

# MASTERARBEIT

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“Tolerance predicts raven cooperation in a loose-string  
paradigm”

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## **1. Zusammenfassung**

Kooperatives Verhalten gilt als äußerst wichtiges Merkmal von sozial lebenden Arten. Zahlreiche Studien zum Thema Kooperation legen hierbei ihren Focus vor allem auf evolutionäre Gesichtspunkte. Diese beschreiben häufig einen möglichen Einfluss kooperativen Verhaltens auf die Evolution menschlicher Kultur, als auch auf die Ausbildung einer Reihe höherer kognitiver Fähigkeiten. Betrachtet man jedoch experimentelle Untersuchungen von kooperativen Problemlösungen, so sind die kognitiven Grundlagen umstritten; außerdem wurden die meisten Tests vorwiegend an Menschen und anderen Primaten durchgeführt. In den letzten Jahren häuften sich Hinweise, dass vor allem Rabenvögel kognitive Fähigkeiten entwickeln konnten, welche denen von Primatenarten äußerst ähnlich sind. Diese könnten es ihnen erlauben, ihr Verhalten in dem Maß mit anderen Individuen zu koordinieren, dass für beide Parteien ein nützliches Resultat entsteht. Desweiteren wird davon ausgegangen, dass unterschiedliche Toleranzschwellen gegenüber anderen Individuen, sowie ein bestimmtes Maß an positiven Beziehungen als Randbedingung zur Lösung kooperativer Aufgaben existieren können. Aus diesem Grund haben wir entschieden eine Studie zu diesem Thema durchzuführen. In unserem Experiment testeten wir Kolkraben (*Corvus corax*) im sogenannten Loose-string Paradigma, um zum Einen herauszufinden, ob Raben fähig sind ihre Handlungen mit anderen Individuen zu synchronisieren bzw. in Folge dessen zu kooperieren und des Weiteren um gleichzeitig zu überprüfen, ob sie die Bedeutung des Partners verstehen. Dafür haben wir die Raben in der gesamten Gruppe und innerhalb aller Dyaden getestet. Zusätzlich haben wir einen sogenannten Verzögerungs-Test und einen Test in welchem die Tiere ohne Partner getestet wurden mit in die Versuche integriert. Mit Hilfe dieser Kontrollen konnten wir sehen, ob Raben die Notwendigkeit des Partners mit einbeziehen, indem sie entweder auf die Ankunft des Partners warten oder nicht mehr ziehen, sobald kein Partner vorhanden ist. Unsere Resultate weisen darauf hin, dass Raben ihre Handlungen mit anderen Individuen soweit synchronisieren können, sodass sie auf kooperative Weise erfolgreich eine Belohnung erhalten. Jedoch scheint es, dass sie innerhalb dieses Set-up die Wichtigkeit des anwesenden Partners nicht einbeziehen oder verstehen. Dies zeigte sich dadurch, dass Individuen auch dann gezogen haben, wenn kein Partner anwesend war und dadurch, dass sie nicht auf die Ankunft des Partners während des Verzögerungs-Tests warteten.

Desweiteren verdeutlichen unsere Ergebnisse, dass sowohl während der Gruppentests, als auch während der dyadischen Tests, Toleranz als wichtiger Faktor, den kooperativen Erfolg vorhersagt. Interessanterweise zeigte sich während der Gruppentests ausschließlich Toleranz als Einfluss nehmender Faktor, wobei die Leistung in den dyadischen Tests zusätzlich von anderen Faktoren beeinflusst wurde. Dazu gehören Verwandtschaft, Rangordnung, und Geschlechterkombination der Individuen innerhalb eines Paares. Daraus lässt sich schließen, dass Raben, wenn man ihnen die Wahl lässt, am besten mit Individuen kooperieren, zu welchen sie im Allgemeinen toleranter sind. Zwingt man sie jedoch in bestimmte Dyaden, so scheinen auch verschiedene andere Faktoren eine wichtige Rolle zu spielen und damit Einfluss auf den kooperativen Erfolg zu nehmen.

## **2. Abstract**

Cooperative behavior is a very important trait among different social species. Most studies on cooperation focus on its evolutionary origin, indicating a possible influence on both the evolution of human culture as well as on a variety of higher cognitive skills. So far, experiments focusing on cooperative problem solving abilities have revealed mixed results and were mainly carried out on humans and non-human primates. However, there are indications that corvid species might share with primates the same cognitive abilities that allow them to coordinate their actions with others to bring about a beneficial result for both acting parties. Despite this, few conclusions can be made on corvid cooperation as current knowledge is based on two studies. Therefore, we tested 9 captive ravens (*Corvus corax*) in a loose string paradigm to study whether they are able to synchronize their actions and cooperate, while in parallel testing whether they understand the need of a partner in this paradigm. We tested the ravens in a group setting and in all possible dyads to see whether they can cooperate during the task. Additionally we included a delay control phase and alone trials, to see whether they consider the need of the partner by waiting for its arrival or by refraining from pulling when tested without the partner. Our results indicate that ravens can be successful in synchronizing their actions in order to cooperatively gain a reward. However, they don't seem to understand the importance of a partner in the loose string paradigm, as they keep pulling the string when they are alone and also do not wait for the partners' arrival in delay trials. Furthermore, our results suggest that both in a group and in a dyadic setup tolerance predict cooperative success. Interestingly, tolerance was the only predictor in the group setting, whereas in the dyadic set-up cooperation was also affected by kinship, rank and the sex-combination of the dyad. This suggests that when given the choice, ravens choose to cooperate with individuals with whom they have high levels of tolerance, yet that when forced within a certain dyad, other factors also play a role in generating successful cooperation.

### **3. Introduction**

#### **3.1 What makes cooperation interesting? Definitions and underlying mechanisms**

In human societies, cooperative behavior has long been studied and described as a highly important pattern in a variety of social contexts (Rand and Nowak 2013). Moreover, cooperation has been suggested to shape, or in some cases even create, cognitive abilities in human infants (Carleton 1980). Its influence on human culture, environmental adaptations and its evolutionary origins has been in the centre of interest of cognitive research. Despite that humans' cooperative abilities seem exceptional, and given that cooperation might play such an important role in developing further cognitive skills in social groups, its evolutionary origins might best be understood by studying several animal species (Boyd 2006). As such, investigating cooperative behavior in different animal species has been an important focus of cognitive research during the last years.

In general, cooperation can be described as an interaction of at least two individuals which depends upon accurate responses of all individuals (Hake and Vukelich 1972). Including these aspects, cooperation can be defined with both the intention of an action as well as the outcome of it (Brosnan and de Waal 2002). Here, while paying attention to our study goal, we define cooperation based on the intention of an action as "... the voluntary 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 indicates that cooperation always requires at least two individuals acting closely together and, moreover, that it is based on a certain synchronization of behavioral patterns (Boesch and Boesch 1989, Boesch 2002). From an ultimate perspective, cooperation can be investigated by its evolutionary background in which it is considered to be based on kin selection, mutualism or reciprocity (Trivers 1971, Dugatkin 2002).

Following a proximate perspective, defining the cognitive abilities used in cooperative behaviors, is highly important (Brosnan and de Waal 2002). So far, it is still uncertain under which condition animal cooperation can develop and whether it needs to be based on complex cognitive abilities that require the understanding of another's intentions and the need of the partner.



Additionally, the questions about any constraining factors that are likely to influence an individual's success in solving a cooperative task and its choice on with whom to cooperate with are not yet fully answered (Nowak 2006).

### **3.2 Cooperative behavior in different animal species**

Cooperative behavior is widespread among animal species (Nowak 2006, Snowdon and Cronin 2007, Drea and Carter 2009, Heinrich 2011, Plotnik et al. 2011, Suchak et al. 2014). Especially species living in groups, which are structured by different types of social relationships, use cooperation in a variety of different ecological situations, which has been confirmed in the laboratory with experimental tasks in which they are confronted with a cooperative problem. Tested species include humans, great apes, different species of monkeys as well as wild dogs, hyenas, lions, rooks, elephants and wolves (Creel and Creel 1995, Chalmeau and Gallo 1996, Chalmeau et al. 1997b, Boesch 2002, Dugatkin 2002, de Waal and Davis 2003, Hare and Tomasello 2005a, Melis et al. 2006b, Nowak 2006, Snowdon and Cronin 2007, Hare et al. 2007, Seed et al. 2008, Drea and Carter 2009, Scheid and Noe 2010, Plotnik et al. 2011). However, field observations have also found cooperation within a variety of different social contexts in different species; i.e. cooperative hunting (Stander 1992, Creel 2001, Boesch 2002, Luhrs and Dammhahn 2010, Yosef and Yosef 2010) or breeding (Kullberg and Angerbjorn 1992, van Kesteren et al. 2013, Xu et al. 2014), territory defense (Farabaugh et al. 1992, Heinsohn and Packer 1995, Booksmythe et al. 2012) or social support within agonistic interventions (Koyama et al. 2006, Schino 2007, Schino et al. 2007a, Schino et al. 2007b, Fraser and Bugnyar 2012). Among these, group hunting may be one good example to describe cooperative behavior in the field within social contexts. With this, social carnivores, such as African wild dogs, that hunt large prey together and defend it from scavengers by showing different strategies of cooperative behavior can increase their hunting success even if a larger prey is followed (Creel and Creel 1995, Creel 2001). Additionally, the chimpanzee's cooperative hunting behavior has been well observed, in which it has been shown that group hunting requires an elaborate coordination with other members of the group (Boesch and Boesch 1989, Boesch 2002). Furthermore it has even been suggested that chimpanzees should be able to cooperate better than other primate species based on their natural ability to hunt together (Hare et al. 2007).

