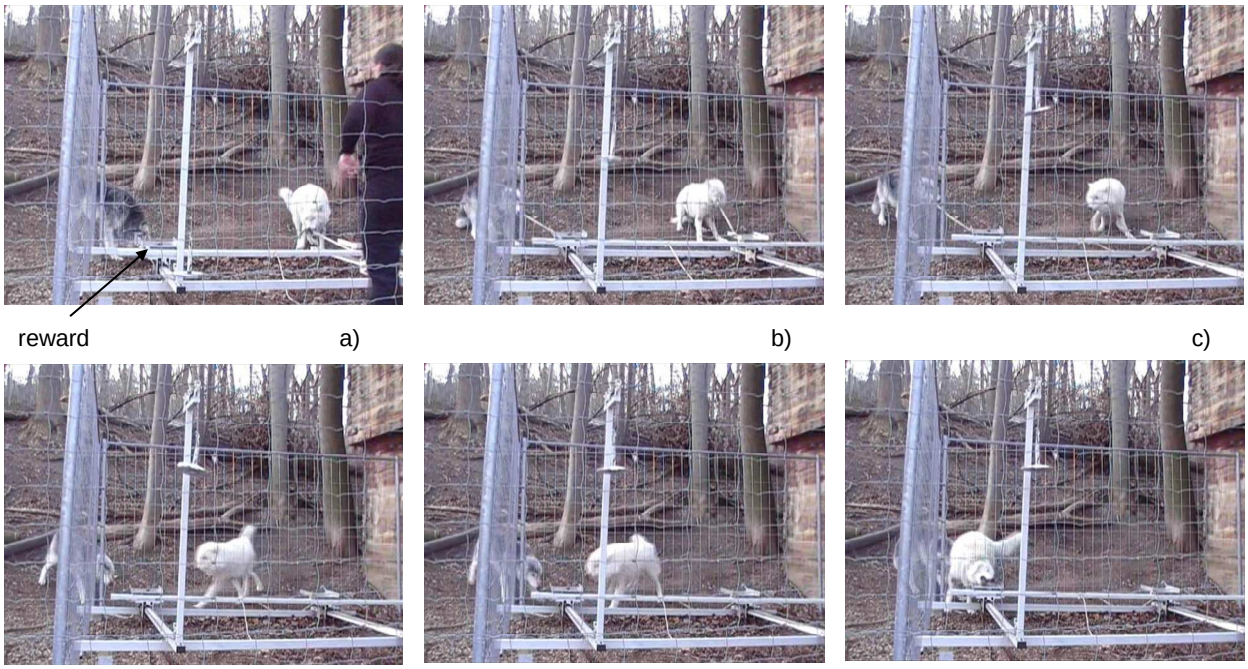


Figure 17. A trial in the connected one side baited condition. The arrow shows the position of the reward. Black was pulling on the baited side and White on the unbaited side (a-b). After pulling the platforms forward White immediately released the rope and swiftly moved to the baited side (c-e). White stretched its head through the hole to receive the reward (f).

4.2.4 Cooperative task but only one wolf present

The free access of the wolves to the apparatus led to different situations at the beginning of a trial. So far, we have analyzed only those trials where both animals were present at the beginning. However, to investigate whether the wolves were attentive towards the presence of the partner (within area 1) or not, we compared the latency until a wolf pulled for the first time when it was alone at the apparatus with the latency until the first pull when both wolves were at the apparatus at the beginning of the trial. The analyses were restricted to the CBB trials to ensure that the varied amount of food in the COB condition would not influence the behaviour of the wolves. Moreover, only trials were compared from the same day. Wolves started pulling later when they were alone at the apparatus than when they were together at the apparatus at the beginning of the trial. White started pulling after 2.24 (1.61; 3.42) seconds when he was together with Black at the apparatus and after 2.84 (2.11; 4.60) seconds when he was alone (Wilcoxon Signed Ranks Test, N=70, z=-3.097, p=0.002). Black needed twice as long to start pulling when he was alone at the apparatus (6.52 (4.08; 12.88) seconds) than when he was to-

gether with White (3.60 (2.60; 6.90) seconds) (Wilcoxon Signed Ranks Test, N=61, z=- 3.953, p<0.001) (Fig.18).