Unfortunately, most studies on the experimental basis of cooperation have mainly been carried out with humans and different primate species (Chalmeau et al. 1997b, Mendres and de Waal 2000, Cronin et al. 2005, Melis et al. 2006a, Hare et al. 2007, Snowdon and Cronin 2007, Rand and Nowak 2013). The first experimental evidence for cooperative problem solving in a mammal species other than primates was presented by Drea et al. in 2009. Here, spotted hyenas coordinated their behavior spontaneously and repeatedly when tested in a dyadic set up in order to reach hidden food rewards. Later, Plotnik and colleagues (2011) tested elephants on a cooperative problem solving task in a dyadic set up and were able to show that elephants can synchronize their actions in order to get a reward as well. Finally Seed et al. (2008) and Scheid and Noe (2010) found that rooks are able to coordinate their actions when tested with different partners in a cooperative task (Seed et al. 2008, Scheid and Noe 2010). To sum up, cooperative problem solving occurs in different group living mammals and birds, raising the possibility that this trait might be widespread among animal species. Therefore, the question is not only if a species can solve such problems but how much individuals differ in how well they perform in cooperative tasks. We furthermore need to ask whether all these species actually do understand the cooperative character of the task; i.e. that a partner is required. Finally we need to consider questions about other proximate factors like kinship, sex, age, rank, tolerance or affiliative relationships that might influence their performance during these experiments.

### **3.3 Cognitive and constraining factors during cooperation**

Focusing on cognitive aspects of cooperation, we need to distinguish between solving the task by associative learning (e.g. to do behavior x in situation y to achieve a reward) or by understanding the basic principle of the set up, i.e. to do behavior x together with another individual in situation y to achieve a reward. The important addition in the latter case is the understanding of the need of the partner. With this, experimental results are contradictory. It has been shown that some primate species including chimpanzees, capuchin monkeys and cottontop tamarins are able of taking the presence or absence of the partner into account by either stopping to work when the partner was absent or by waiting for the partner's arrival (Mendres and de Waal 2000, Cronin et al. 2005, Melis et al. 2006a).

In contrast, other studies on baboons, certain macaque species as well as capuchin monkeys did not find evidence for any understanding of the need of the partners (Fady 1972, Petit et al. 1992, Chalmeau et al. 1997a). Other than primates, elephants are reported to inhibit their action for up to 45 s while waiting for the arrival of their cooperation partner (Plotnik et al. 2011). In contrast, rooks and hyenas did not wait for the arrival of the partner or went on pulling when no partner was present (Seed et al. 2008, Drea and Carter 2009), suggesting that they may lack an understanding of the need of partner.

Aside from cognitive constraints, cooperative problem solving may be influenced by factors such as age, sex, kinship, temperament, rank position, tolerance levels or affiliative relationships. Only a few studies have included some of these factors into their investigations. Even though there is hardly any data on the influence of sex or age, there is some evidence that kinship and temperament might influence the likelihood of cooperation and cooperative success in chimpanzees and rooks (Langergraber et al. 2007, Scheid and Noe 2010). Related chimpanzees work together better than non-related individuals (Langergraber et al. 2007). Even though there is no direct data on the influence of temperament on cooperation of chimpanzees, it was found that personality similarities in sociability and boldness at least increase contact sit in chimpanzees and therefore can enhance friendly relationships (Massen and Koski 2014). This might increase cooperative success as well. During a cooperative task, rooks that scored high in boldness performed better compared to shy individuals and moreover did increase the success of shy individuals when paired with in a dyadic set up (Scheid and Noe 2010).

Some studies could indicate the importance of tolerance for cooperation (Werdenich and Huber 2002, de Waal and Davis 2003, Brosnan et al. 2005, Melis et al. 2006a, Hare et al. 2007, Seed et al. 2008, Scheid and Noe 2010,). Interestingly, rooks (Seed et al. 2008), chimpanzees (Melis et al. 2006a) and bonobos (Hare et al. 2007) increase their performance when within-dyadic tolerance levels were higher. Accordingly, Melis et al. (2006b) based their study with chimpanzees on the so called tolerance hypothesis that "...suggests that pairs of individuals with the highest level of interindividual tolerance will be the most successful at solving novel instrumental tasks that require joint effort".

Additionally they predicted that cooperation can also be a form of out-competing another individual that should furthermore lead to a better cooperation if there is a higher amount of tolerance (Melis et al. 2006a). Their results showed that chimpanzee dyads that scored high in tolerance also performed with a higher success during the cooperative task.

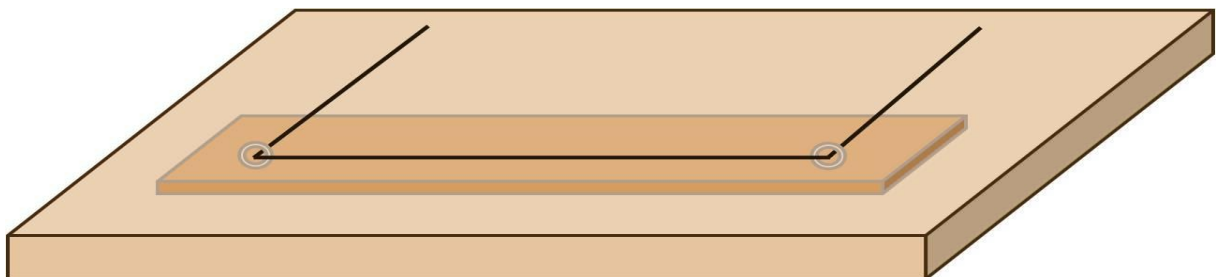
Additionally Hare et al. (2007) directly compared the performance of chimpanzees and bonobos in a simple food sharing task as well as in a more complex cooperative problem solving task. The results showed a clear advantage of bonobos compared to chimpanzees in both tasks leading to a higher success in retrieving food for the bonobos (Hare et al. 2007). Hare and colleagues based the explanation of their results on the emotional-reactivity hypothesis. This hypothesis assumes that the selection on social-emotional systems can cause a wider social cognitive evolution in different species (Hare and Tomasello 2005b).

Considering that tolerance might enhance cooperative ability and additionally the possibility to reciprocate, we also have to ask how individuals choose to cooperate with certain partners (Trivers 1971). In 2008, Rutte and Taborsky examined direct reciprocity in rodents and could show that in non-related rats the tendency to act cooperatively seems to be influenced by social experience and partner-specific information, in which rats prefer to help individuals from whom they received help before (Rutte and Taborsky 2008). Other studies indicate that some species base their decision whether or not to cooperate on the quality of long-term relationships. This would indicate an emotional mechanism rather than a complex cognitive basis (Schino et al. 2007a). Additionally it seems that at least some species are well aware of their type of relationship to others and therefore develop selective social bonds with other individuals leading to different social responses during several tasks and situations (Cords 2002, Brosnan et al. 2005, Connor 2007, Emery et al. 2007, Cameron et al. 2009, Fraser and Bugnyar 2010a, Massen et al. 2011). One could assume that a deeper social relationship between two individuals might enhance their performance in solving novel instrumental tasks including cooperative tests. Finally there is hardly any evidence that rank position and rank distance might influence cooperative success (Gilby 2007, Benenson et al. 2014). One could assume that, dyads that share a wider rank distance might perform better due to less in-between competition as their rank order is considered to be clearer; i.e. individuals with a higher rank when paired with a lower ranked individual would stress their dominance rank less through monopolization as when paired with other higher ranked individuals.

### 3.4 Investigating cooperation experimentally: The loose string paradigm

Many studies on cooperative problem solving have been conducted using a cooperative pulling task; i.e. the fixed-string paradigm (Drea and Carter 2009), a paradigm in which individuals would need to pull two bars (Chalmeau and Gallo 1996, Chalmeau et al. 1997b) or the so called loose-string paradigm (Hirata and Fuwa 2007). With the loose-string paradigm two individuals need to pull simultaneously on two ends of a string that is attached to a sliding platform. The platform contains food pieces that individuals can only reach after pulling the platform near enough. In case only one individual is pulling at a time, the string gets loose and the other end will get out of reach for the partner (Figure 1).

This basic set-up of the task tests whether individuals are able to solve the problem cooperatively. To test for the understanding of the partner additional control conditions have been implemented. During these controls the individual is either presented with the apparatus alone, in which pulling the string would not lead to any reward (as the string would go loose), or it needs to wait for the arrival of the partner in order to solve the task. When comparing certain studies that used these control conditions, slight differences in methods occurred; i.e. for elephants the delay increased stepwise from 5s to a maximum of 45s in which dyads needed to pass a certain criterion in order to move to the next step (Plotnik et al. 2011), whereas in rooks the delay was instantly between 1 and 2 minutes and no criteria needed to be reached (Seed et al. 2008, Scheid and Noe 2010). These differences might reflect the great variation in performance of several species within these control trials.



**Figure1:** Schematic drawing of an example for the loose string paradigm that is used to test cooperative behavior in different animal species

### 3.5 Investigating cooperation: why test ravens?

It has been suggested that some birds, and specifically corvid species, developed cognitive features that show a certain similarity with those of human and non-human primates (Emery and Clayton 2004, Emery et al. 2007). Several tests presented evidence that corvids are highly successful in performing problem solving tasks of different type (Heinrich and Bugnyar 2005, Werdenich and Huber 2006, Colbert-White et al. 2013). However, the performance of group-living corvids in a cooperative problem-solving task has hardly been investigated yet. The exceptions are two independent studies on rooks by Seed et al. (2008) and Scheid et al. (2010). Results suggest that corvids are able to solve a loose string task and possibly might exhibit cognitive abilities which are required for understanding the need of the partner (Seed et al. 2008, Scheid and Noe 2010).

In this study we chose to test ravens (*Corvus corax*) in the loose-string paradigm. Ravens are foraging generalists, but also specialists on carcass feeding. They mainly live in larger fission-fusion societies and share affiliative relationships of different degrees with different individuals in the group (Seed et al. 2007, Fraser and Bugnyar 2010a). They therefore seem to be able to build closer relationships to some individuals reflected in a higher amount of affiliative behavioral patterns such as food-sharing, preening or social support during agonistic interventions (Seed et al. 2007, Fraser and Bugnyar 2010a, b). Playback studies revealed that ravens understand their own relationship to others (Boeckle and Bugnyar 2012) and they understand the in-between relationship of others (Massen et al. 2014). Furthermore, social bonds (notably to kin) seem to enhance different forms of social learning (Fritz and Kotrschal 1999, Schwab et al. 2008). It therefore might also influence cooperation during problem solving tasks. All these aspects would also mean that their tolerance level might vary among dyads in a group based on their intensity of social bonds. This social background can lead to the possibility that ravens actively choose with whom they want to cooperate or not. However ravens might also be able to cooperate with unfamiliar members of a larger group in finding food. Testing ravens, therefore, provides a unique possibility not only to clarify whether these corvids are able to solve a cooperative string-pulling task, but moreover, identify some rules of decision making and its underlying mechanisms by investigating constraining factors.

### 3.6 Research question and hypothesis

In this study we provided ravens (*Corvus corax*) with a cooperative solving task in a dyadic and group test set up to answer three main questions.

Q1: Are ravens able to synchronize their pulling behavior and therefore cooperate with each other in order to get a food reward?

Based on observational studies on raven cooperative behavior under captive and field conditions (Fraser and Bugnyar 2010a, b, Heinrich 2011, Braun and Bugnyar 2012) we predict that ravens are able to successfully solve the task.

Q2: In case they are able to pull simultaneously, do they understand the need and importance of the partner?

If ravens understand that a partner is needed to solve the task they either should wait for the partner to arrive or stop pulling when tested alone. In case they do not do so, simpler mechanisms may be at work. For instance, ravens may individually learn to pull on the string to get the reward; the coordination between two birds would thus be a byproduct of each individual acting separately but simultaneously towards the reward (Noe 2006).

Q3: Which constraining factors do influence cooperative success in ravens?

We will test which patterns might enhance or reduce their cooperative success. Specifically, we will focus on different tolerance levels as well as kinship, rank, rank distance, sex and sex combination. As tolerance seems to increase the likelihood of cooperation to occur in different species such as chimpanzees (Melis et al. 2006a), capuchin monkeys (de Waal and Davis 2003) and rooks (Seed et al. 2008) we predict that also in ravens, dyads with a higher interindividual tolerance, that readily share food, will cooperate successfully, more spontaneously and with a higher rate. We furthermore predict that kin cooperate better than non kin and that lower ranked individuals cooperate better than higher ranked individuals as their competition might be less towards each other.

We also assume that dyads that share a greater distance in rank might perform better during the test as their rank situation might be clearer and therefore their competition might be less as well. Regarding sex and sex combination, no assumption can be made as there is hardly any data to base the predictions on.



## **4. Methods**

### **4.1 Subjects and housing condition**

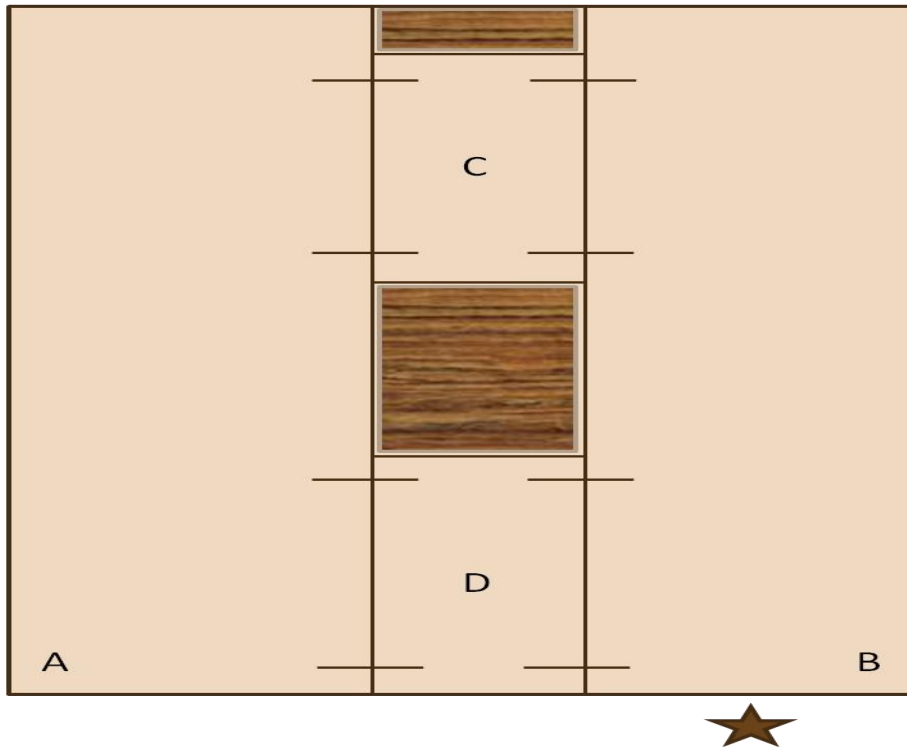
We tested ravens (*Corvus corax*) at the Haidlhof research station of the University of Vienna and Veterinary University of Vienna in Bad Vöslau, Austria in a series of repeated tolerance and cooperative string-pulling tasks. The tested group included 10 sub-adult individuals hatched in 2012, which derived from four nests in captivity (Stockholm, Bayerischer Wald, Wels and Haag; Table 1). All individuals arrived at Haidlhof research station as nestlings at the age of 3 to 5 weeks, were hand-raised to fledglings and kept in this social group ever since. Additionally, all individuals were marked with different colored rings for individual identification and were trained to participate in behavioral experiments. The current study was performed between September 2013 and March 2014. The lowest ranked male (Max) never participated in any of the tests and therefore was excluded from all analyses.

**Table 1:** Overview of all the birds that belonged to the group and were kept together. All participated in the tests except Max, who did not participate in any of the tests. The table includes sex, age, origin and kinship.

<b>Name</b>	<b>Sex</b>	<b>Age</b>	<b>Origin</b>	<b>Kinship</b>
Laggie	M	2 years	Germany	Group 1
Tom	M	2 years	Germany	Group 1
Adele	F	2 years	Germany	Group 1
George	M	2 years	Sweden	Group 2
Horst	M	2 years	Sweden	Group 2
Louise	F	2 years	Sweden	Group 2
Nobel	F	2 years	Sweden	Group 2
Rufus	M	2 years	Austria (Haag)	Group 3
Paul	M	2 years	Austria (Wels)	Group 4
Max	M	2 years	Austria (Wels)	Group 4

For most of the time during the day, the whole group of 10 birds was housed together in one outdoor aviary complex which included several compartments that could be used either for testing or for separation of one or more individuals from the group.

During the day, all birds had excess to all of these compartments (Figure 2). All individuals had experience with being separated from the group for several minutes, hours and even days, due to previous studies.



**Figure 2:** Overview of the aviary complex ‘Ludus’ including all compartments that can be closed if needed. A: left living compartment, B: right living compartment, C and D: additional compartments, all compartments can be used as living compartments, for testing or separation, D was used to keep the partner during the dyadic cooperation tests, Star: position of apparatus, all compartments were connected through doors

All birds were fed twice a day with a wide variety of proteins (e.g.: meat, bones, curd, yogurt, egg), bread and fruits. Water was provided ad libitum in the form of small water bowls and wider basins for the birds to bathe. Training and testing were conducted exclusively with positive reinforcement in which every individual could choose whether to participate or not. Furthermore to ensure highly motivated and less nervous birds, a previous habituation to both experimenters and testing apparatus took place before any training or testing started.