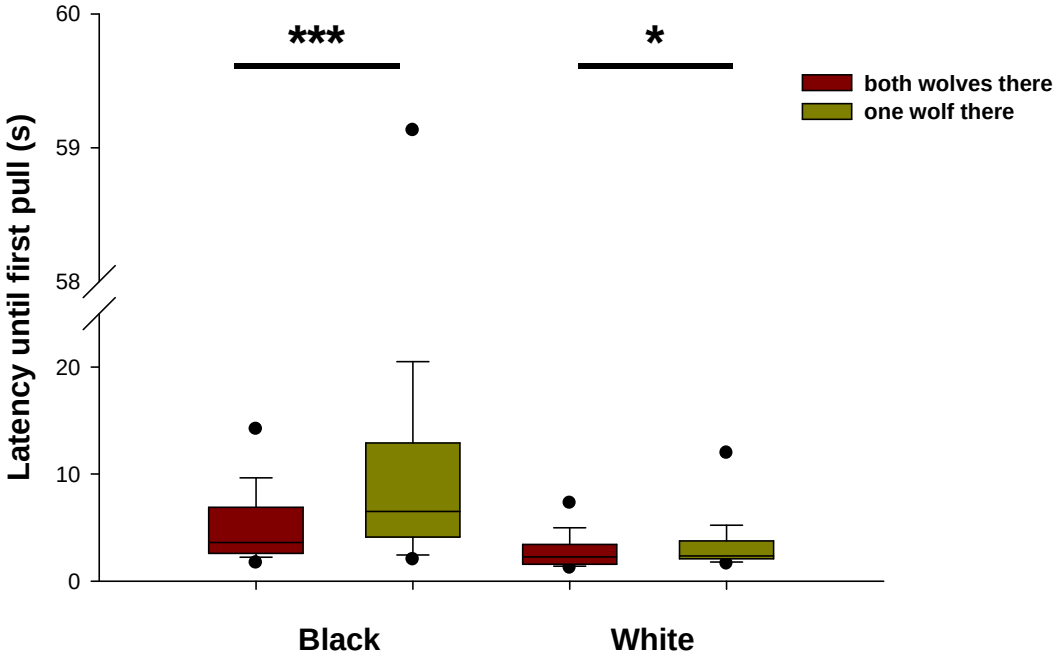


Figure 18. Latency of the first pull in the CBB trials when either one wolf was at the apparatus or both were at the apparatus at the beginning of the trial. Wilcoxon Signed Ranks Test * P<0.05; *** P<0.001

4.3 Means-end understanding

In the means-end understanding condition the rope was fixed to the unbaited platform and the platforms were not connected. Thus, pulling the rope could not lead to getting the food. When both animals were within area 1 at the beginning of the trial, White pulled six of eight trials and Black pulled once. When only White was at the apparatus, he pulled in eight of twelve trials. This parallels previous results that White is more prone to pull independent of outcome relative to black. To see whether White perceived on which side the food was we had a look to which side White went first. He indeed, went in all twelve trials first to the baited side where no rope was present before he went to the unbaited side (in 11 trials) where a rope was present and pulled the rope eight times. That might have shown that White knew from the other conditions that pulling on the baited side led to reach the reward, but may not have understood the connectivity.

4.4 Interaction

4.4.1 Agonistic behaviour

Dominant approaches were only directed from White to Black. To find out whether the high success rate in the cooperative tests was based on the voluntary participation of the wolves or rather because Black was forced by White to start pulling, the numbers of trials were calculated in which White dominated Black before Black pulled the first time or in trials Black never pulled. White dominated Black in 7.5% of the cooperative trials (N=614) whereas it was more often the case in the COB task (11.02%) than in the CBB task (6.57%). The trials in the CBB task (N=32) were solved successfully whereas in the COB task 9 of 14 trials were not solved. In all these COB trials (N=14) White displaced Black through the dominant approach from the baited side and not to force him to pull on a rope.

4.4.2 Interactions far away of the apparatus

As mentioned above the wolves could move freely in the enclosure and could leave area 1 during a trial. Whether the wolves left area 1 to recruit another one to participate when this one was apart from the apparatus out of area 1, the number of trials the wolves interacted with each other during a trial were calculated. During an interaction the wolves greeted each other by standing next to each other and rubbed on each other on the side, smelled at each other and put one's heads together. From all the cooperative trials (N=723), those 162 trials were analyzed in which the wolves left area 1 at least once during a trial. The wolves interacted in 18.52% of these trials with each other and solved 10 of these 30 trials within 4 minutes after the interaction. This hints at the possibility that through social interactions the wolves came together back to the apparatus to solve the task.

5 Discussion

This study showed that the wolves cooperated with each other to solve the task irrespectively whether both or only one wolf got the reward, although they cooperated slightly less in the one-side baited condition. Furthermore, they synchronized their behaviour in order to start pulling together and cooperated quicker over time. Moreover, both wolves started pulling later when the partner was absent (out of area 1) compared to the trials when they were together at the apparatus (within area 1). In the connected and one side baited (COB) condition Black pulled less often than in the connected and both sides baited (CBB) condition. In the disconnected and one side baited (DOB) condition White always pulled, even on the unbaited side, which was not necessary to solve the task. Black never did so if the platforms were disconnected, but he pulled the unbaited side in cooperation (COB) trials. Therefore Black might have recognized when it was necessary to pull with White to solve the task. In the COB and DOB conditions White mostly received the food even when he pulled on the unbaited side.

5.1 Did the wolves cooperate?

According to our definition (see section 2.1) two of the three wolves cooperated: they voluntarily acted together and therefore produced a situation that benefited one or both of them, in the both sides baited and in the one side baited tasks, respectively. In the cooperative trials this end situation of pulling the platforms within reach could not be achieved alone. The successful cooperation of these two wolves probably reflects the tolerant relationship between them. Several studies have shown that animals work with lower success with less tolerated individuals than with highly tolerated individuals (Melis et al. 2006b; Mendres and De Waal 2000; Petit et al. 1992).