#### 4.2 Experimental Apparatus

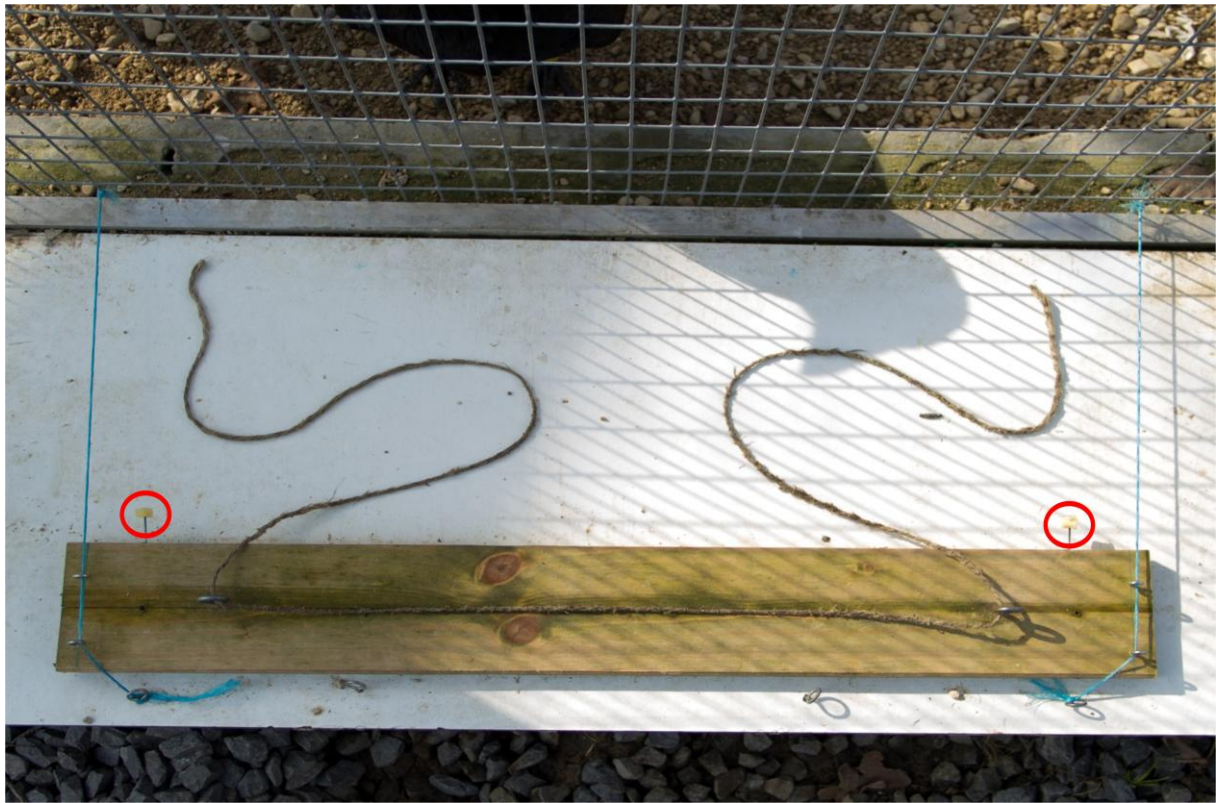
Both tolerance and cooperation tests took place in the right living compartment B of the aviary (Figure 2). The apparatus itself remained outside the aviary and was placed in front of the mesh fence. It consisted of one wooden panel (200cm x 60cm x 1,5cm) which was fixed outside the compartment in a way that it provided the same level as the inner ground floor of the aviary. For testing tolerance behavior, two 1m long strings were attached at the opposite end of the panel with the help of two eye bolts. For each test session the distance between these two strings varied according to the different test conditions, either 120 cm, 60 cm or 30 cm (Figure 3).



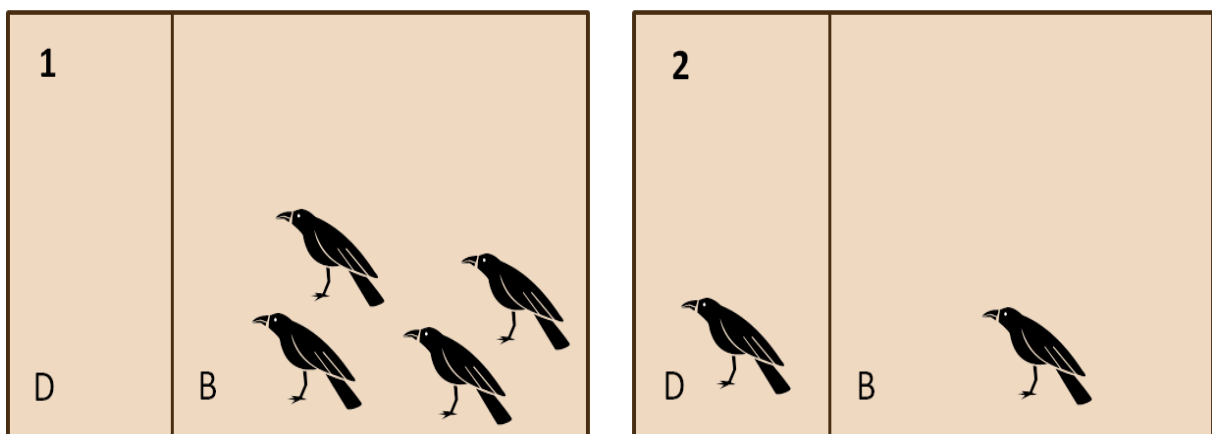
**Figure 3:** Schematic drawing of the experimental set up for the tolerance test with 120cm distance. The experimenter and the apparatus are outside the aviary, and the brown circle represents the reward that is connected to the string. The two ends of the string are placed into the aviary.

During the cooperation tests another smaller panel (78cm x 10cm x 1,0cm) was fixed on top of the first one. Two blue strings were used as rail to keep the moving panel in line. To hold the string for the ravens to pull in place and to make sure that the panel moves in the right direction when pulled, two eye bolts were attached on the top of the panel at 60 cm apart. Both ends of this one string then were placed in the aviary. Food was attached to two nails on each side at the front part of the panel (Picture 1).

During a cooperative group test, all individuals of the group had access to the apparatus. In contrast, during the dyadic cooperation test only one or two individuals, depending on the test condition, had access to the apparatus. The partner during all dyadic cooperation tests was kept in the additional compartment D while waiting for the cooperative trials (Figure 4).



**Picture 1:** Picture of the experimental set up is shown for the cooperation tests, in which the red circles mark the reward. The both ends of the string would be placed into the aviary at the beginning of a trial. The blue strings were used as form of rail in order to keep the moving slide in line (Alexandru Munteanu©).



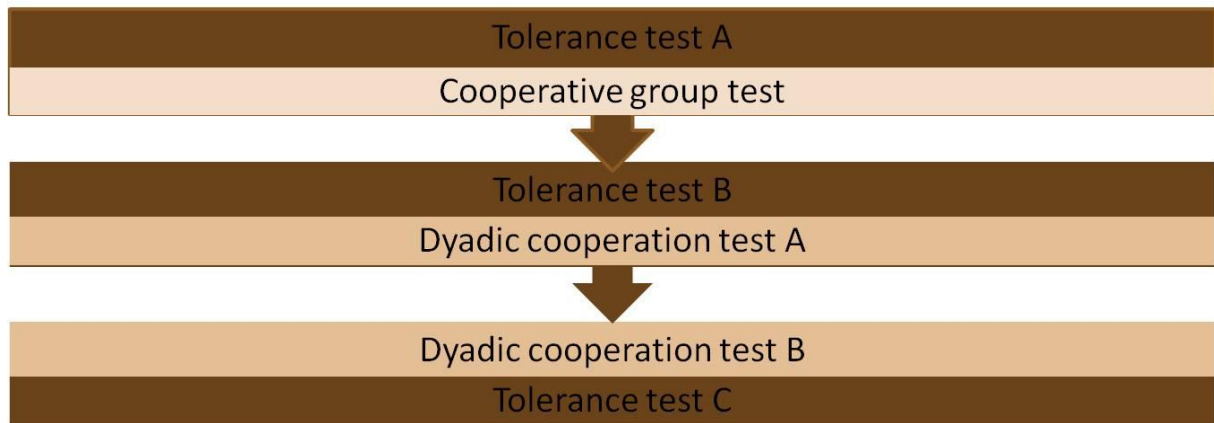
**Figure 4:** Experimental set up for the cooperation test drawn in a plan view. 1: experimental set up during the cooperative group test, 2: experimental set up during the dyadic cooperation test, D: additional compartment, B: right living compartment

#### **4.3 Training and Piloting**

We know from previous studies that all ravens were capable of solving simple problems involving the pulling of a string with their beak. Taking into account possible effects of neophobia, the whole group was habituated first to the big panel and later on to the small panel 2-3 weeks before the experiment started. During this time the panel was set up and all strings were baited with food several times such that all individuals had direct excess to the apparatus and could get the food without pulling. After the birds did not show any fear or avoidance of the panels anymore, the pilot phase started. For the tolerance tests, we ran a total of 9 pilot sessions on 3 days to define the number of trials, inter trial interval and inter session interval as well as the length of the strings or the general procedure. Similarly, 5 sessions on 4 days were used to pilot the cooperation test. In addition to this training, beforehand several monopolization experiments were run from the beginning of 2013 until the beginning of 2014 to define a hierarchy between all individuals. During these tests the whole group had excess to one big piece of meat, usually a pig leg, for 30 minutes. This piece was attached to a wooden plate in order to prevent the ravens from moving it around. They therefore only had the possibility to feed from it at a certain spot, similar to a carcass feeding.

#### **4.4 General procedure of testing**

Throughout all tests we did a total of three rounds of tolerance tests, one cooperative group test and two rounds of dyadic cooperation test. Test sessions took place between October 2013 and March 2014. We started our testing with a tolerance test, followed by the cooperative group test, the second tolerance test, the first and the second round of dyadic cooperation test and ended the testing with the third tolerance test (Figure 5).



**Figure 5:** Overview of the order of all test phases. The whole experiment consisted of three rounds of tolerance tests, one round of cooperative group test and two rounds of dyadic cooperation test.

Seven out of the 10 individuals participated during all test phases. Rufus and Paul only started from the second tolerance test on, as they were temporarily separated from the group during the first tolerance test and the cooperative group test. Table 2 represents an overview of which individuals participated during which test phases.

**Table 2:** Represents an overview of the participation of all individuals during the test phases. The check means that the individual did participate in this test. The cross means that this individual did not participate in the test. Max had access to the apparatus but did not participate

Name	Tolerance 1	Group Test	Tolerance 2	Dyadic Test	Tolerance 3
Laggie	✓	✓	✓	✓	✓
Tom	✓	✓	✓	✓	✓
Adele	✓	✓	✓	✓	✓
George	✓	✓	✓	✓	✓
Horst	✓	✓	✓	✓	✓
Louise	✓	✓	✓	✓	✓
Nobel	✓	✓	✓	✓	✓
Paul	✗	✗	✓	✓	✓
Rufus	✗	✗	✓	✓	✓
Max	✗	✗	✓	✗	✓

#### **4.5 Experiment 1: Tolerance test**

Tolerance tests took place before and after the cooperative group test and after the dyadic cooperation test, respectively (Figure 5). Here a reward (pieces of Frolic<sup>®</sup> dog food) was directly attached to the ends of two separate strings. Birds thus had to pull on one of the strings to reach the reward, without the need of a cooperation partner. Both ends were simultaneously moved into the aviary. The strings were placed in a way that the ends were either, 30cm, 60cm or 120cm apart from each other. Each day, a maximum of 3 sessions took place, each with a different distance. One session consisted of 20 trials with a 20s inter-trial interval and 5min inter-session interval. All distances were counterbalanced over 9 sessions, providing all possible combinations per round. Therefore, each distance was tested 6 times in every round and 18 times altogether. In total, 54 Sessions and 1080 trials were carried out. During each session and round all individuals of the group had access to the test apparatus, except during the first 18 sessions in which Rufus and Paul did not participate. Therefore the sample size during the first round was  $n = 7$  and during the second and third round was  $n = 9$  (Table 2).

#### **4.6 Experiment 2: Cooperative group test**

The cooperative group tests followed the first tolerance tests (Figure 5). Here the string was looped through the rings of the sliding platform and to reach the reward subjects had to pull on both ends simultaneously. To increase the motivation within the cooperation tests, pieces of cheese instead of Frolic<sup>®</sup> dog food, were used for all trials. Similar to the tolerance tests, both ends of the string were moved into the aviary simultaneously so that the birds could pull (Picture 2). Per day about 3 sessions, maximum 9 with at least a 1hour break after every third session took place. Each session consisted of 20 trials with a 20s inter-trial interval and 5min inter-session interval. In total one round of 30 sessions and 600 trials was carried out. During all sessions the whole group had permanent access to the apparatus, except Paul and Rufus (Table 2). Therefore the sample size of the group test was  $n = 7$ .





**Picture 2:** During every test trial both ends of the string were moved into the aviary simultaneously (Alexandru Munteanu©).

The distance between both strings was always set with 60cm. For the birds to successfully pass a cooperation test, two individuals had to pull each on one end of the string simultaneously in order to move the panel as far to the fence so the food was in reach (Picture 3). The experimenter was only allowed to move the panel further to the fence when it got stuck or when it already moved more than half of the way. A trial was repeated as soon as the panel happened to be lopsided, so one individual could reach the food first and stopped pulling, or the string got stuck in any of the eye bolts (Picture 4). A trial was considered unsuccessful when the string got loose, which means that the other end of the string was pulled back out of the aviary and like this out of reach for the partner (Picture 5).





**Picture 3:** Two individuals needed to pull the panel until the food was in reach in order to be considered successful. The two pictures show a pulling action of two individuals that ended successful (Alexandru Munteanu©).





**Picture 4:** Example of when the trial was repeated is shown. One trial was repeated as soon as the panel was lopsided so that only one individual could reach the food and then stopped pulling (Alexandru Munteanu©).

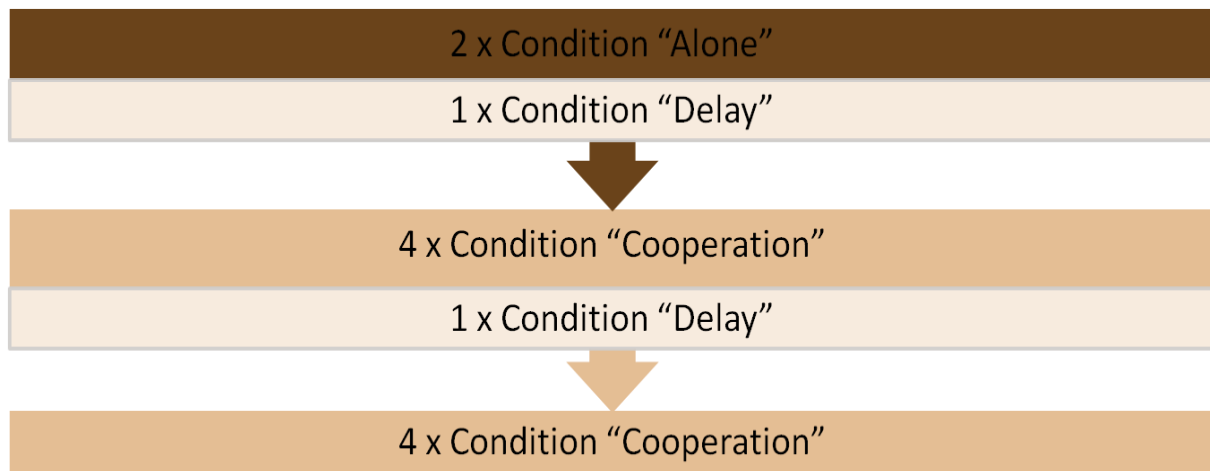


**Picture 5:** The picture shows a unsuccessful trial. Only one individual did pull the string which therefore got loose. The other end was pulled out of the aviary (Alexandru Munteanu©).

#### **4.7 Experiment 3: Dyadic cooperation test**

Dyadic cooperation tests were carried out the same way as the group tests but instead of all birds, only two birds were in the test area. Additionally, we included two different types of control trials, alone trials and delay trials. During the alone trials only the focal individual had access to the apparatus. Here we could see whether birds continued pulling even though that no partner was present. In the delay test, the focal animal had access to the apparatus before the partner did. Therefore, the string was moved into the aviary in which the focal individual remained at the same time as the door opened to release the partner. The delay test was used to examine whether birds are able to wait for the arrival of the partner. We used cheese as reward and a maximum of 8 sessions per day were possible using four different dyads. Every individual was tested with every other individual of the group two times within two different test rounds leading to a total of 36 dyads. Altogether, each dyad was tested 4 times in which both individuals remained as focal individual two times, one time during the first round and the second time during the second round. The order of dyads was randomized during both cycles. Each individual was only tested once per day as focal and once as partner within one and the same dyad, respectively in two session right after the other. The order of which individuals participated as focal or partner during a session was counterbalanced over the two rounds. Each session of a focal individual consisted of 12 trials in total with a 20s inter trial interval. First the focal individual was tested alone during two trials, after which one delay trial, four cooperation trials, again one delay trial and four cooperation trials followed (Figure 6). In total dyads were tested in 144 sessions and 1728 trials, in which each individual only participated in 352 trials. After we finished the protocol for one individual of a certain dyad, we carried on with the same protocol for the second individual of a dyad. The same rules apply as in the group tests according to successful and unsuccessful trials, intervention of the experimenter and repeated trials.

Note that during the alone control, one trial was considered to be successful when the focal individual did not pull the string. During the delay control, a trial was considered to be successful when the focal individual did wait for the partner's arrival so that both birds could cooperate and get the food reward. A trial during each condition ended as soon as the food was eaten or after 2 minutes.



**Figure 6:** The figure represents an overview about the sequence of the dyadic cooperation test including 8 trials of cooperation, 2 delay trials and 2 alone trials.

#### 4.8 Measurements

In order to analyze the data of the monopolization tests and with this to assess a dominance hierarchy within the group all unidirectional displacements were scored (Gwinner 1964). Data were arranged in matrices and dominance order was determined with the most consistent linear hierarchy, calculating Landau's linearity indices ( $h'$ ) using MatMan 1.1 (de Vries et al. 1993) and reordered matrices to best fit a linear hierarchy (de Vries 1995; 1998). We found a significantly linear hierarchy in the group ( $h'=0.858$ ,  $n=9$ ,  $p < 0.001$ , based on 524 interactions and with 5.56 % unknown relationships).

All pilot and test sessions were video-recorded with at least one or two cameras that were focused on the apparatus. In order to statistically analyze the data all test videos were coded to define the number of pulls per individual during all test phases.

Tolerance scores were calculated from all three rounds of tolerance tests. Therefore, all rounds in respect to the total number of pulls for each individual together with each other individual were compared. With this, it was possible to examine differences in behavior and tolerance levels according to different distances as well as changes of tolerance scores due to successful cooperation before and after the group test as well as after the dyadic cooperation test.

In both the cooperative group test and dyadic cooperation test the total number of successful cooperation per dyad was determined by calculating the total number of successful pulls per dyad.

Additionally, the rate of pulling when tested alone and unsuccessful as well as successful trials during the delay control were calculated. Finally, we examined differences in performance that are related to characteristics such as to rank, rank distance, sex, sex-combination and kinship. Here we also used the total number of successful cooperation (number of successful pulls) per individual.

#### 4.9 Statistical Analysis

Statistical analyses were done with the IBM SPSS 20.0 for Mac OS IBM-software, including  $\alpha = 0.05$  and two-tailed p-values. First we calculated Wilcoxon-Signed-Rank-tests and Mann-Whitney-U-tests for general comparisons, for a non-normally distributed data set, or Chi-Square tests. Here we used the Wilcoxon-Signed-Rank-test to assess differences in performance during the first and second round of the dyadic cooperation tests by comparing the mean number of pulls of all individuals. We used the same test to compare the mean number of pulls during all alone trials for every individual within the first and the second round of the dyadic cooperation test. Additionally we compared the performance between kin and non-kin, as well as the performance between male-male and female-male or female-female and female-male dyads with the help of the Wilcoxon-Signed-Rank-test. In order to compare the performance of female-female and male-male dyads we used the Mann-Whitney-U-test. For all these comparisons, the mean number of successful pulls for every dyad was used. To see whether there is a difference of the relative number of successful cooperation between the group test and the pair-wise tests, and therefore a difference in performance, we calculated a Chi-Square-test. In order to see which factors might influence whether a dyad might be successful or not and to examine in which combination they provide an influence, generalized linear mixed models (GLMM) were calculated for the influence of tolerance levels, hierarchy, rank distance, sex, sex-combination and kinship as fixed effects.

With this we also could investigate the influence of the session number on the performance to see whether individuals get better over time. By using the GLMM we could combine all possible factors and control for repeated measures by including the focal and partner as random effects.