The wolves solved the cooperative task (CBB) right from the start with a high success rate and did so without any training as it was found in capuchins (Cronin et al. 2005) chimpanzees (Melis et al. 2006b), rooks (Seed et al. 2008) and hyenas (Drea and Frank 2003). Of course the wolves might have learned in the training that if there was a rope – then pull on it. For this the wolves always should have

pulled even in the condition when only one reward was presented and irrespectively whether the partner was present or not. Therefore we analysed whether the wolves continued cooperation when only one reward was presented and whether they paid attention at the other one and whether they synchronized their behaviour.

In the connected one side baited (COB) condition the wolves continued to cooperate but were less successful than in the mutual rewarded cooperative task (CBB). Similar results were found in a lot of primate studies (Cronin and Snowdon 2008; de Waal and Berger 2000; de Waal and Davis 2003). That might have shown that the wolves perceived that pulling together was needed to solve the task successfully. The unequal presentation of only one reward might have allowed them to understand whether they would get rewarded after a trial or whether they would get nothing, which may have affected the success rate was less when food was presented only on one side.

5.2 Did the wolves take their partner into account?

5.2.1 Synchronization of the behaviour

From field it is known that synchronization during a hunt increases the chance of success (Creel and Creel 1995). In cooperative problem-solving experiments it was further shown that a high degree of synchronisation led to success (in primates e.g. Melis et al. 2006a, Melis et al. 2006b, Hirata and Fuwa 2007; rooks Seed et al. 2008). Especially in these studies the animals had to pull the two ends simultaneously to move the platform because if they only pulled on one side, the rope got unthreaded and they could not reach the reward anymore. Therefore, the animals had to be attentive towards the others behaviour. Mendres and De Waal (2000) found out that if pulling together was necessary the capuchin more often glanced at the partner than when it could pull it alone. However, a study on rats (Schuster 2002) showed, that coordination can be based either on social interactions or on non-social cues. In this study the rats were tested either individually or paired with or without a non-social light cue. The rats had to coordinate their movements to receive a reward. The results showed that if a non-social cue, a

light, was given, the rats coordinated their behaviour individually as fast as if tested in the paired condition with the light cue. However, when they were tested without the non-social light cue they coordinated their behaviour faster when they were tested paired then when they were tested individually and social interaction was not possible. Thus, in this study the non-social cue a light was the dominant stimulus that controlled coordination and not the presence of the partner. Although without the light cue the presence of a second actor was important to improve coordination (Schuster 2002).

In our study, the wolves could solve the task if the two of them pulled alternately without synchronizing their behaviour. When the wolves pulled the platforms forward by pulling alternately the platform got stuck after each pull. When both wolves pulled at the same time on the ropes then the platforms moved consistently forward and therefore pulling was easier. Nevertheless, the wolves did synchronize and coordinate their behaviour. The time difference between the first pulls of the two wolves decreased so that they started pulling more synchronized. Additionally, they solved the cooperative task faster over time as it was shown in Orang-utans (Chalmeau et al. 1997).

With the rat study in mind, one could assume that the wolves coordinated their behaviour based on the consistent movement of the apparatus after simultaneously pulling the rope than by paying attention to the other wolf. To test for that, further research should be done with an opaque partitioning between the animals. In capuchin this method was useful to show that the animals showed less performance when they were tested with the visual barrier between them, than when visual contact was given. Therefore, for the capuchins it was important to see each other to synchronize their behaviour (Mendres and De Waal 2000) or at least to be motivated to perform. In our study social interaction and visual contact was possible among the wolves.

5.2.2 Need for a partner

Synchronisation with other animals could also be learned and to control for it animals were tested without the partner presented (Mendres and De Waal 2000). Some studies with primates showed that they waited until the partner was present

before starting to pull (Chalmeau 1994; Chalmeau et al. 1997; Hirata and Fuwa 2007; Melis et al. 2006a), whereas in other studies though they pulled when they were alone they did so more often in presence of the partner than in its absence (Chalmeau and Gallo 1996; Cronin et al. 2005; Mendres and De Waal 2000). The wolves also pulled when they were alone at the apparatus but did so later, as compared to trials when the partner was present in the connected both sides baited condition. Thus, they might have perceived the absence of the partner but maybe they still pulled because it was simply too difficult for them to inhibit the learned response to pull on the rope (Seed et al. 2008; Stevens and Hauser 2004).

Alternatively, the wolves may have been more variable in performance than the animals in some of the studies mentioned above. In those experiments the subjects were tested in a chamber where the second animal was either there or not (e.g. Hirata and Fuwa 2007, Melis et al. 2006b, Mendres and De Waal 2000). However, our wolves could move freely in their enclosure, and therefore, their distance to the apparatus varied e.g. the second wolf was once only 5 m away and another time 20 m, and also, they had the opportunity at any time to join the other wolf at the apparatus. This also might have also influenced the behaviour of the present wolf. More detailed analysis and further research would be needed to address this question.