In order to find the best fitting model, we used a backward step-wise approach and we based our decision on which model to use for both the group and the dyadic cooperation test on the corrected Akaike Information Criterion (cAIC).

Finally we calculated post-hoc correlations (Spearman rank order correlation) in order to see the relationship between the mean tolerance levels and the total number of successful cooperation as well as between the dominance rank and the total number of successful trials. Additionally, we used Wilcoxon signed ranks tests and Mann-Whitney U test for post-hoc comparisons and used a Holm Bonferroni (Holm 1998) correction for calculating corresponding p-values when multiple comparisons were made on one data-set.

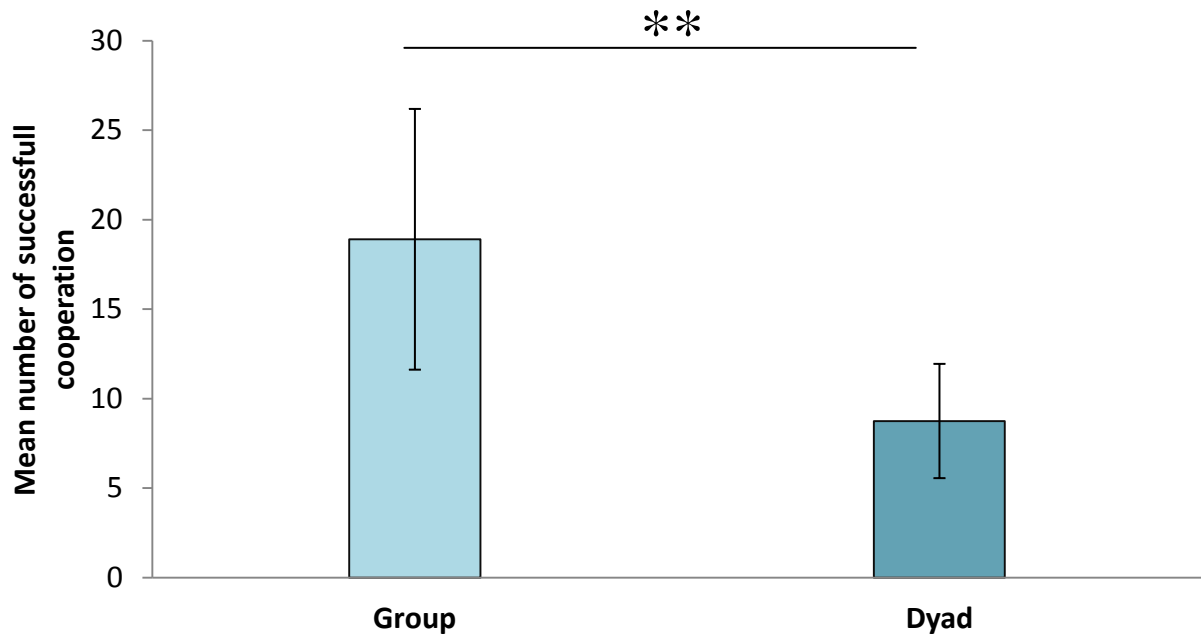


## **5. Results**

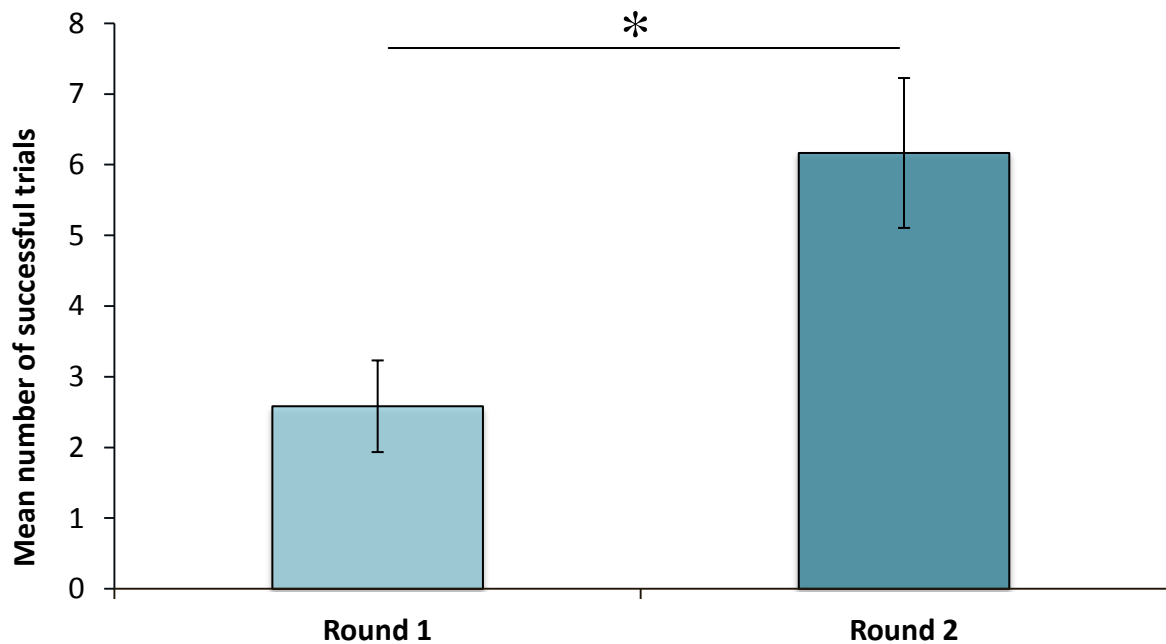
### **5.1 Q1: Are ravens able to synchronize their pulling action and therefore cooperate with each other in order to get a food reward?**

The results of our experiments show that the ravens in general performed with a high level of success in this loose string paradigm. They were spontaneously able to solve the problem and get the food reward when tested first in the group and later in a dyadic set up. Interestingly, there are clear differences when comparing the number of successful cooperation during the two test phases (Figure 7). During the group test individuals ( $n=7$ ) were successful in 397 trials out of 600 trials (66.17%). In the group experiment every individual was successful at least 32 times, but not all dyads could solve the problem (3 out of 21 dyads). In the dyadic cooperation tests, pairs were successful in 315 out of 1152 (27.34 %). Here all individuals ( $n=9$ ) were successful at least once, but again not every dyad could solve the problem (15 out of 36 dyads). Using a Chi-Square test we statistically compared both test phases with each other. The result shows that the ravens performed significantly better during the group test when compared with the dyadic tests (Chi-Square;  $\chi^2 = 675.8$ ,  $DF = 1$ ,  $p < 0.001$ , Figure 7).

To see whether there is a possible learning effect over time, we compared the mean number of successful trials during the first and the second round of the dyadic cooperation tests. We found that ravens performed better during the second round than during the first round; i.e. the number of successful trials was significantly higher in the second round of the dyadic cooperation tests (Wilcoxon Signed Rank;  $T^+ = 44$ ,  $N = 9$ ,  $*p = 0.05$ ; Figure 8), indicating a possible learning effect.



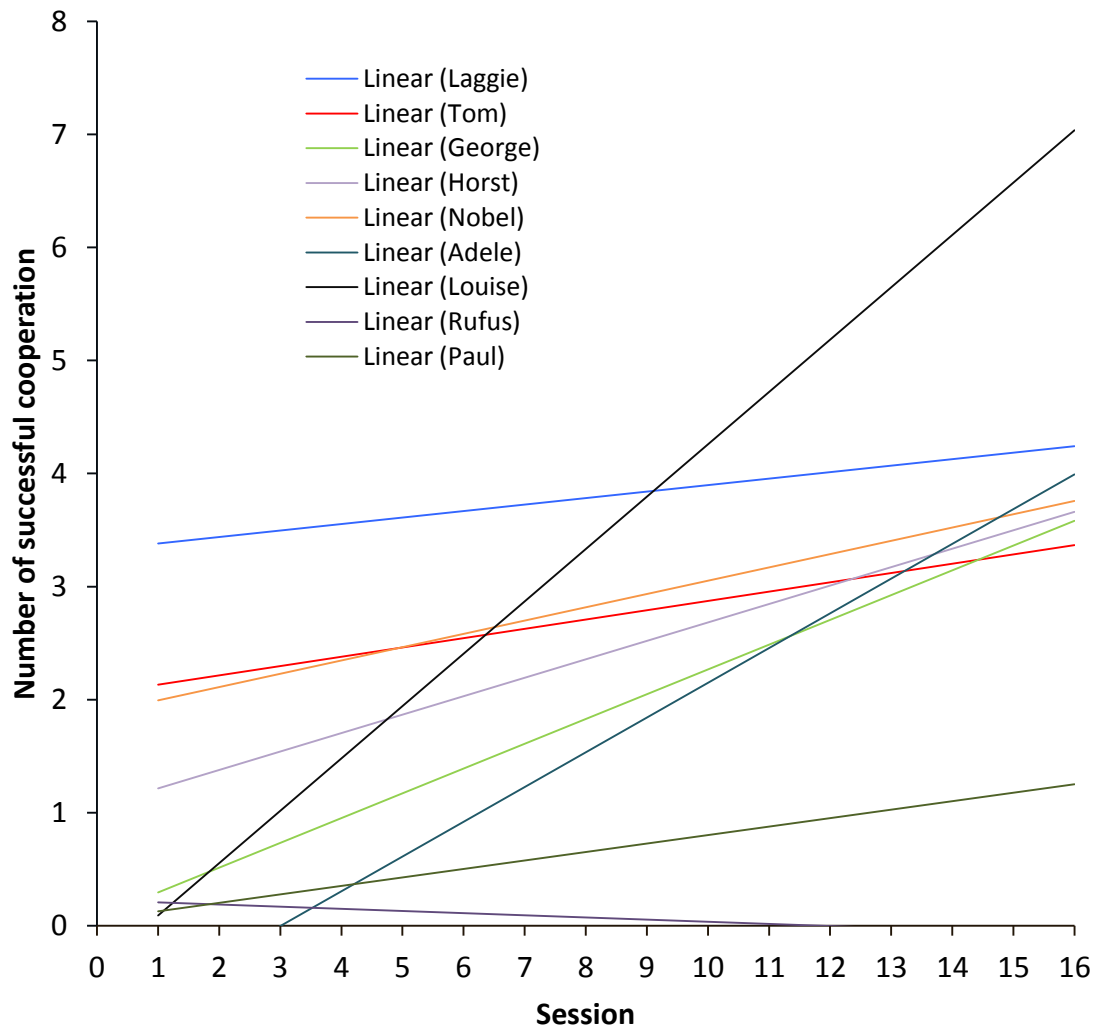
**Figure 7:** Mean  $\pm$  S.E.M. number of successful trials of all individuals during the group test and the dyadic cooperation test, group-test N=7, dyadic-test N=9 , \*\*p < 0.001.