5.2.3 Did the wolves recognize in which condition cooperation was needed?

When comparing the COB and DOB condition the behaviour of Black on the unbaited side suggested that Black might have also recognized when cooperation was necessary and when not. Black did not pull the unbaited side in the disconnected condition but pulled there in the connected condition when White alone could not solve the problem. Interestingly, White always pulled irrespectively whether it was necessary or not.

Black might have learnt when the platforms could be moved individually or when cooperation was needed. The apparatus looked different in the connected and in the disconnected trials, since the connecting steel was horizontally connected on the platforms in the former case while it was leaning visible for the wolves against

the visitor's house in the later case. Beyond these already conspicuous discriminative cues, after disconnecting the platforms at least one DBB trial was conducted before a DOB trial, even in the connected condition in which at least one CBB trial was before a COB trial. Thus Black might have recognized in the first both side baited trials that at the moment pulling alone was or was not possible.

If Black understood the apparatus he might have pulled motivated by reciprocity. In reciprocity animals help each other in turns (Trivers 1971). Actually, Black's decision to cooperate might be based on past interactions with White and may have been based on the expectation of future help by White (Rutte and Taborsky 2007) in this task, Black and White pulled highly successful together at the beginning of the COB condition. Then White mostly got the reward and Black less often join White. When Black then again received more often the reward he pulled again more often and the teams' success rate increased. However, it remained unclear whether White allowed Black to take the food more often and therefore Black started pulling again.

However, White pulled the unbaited side in the COB as well as in the DOB condition although in the disconnected condition it was not needed. One explanation could be that through the learnt response to pull when seeing a rope White could not restrain to pull even when no food was presented. Another explanation could be that White did not care whether the platforms were connected or not and just pulled. After all, he often got the reward even when he pulled the unbaited side irrespectively whether the platforms were connected or not.

5.3 Who got the food when only one reward was presented and did it influence their performance?

As mentioned above after a while Black pulled less often in the COB condition but as he received again more often the reward he continued pulling again more often. Both wolves were attentive to the amount of food presented and they could distinguish whether a platform was baited or not because both wolves increased the latency to start pulling on the unbaited side versus the baited side.

White pulled more often on the baited side although in the successful trials in the COB condition both wolves had more or less the same chance to get the reward by pulling the baited side. However, White got always the food if he pulled the baited side but when Black pulled the baited side and White helped Black by pulling the unbaited side White often stole the food by moving quickly to the baited side and taking the food before Black could take it. Similarly, capuchins also grabbed the reward of the partner by swiftly moving over to its side (Visalberghi et al. 2000). Hence, White behaved like a scrounger which used the behavioural investment of another individual (producer) to obtain a limited resource (Barnard and Sibly 1981). As mentioned above this behaviour of White might also have influenced the motivation of Black to pull, which caused further a decrease in success.

The reason why the reward was stolen more often in the disconnected one side bated condition than in the connected one side baited condition might be due to the fact that when White pulled the unbaited side in the disconnected condition he did not have to pull the platform forward completely. He could stop pulling earlier since there was no food anyhow and therefore increased the chance to get the food before Black got it. While in the connected condition he had to pull the platform forward completely together with Black or the food would not be accessible - for none of them. As in other studies (Chalmeau 1994; de Waal and Davis 2003) the dominant animal, in this case White, got most of the rewards. Black let White take the food without resistance - he never attacked White after White took the food from its platform.

5.4 Did the wolves have a means-end understanding?

Unfortunately, no clear conclusion could be reached concerning the wolves' means-end understanding in this task. There was no chance for the wolves to reach the reward in this task still they tried to get access to it either by searching for the rope on the baited side or pulling on the unbaited side. In trials in which White approached the baited side where no rope was offered he might have known that by pulling on the baited side he would get the reward but because of the absent of the rope he could not get the food. Therefore, he sometimes pulled later on the empty side maybe just to try something out to get the reward. This can

be explained by persistence to reach food typical in wolves' predatory behaviour. Wild living wolves have to be persistent when hunting because they test prey before they definitively hunt (Mech 1970). Frank and Frank (1985) showed experimentally that young wolves tried to solve a problem immediately and persisted until either they solved the problem or the task was ended (Frank and Frank 1985). Alternatively the pulling behaviour of White could also be explained by task-specific learning to respond to a rope by pulling. As the other results showed it seemed that White did not perceive the difference between connected and disconnected apparatus. Thus White might have just pulled because in the COB and DOB conditions, having Black pull on the baited side, he often got the reward despite of pulling on the empty side.

However, Black did not pull on the unbaited side in the DOB condition and also in the means-end condition, which could be an indication for a means-end understanding (Osthaus et al. 2005). This also can be explained by the fact described above, so that Black could distinguish between connected and disconnected condition because of the fact that the connecting steel was leaning visible against the visitor's house and therefore pulling on the unbaited side was not needed to access the reward.

5.5 Did they force each other to cooperate?

Another question was whether the animals participated voluntarily or whether one animal forced the other one to pull the rope. In the study by Chalmeau (1994) the dominant male chimpanzee forced the other individual by carrying it to the apparatus. In the study with two subadult male orang-utans one pushed the other one to the handle to pull on it (Chalmeau et al. 1997). However, in this study White rarely dominated Black and if, it was to displace Black from one side of the apparatus, especially in the COB condition from the baited side. In more than half of these trials when White dominated Black in the COB condition were not solved. Probably because if White displaced Black from the baited side Black did not join White with pulling on the unbaited side because then he could be sure that he would not get the reward and again, maybe it depended on who helped whom before.

Furthermore the observations of interactions in the upper area of the enclosure during a trial could be a kind of recruitment of the partner to help to solve the task together. But it could also be that it happened just by chance.

5.6 General Discussion

Our results show that zoo wolves, even in an old age and without special socialization by humans, can be tested with a cooperative sting-pulling task in presence of an experimenter. Our two wolves cooperated even for two small pieces of food, and continued cooperation when only one of the wolves got rewarded. Additionally it could be shown that the wolves were attentive to the amount and location of the food presented on the two platforms and also to the presence of the other wolf. Black, at least, also might have recognized in which condition he should join White to pull and even more that in the means-end condition pulling would not led to success. White mostly pulled, irrespectively whether he pulled on the baited or unbaited platform. Even in the means-end condition in which pulling would have never led to success he pulled the platform forward. This might have come from the long training period before the experiment started. It caused by the fear of Black to a cleaner from the Zoo Schönbrunn. The man came close to the enclosure to clean the path or just passed the enclosure on eight following days after the first training day with the rope. As soon as the man came near to the enclosure Black run around in a crouched posture and watched the man and Black often hid from him in a hole in the enclosure. Therefore to ensure that both wolves had the same starting conditions for the experiment of trials more days were used to test the wolves individually. For further studies it would be helpful to exclude such factors from the beginning on.

Although only two wolves could be tested, a proper study now can be much better planned. Therefore ongoing studies on wolves, like the one investigating cooperation in hyenas (Drea and Frank 2003), will probably significantly contribute to our insights in the proximate mechanism of cooperation. Further on, comparing cooperation in carnivores with that of non-human primates and contemporary hunter-gatherer groups can improve our knowledge on the evolution of cooperation of today living humans (Schaller and Lowther 1969).

6 In retrospective

I enjoyed testing the wolves, because I never was so close to wolves before, especially when Black tried to come into the experimental area at the beginning. But over time I got to know the wolves, and he also did not try it anymore.

I worked with Grey, the female, until the end of the experiment because at the beginning she took the food out of the hole. During the experiment, however, she refused to come closer than one meter. When the males were not interested to do some more tests I worked with Grey and I managed to bring her close again, and once more she took the food from the platform through the hole.

Furthermore, it was nice to observe the behaviour of the wolves. I had the impression that they liked to participate although they got just small pieces of food. Sometimes especially White was just waiting and touching the experimental enclosure fence with his foreleg between two trials similar to what dogs do when they would like to get more of something. Sometimes I observed White resting near the apparatus and as soon as Black was at the apparatus he got up and came to the apparatus too. Then Black sometimes did not pull immediately, but waited until White was there and started pulling on one side. They were only two wolves but a lot of things were going on, and it would be very interesting to do further research in this direction.

Finally I would like to say that this task was an enrichment in the zoo life of the wolves, and brought some liveliness in their enclosure. For me it seemed that the wolves became more active, especially White who had already some problems with his haunches. It was clear to see when he got up after a longer resting phase. Unfortunately two of the wolves died in June 2008, White the dominant one and Grey. She was the oldest one.

7 Supplement

7.1 Ethogram

Resting

sleeping individually - slin: the wolf lies more than 5 m away from the others and has its head down on the ground or on its foreleg and the eyes are closed

sleeping in group – slgr: The wolf lies and has its head down on the ground or on its foreleg and the eyes are closed and the other wolves are less than 5m away from the observed individual (I note who is the individual within 5m distance)

resting individually - rei: the wolf lie more than 5 m away from the others and have its head held high and looks around, the wolf sit and looks around or the wolf stand and looks around with a neutral posture

resting in group – regr: the wolf lies and has its head held high and looks around, the wolf sits and looks around or the wolf stands and looks around with a neutral posture and the other wolves are less than 5 m away from the observed individual (I note who is the individual within 5m distance)

grooming individually – gri: the wolf lies or sits down and nips or licks itself anywhere on its body