**Figure 8:** Mean  $\pm$  S.E.M. number of successful trials during the first and the second round of the dyadic cooperation test, \*p = 0.05.

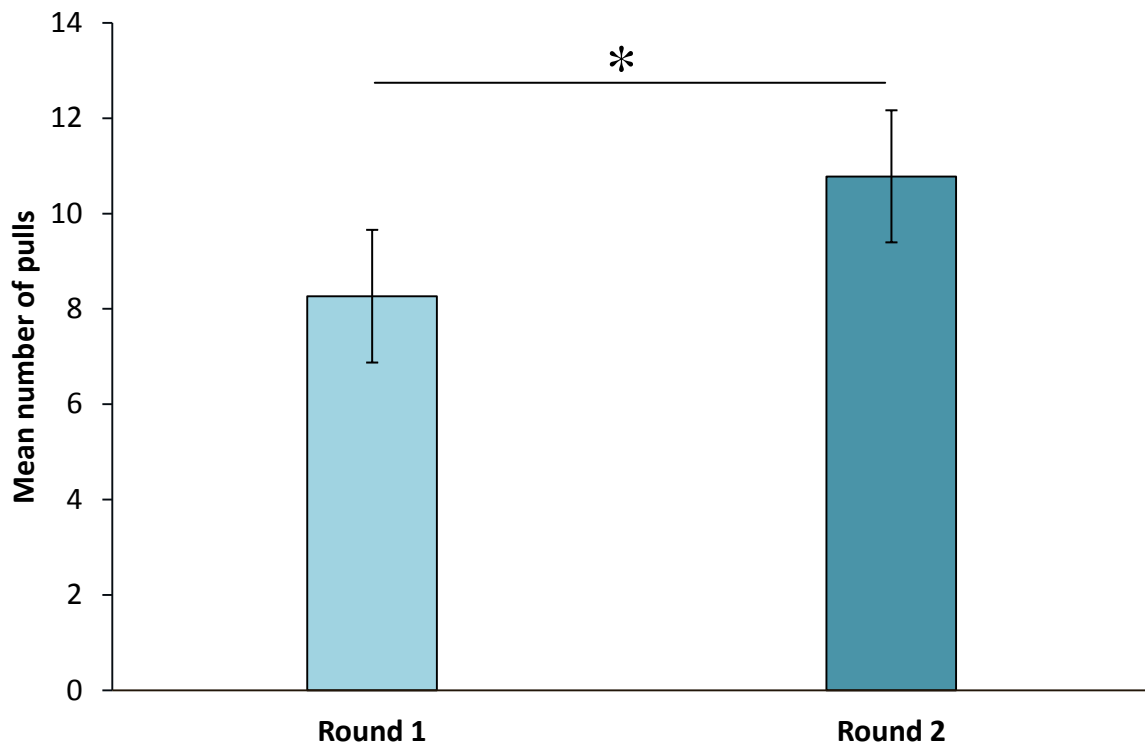


Additionally, when running a GLMM including session number we found that this pattern is not only true for the direct comparison of the first and the second round of the dyadic test, but also across all sessions of the dyadic cooperation test; i.e. there is a strong relationship between the number of successful trials and session number (GLMM;  $F_{1, 142} = 14.297$ ,  $\beta = 0.165 \pm 0.044$ ,  $p < 0.001$ ; Figure 9), indicating that individuals solve the problem with significantly higher success over time.

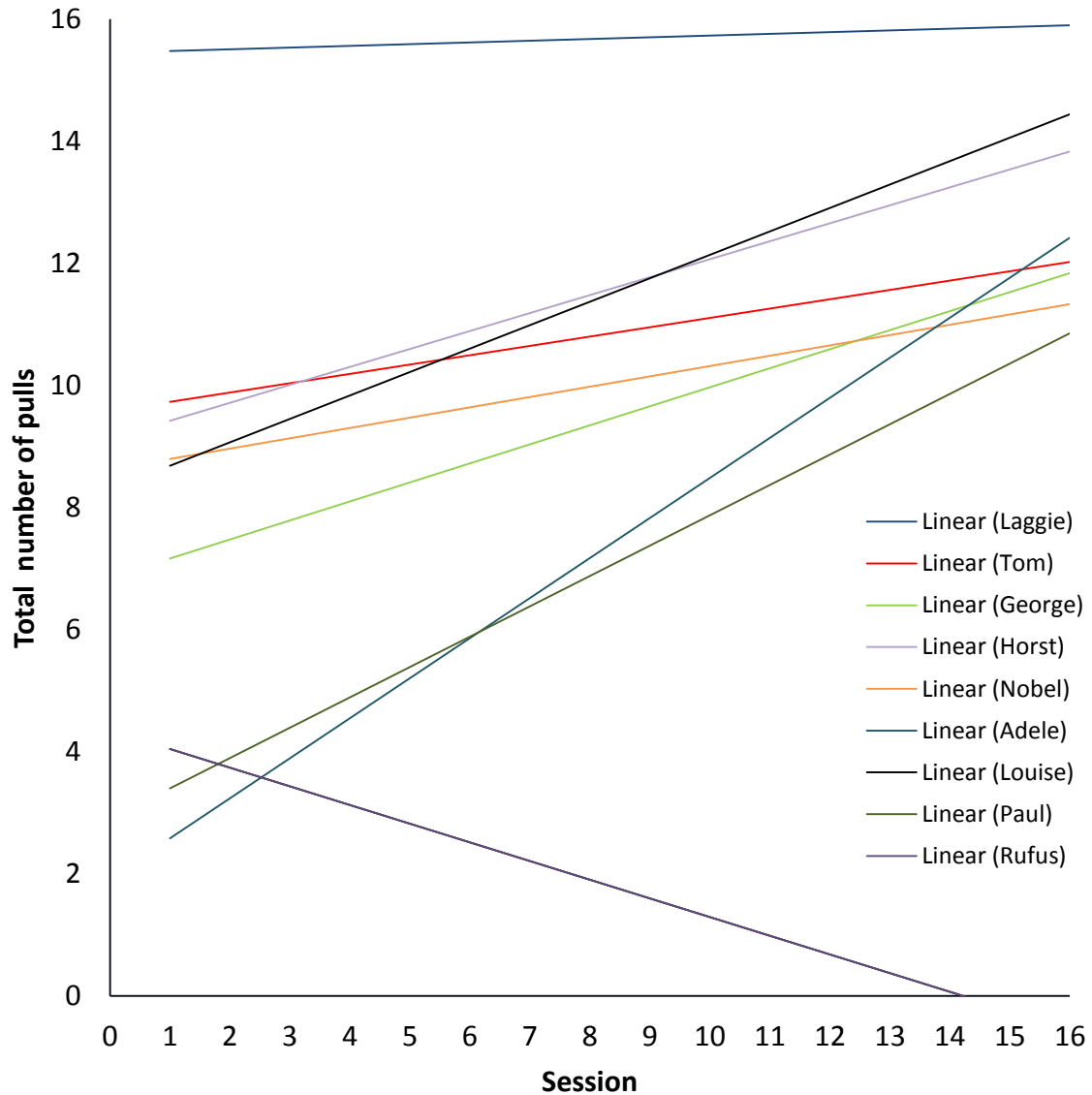


**Figure 9:** Relationship between session number and the number of successful cooperation during the dyadic cooperation test per individual. Session number 1 to 8 represents the first round of the test phase and session number 9 until 16 represents the second round of the dyadic test phase. The data only includes the total number of successful cooperation in which the described individual was tested as focal individual but not as partner. Therefore each focal could cooperate successfully 8 times per session.

To investigate whether this effect is truly a learning effect or might be due to motivational effects, we ran the same statistics with the total number of pulls for every individual, leading to successful and unsuccessful cooperation. This shows exactly the same pattern as the first comparison; i.e. when comparing the mean number of total pulls, the birds generally pulled significantly more during the second as compared during the first round (Wilcoxon Signed Rank;  $T^+ = 40$ ,  $N = 9$ , \*  $p = 0.03$ ; Figure 10). Again this pattern is also true when running a GLMM, including the performance across all sessions. There is a strong positive relationship between the total number of pulls and the session number (GLMM;  $F_{1, 142} = 8.731$ ,  $\beta = 0.244$ ,  $p < 0.004$ ; Figure 11), indicating that birds in general pull more over time.