Feeding

eating – ea: to bite and swallow food items for ingestion

take food – tf: the wolf takes the food from the feeding place and goes or runs away with it and lies down with it

licking - li: the wolf licks or sniffs the food with its tongue or its nose

cache - ca: to hide or bury food items, the actor digs a hole with its front paw and places the item inside it or the actor places the food under a bush

dig up – diup: the actor digs up a food item with its front paw

regurgitate – reg: the actor retches and regurgitates the food and eats it afterwards

walk with food - wwfo: the actor has the food in its mouth and walks a few rounds inside the enclosure without avoiding an other wolf

to door – todo: the wolf walks to the door where they get their food and sniffs on the ground or on the door, or it pushs with its front paws against the door (I note whether it come at feeding time)

drinking-drnk: the wolf goes to the water hole and laps up water with the tongue

beg – beg: a wolf wants to take the food out of the mouth of an other wolf

Defecation and peeing

mark – m: the wolf urinates with its hind leg lifted up in the air mostly near or on bushes or on a tree

pee – pee: the wolf urinates with its hind leg on the ground anywhere in the enclosure not especially on an object

defecate – def: to evacuate solid waste and afterwards the hind paws are often scraped backwards on the ground

rub on ground – rog: the wolf sits on its bottom and slides forward by going forward with its front legs

Affiliative Interaction

grooming – gro: the wolf excitedly nips and licks the another wolf's mouth or neck or the wolves lie or stand calm next to each other and lick or groom the other one

greeting – gre: all three wolves stand next to each other and rub on each other on the side, smell at each other and put one's heads together

playing:

jump – ju: the actor beards down his chest with its ears drawn way back and holds its tail normal and maybe wags and jumps around an other wolf

kick – ki: the actor raises its paw and extends it toward the receiver or the actor pressed its nose or cheek against the receiver and wags its tail

chase leaves – chlv: the wolf pawing with its front paw blowing leaves or jumps at a tree

stand friendly- stfr: the wolf stand with its tail perpendicularly or above the plane of the back and wag it, its ears pointed forward, while the actor approach

ride up – ru: the wolf mount another one from behind

Agonistic interaction

Threats

displace – displ: aggressor causes opponent to move away from a resource or goal (Schenkel 1947)

attack – att: a running or jumping approach toward the receiver with its tail, ears and sometimes hackles up

stand over – stdov: aggressor stands next to an opponent and holds its head over opponent’s body, or more extremely places its forepaws on the opponent and raises its own head and chest over the body of the opponent and has its tail above and its ears erects and pointed forward

bite - bi: the wolf quickly moves forward and makes snapping movements or actually bites, possibly accompanied by showing the teeth and /or growling and/or barking

stand erect – stder: aggressor raises itself to its full height, hold its tail perpendicularly or above the plane of the back and its ears erects and pointed forward and raised its head (sometimes raised hackles)

stare – star: aggressor looks directly at opponent maintaining eye contact

flee – fl: submissive wolf walks or runs with its tail tucked and its body ducked away from the aggressor

follow – fol: to match speed and direction while following behind another usually within two or three body lengths. This often occur after an interaction

pilfer food – pilf: the actor takes the food from another wolf which ate before on them

approach – ap: actor approach with its tail perpendicularly or above the plane of the back and its ears erects and pointed forward and its head held high

muzzle bite – mb: grabbing the muzzle of another wolf with enough pressure to make the grabbed wolf whimper

jaw spar- js: two wolves “fencing” with open jaws

chase – ch: a wolf run after another wolf to catch them

Submission

crouch – cro: the wolf lowers its head and body, often tucking its tail between the legs

friendly submission - frisub: receiver lies on the back and stretches its font legs to the actor and maybe wags its tail and has its mouth open

passive submit – passub: the wolf lies on its back demonstrates its stomach and has its tail between its legs and the ears are directed backwards and lie close to the head

active submit – aktsub: submissive animal approaches aggressor, in a crouched position, with the tail tucked between the hind legs and may attempt to licks the side of the aggressor's muzzle

approach submissive – apsub: submissive animal approaches aggressor (stand erect) with its tail tucked between the hind legs, its ears directed backwards and its head lowered

Locomotion

walking – walk: the wolf goes or runs neutral around in the enclosure its tail neutral so it hangs loosely form a raised base either in a convex or concave curve and maybe the wolf looks around without an apparent goal

sniffing – sn: the wolf goes around with its nose pointed down on the ground

approach

interested – apint: the wolf goes or runs nervously forward until it reaches the goal maybe pointed its ears forward and wags its tail

fearful – apfea: the wolf goes slowly forward maybe ducked, maybe in wavy line and sometimes stops and looks directly at the object

neutral – apneut: the wolf goes in a relaxed manner forward maybe it does more or less ignore the object

reaching – rea: the wolf grasps with its front paw an object behind the fence or inside the enclosure an object under the branches

digging under fence – digfe: the wolf scrapes with its front paw the ground under the fence back, or the actor stands in front of the fence and sniffs at them

avoidance

ignore – avig: the wolf ignores the object so it has its posture in a neutral manner but it does not approach

fearful – avfea: muscles in the body are tense, the wolf keeps away from another animal or situation, usually by walking and often looks stiff at the object or goes nervous back and forth, maybe holds its tail tucked between its hind legs

attending to someone/-thing outside – attend: the wolf looks at the object outside of the enclosure and follows them with its movement

leave – le: after an interaction (affiliate or agonistic) the actor leaves the opponent with a neutral posture

Vocalisation

growl – g: a very low frequency, noisy vocalization of widely varying length

barking – ba: a short explosive outburst and coarse voice

howling: a wolf points its muzzle upward and forward, the moth open and makes a sound (half second to 11 seconds in length) with a frequency between 150 to 780 cycles per second and lasts an average of 35 seconds by a single wolf (S. 97 Mech 1970)

howling individually – hoin: the wolf howls alone

howling in group – hogr: all wolves howl at the same time

whimper – wi: a high tough soft and plaintive sound with a frequency of 760 cycles per second (S. 93 Mech 1970)

New, apparatus oriented behaviours

chew – cw: wolf bite with its molars on the rope

exploration - ex: wolf sniff lick and /or kick the apparatus

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9 References

Barnard, C. J., and R. M. Sibly. 1981. Producers and Scroungers: a general model and its application to captive flocks of house sparrows. Animal Behaviour 29:543-550.

Boesch, C. 2002. Cooperative hunting roles among taï chimpanzees. Human Nature 13:27-46.

Boesch, C., and H. Boesch. 1989. Hunting behavior of wild chimpanzees in the Taï National Park. American Journal of Physical Anthropology 78:547–573.

Boyd, R. 2006. The Puzzle of Human Sociality. Science 314:1555-1556.

Brosnan, S., and F. de Waal. 2002. A proximate perspective on reciprocal altruism. Human Nature 13:129-152.

Chalmeau, R. 1994. Do Chimpanzees cooperate in a learning-task. Primates 35:385-392.

Chalmeau, R., and A. Gallo. 1996. What chimpanzees (*Pan troglodytes*) learn in a cooperative task. Primates 37:39-47.

Chalmeau, R., K. Lardeux, P. Brandibas, and A. Gallo. 1997. Cooperative problem solving by orangutans (*Pongo pygmaeus*). International Journal of Primatology 18:23-32

Creel, S., and N. M. Creel. 1995. Communal hunting and pack size in African wild dogs, *Lycaon pictus*. Animal Behaviour 50:1325-1339

Cronin, K. A., A. V. Kurian, and C. T. Snowdon. 2005. Cooperative problem solving in a cooperatively breeding primate (*Saguinus oedipus*). Animal Behaviour 69:133-142.

Cronin, K. A., and C. T. Snowdon. 2008. The effects of unequal reward distributions on cooperative problem solving by cottontop tamarins, *Saguinus oedipus*. Animal Behaviour 75:245-257.

de Waal, F. B. M. 1989. Food sharing and reciprocal obligations among chimpanzees. Journal of Human Evolution 18:433-459.

de Waal, F. B. M., and M. L. Berger. 2000. Payment for labour in monkeys. Nature 404:563-563.

de Waal, F. B. M., and J. M. Davis. 2003. Capuchin cognitive ecology: cooperation based on projected returns. Neuropsychologia 41:221-228.

Drea, C. M., and L. G. Frank. 2003. The Social Complexity of Spotted Hyenas *in* F. B. M. De Waal, and P. L. Tyack, eds. Animal Social Complexity: Intelligence, Culture and Individualized Societies.

Dugatkin, L. A. 1997. Cooperation Among Animals. An Evolutionary Perspective. Oxford: Oxford University Press.

Frank, H., and M. G. Frank. 1985. Comparative Manipulation-Test Performance in Ten-Week-Old Wolves (*Canis lupus*) and Alaskan Malamutes (*Canis familiaris*): A Piagetian Interpretation. Journal of Comparative Psychology 99:266-274.

Goodmann, P. A., K. Erich, and J. Willard. 2002, Wolf Ethogram, Eckhard H. Hess Institute of Ethology.

Hall, R. L., and H. S. Sharp. 1978, Wolf and Man: Evolution in parallel, Academic Press, INC.

Hauser, M. D., J. Karalik, and C. Botto-Mahan. 1999. Problem solving and functional design features: experiments on cotton-top tamarins, *Saguinus oedipus oedipus*. Animal Behaviour 57:565-582.

Hirata, S., and K. Fuwa. 2007. Chimpanzees (*Pan troglodytes*) learn to act with other individuals in a cooperative task Primates 48:13-21

Mech, L. D. 1970, The wolf: The ecology and behaviour of an endangered species., New York: Natural History.

—. 1995. Summer movements and behavior of an arctic wolf, *Canis lupus*, pack without pups. Canadian Field Nat. 109:473-475.

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

Melis, A., B. Hare, and M. Tomasello. 2006a. Chimpanzees Recruit the Best Collaborators. Science 331:1297-1300.

—. 2006b. Engineering cooperation in chimpanzees: tolerance constraints on cooperation. Animal Behaviour 72:275-286.

Mendres, K. A., and F. B. M. De Waal. 2000. Capuchins do cooperate: The advantage of an intuitive task. Animal Behaviour 60:523-529

Miklósi, A., E. Kubinyi, J. Topál, M. Gácsi, Z. Virányi, and V. Csányi. 2003. A simple reason for a big difference: wolves do not look back at humans but dogs do. Current Biology 13:763-766.

Noë, R. 2006. Cooperation experiments: coordination through communication versus acting apart together. Animal Behaviour 71:1-18.

Nowak, M. A. 2006. Five Rules for the Evolution of Cooperation. Science 314:1560-1563.

Osthaus, B., S. E. G. Lea, and A. M. Slater. 2005. Dogs (*Canis lupus familiaris*) fail to show understanding of means-end connections in a string-pulling task Animal Cognition 8:37-47.

Packard, J. M. 2003. Wolf Behavior: Reproductive, Social and Intelligent, Pages 35-65 *in* L. D. Mech, and L. Boitani, eds. Wolves: Behavior, Ecology and Conservation, The University of Chicago Press.

Packer, C., and L. Ruttan. 1988. Evolution of cooperative hunting The American Naturalist 132:159-198.

Petit, O., C. Desportes, and B. Thierry. 1992. Differential Probability of "Coproduction" in Two Species of Macaque (*Macaca tonkeana, M. mulatta)*. Ethology 90:107-120.

Povinelli, D. J. 2003. Folk Physics for apes. Oxford University Press.

Rutte, C., and M. Taborsky. 2007. Generalized Reciprocity in Rats. PLoS Biology 5:1421-1425.

Schaller, G. B., and G. R. Lowther. 1969. The relevance of carnivore behavior to the study of early hominids. Southwestern Journal of Anthropology 25:307-341.

Schenkel, R. 1947. Ausdrucks-Studien an Wölfen. Behaviour 1:81-129.

Schleidt, W. M., and M. D. Shalter. 2003. Co-evolution of Humans and Canids. Evolution and Cognition 9:57-72.

Schmidt, P. A., and L. D. Mech. 1997. Wolf pack size and food acquisition. The American Naturalist 150:513-517.

Schuster, R. 2002. Cooperative coordination as a social behavior. Human Nature 13:47-83.

Seed, A. M., N. S. Clayton, and N. J. Emery. 2008. Cooperative problem solving in rooks (*Corvus frugilegus*). Proceedings of the Royal Society B: Biological Sciences 275:1421-1429.

Stander, P. E. 1992. Cooperative hunting in lions: the role of the individual Behavioral Ecology & Sociobiology 29:445-454

Stephen, L. E. G., K. Goto, and B. Osthaus. 2006. The logic of the stimulus. Animal Cognition 9:247-256.

Stevens, J. R., and M. D. Hauser. 2004. Why be nice? Psychological constraints on the evolution of cooperation. Trends in Cognitive Sciences 8:60-65.

Trivers, R. L. 1971. The evolution of reciprocal Altruism. The Quarterly Review of Biology 46:35-57.

Trokowicz, L. 1980. Tropienie wilków w dolinie Biebrzy. Przeglad Zoologiczny 24:137-145.

Visalberghi, E. A. B., B. P. A. Quarantotti, and F. A. Tranchida. 2000. Solving a cooperation task without taking into account the partner's behavior: The case of capuchin monkeys (*Cebus apella*). Journal of Comparative Psychology 114:297-301.

Werdenich, D., and L. Huber. 2002. Social factors determine cooperation in marmosets. Animal Behaviour 64:771-781.

Wilkinson, G. S. 1984. Reciprocal food sharing in the vampire bat. Nature 308:181-184.

Curriculum Vitae

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Personal Data:

Born:	06. May 1982; Ried im Innkreis
Nationality:	Austria

Education:

1988-1996	Primary school in Ampflwang
1996-2001	Colleges for agriculture and the food and fodder industry, Elmberg, Linz
Since Oct. 2001	University Vienna, Biology, Zoology

Practical courses:

Summer Semester 2005	The social system of the Timber wolves (*Canis lupus ssp.*) in the Zoo Schönbrunn, Vienna
Winter Semester 2005	Spectral perception in *Cupiennius salei*
Winter Semester 2005	Interaction in crows and squirrels during caching
Winter Semester 2006	Influence of concentration of testosterone in the egg on the behaviour of the chicks (*Gallus gallus domesticus*)

Working experience:

July 2000	Voluntary work as a veterinarian-assistant
Summer 2002-2007	Working assistant at the horse ranch (Pferdehof "Koaser-Minerl", Ampflwang)
Since November 2005	Assistance in looking after seminar groups at the PHYSIO Centrum, Vienna
September 2007 to March 2008	Teaching assistant in an after-school care centre
Since May 2008	Assistance in hand raising timber wolves (*Canis lupus)* and training them in Grünau at the Wolf Science Center, Austria

IT Skills:

Microsoft Office (Word, Excel, PowerPoint), SPSS, Sigma Plot, Endnote, The Observer…

Contributions to Meetings:

Möslinger, H., Range, F., Viranyi, Zs. & Kotrschal, K. (2008) Cooperative string-pulling among wolves. Poster presented at the Canine Science Forum 2008 in Budapest, Hungary