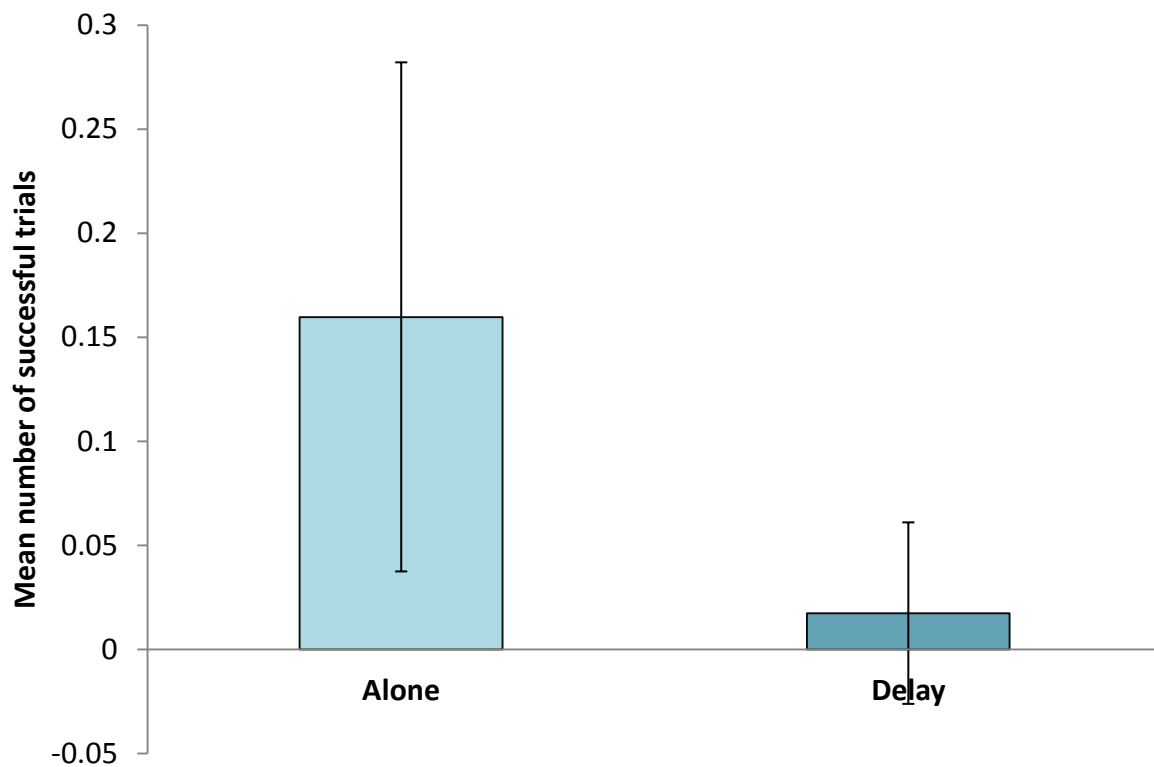
**Figure 10:** Mean  $\pm$  S.E.M. number of total pulls during the first and the second round of the dyadic cooperation test, \* $p = 0.03$ .



**Figure 11:** Relationship between session number and the total number of pulls per individual during the dyadic cooperation test. Session number 1 to 8 represents the first round of the test phase and session number 9 until 16 represents the second round of the dyadic test phase. The data includes the total number of pulls for each individual in which it has been tested as focal and partner individual. Therefore each individual could pull in total 16 times per session.

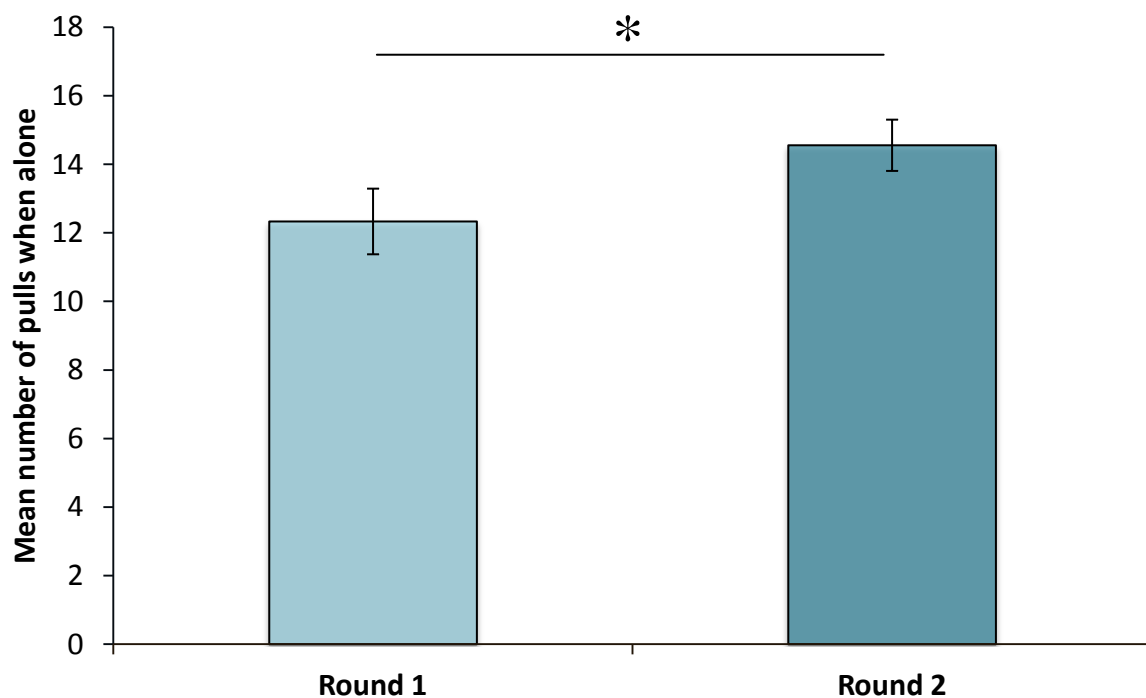
**5.2 Q2: In case they are able to pull simultaneously, do they understand the need and importance of the partner?**

In order to see whether ravens not just solve the problem but also understand that a partner is required for solving it, we included two controls in our experiment, a delay test and trials in which individuals were tested alone. Ravens performed poorly during both control phases. We ran a total of 288 trials of testing individuals alone, in which during 45 trials (15.97%) in total the focal individual did not pull at all when having access to the apparatus without any partner being close. Additionally we run a total of 288 trials of the delay control, in which only during a total of 5 trials (1.73%) individuals waited till the partner arrived and then solved the task successfully (Figure 12). Moreover, this happened only with two different focal individuals (Louise 3 times and Horst 2 times). These numbers illustrate that ravens were not able to hold back their pulling actions in the absence of a partner in this set-up. It therefore also could suggest that they might not consider the need of the partner in our experiment, though can be explained by other reasons as well.



**Figure 12:** Mean  $\pm$  S.E.M. number of successful trials during the alone and delay control trials

Finally we compared the mean number of pulls when birds were alone between the first and the second round. Our results show that the ravens did not decrease their pulling rate over time. In contrast, the number of pulls increased significantly from the first to the second round (Wilcoxon Signed Rank;  $T^+ = 32$ ,  $N = 9$ , \*  $p = 0.04$ , Figure 13). These results indicate that the ravens (have learned to) focus on pulling the string, irrespective of their partner.



**Figure 13:** Mean  $\pm$  S.E.M. number of pulls during the alone control in the first and in the second round of the dyadic test, \* $p = 0.04$ .

### 5.3 Q3: Which constraining factors do influence cooperative success in ravens?

In both group and dyadic tests, we found quite some variation between individuals and dyads in their success and pulling rate (Table 3 and 4). To investigate which factors might explain this variation, we ran several models on the proportion of successful cooperation, including tolerance levels, sex, sex-combination (MM, MF and FF), kinship, rank and rank-distance (1-8), as possible factors. To do so, we first tested whether there was any difference between the different tolerance tests we conducted; i.e. over the different distances (120cm, 60cm and 30cm) and over the different rounds (1-3).

**Table 3:** Represents an overview about the total number of successful cooperation of all dyads during the group test.

<b>Group</b>	<b>Tom</b>	<b>Laggie</b>	<b>George</b>	<b>Horst</b>	<b>Nobel</b>	<b>Adele</b>	<b>Louise</b>
<b>Tom</b>	*	101	33	3	27	18	15
<b>Laggie</b>	101	*	16	15	17	13	20
<b>George</b>	33	16	*	46	25	1	11
<b>Horst</b>	3	15	46	*	18	0	13
<b>Nobel</b>	27	17	25	18	*	0	5
<b>Adele</b>	18	13	1	0	0	*	0
<b>Louise</b>	15	20	11	13	5	0	*

**Table 4:** Represents an overview about the total number of successful cooperation of all dyads during the dyadic test.

<b>Dyadic</b>	<b>Tom</b>	<b>Laggie</b>	<b>George</b>	<b>Horst</b>	<b>Nobel</b>	<b>Adele</b>	<b>Louise</b>	<b>Rufus</b>	<b>Paul</b>
<b>Tom</b>	*	32	0	0	14	15	24	0	0
<b>Laggie</b>	32	*	0	19	21	15	26	0	0
<b>George</b>	0	0	*	20	15	11	20	0	0
<b>Horst</b>	0	19	20	*	13	8	18	0	0
<b>Nobel</b>	14	21	15	13	*	0	19	0	10
<b>Adele</b>	15	15	11	8	0	*	5	0	7
<b>Louise</b>	24	26	20	18	19	5	*	1	2
<b>Rufus</b>	0	0	0	0	0	0	1	*	0
<b>Paul</b>	0	0	0	0	10	7	2	0	*

Therefore, we ran a GLMM on all our tolerance data, and tested the effect of distance and round, while controlling for subject and partner identity. We found that both the distance and the rounds had no significant effect on tolerance (Table 5), indicating that the variation in tolerance between individuals was consistent over the different distances and rounds. Therefore, we choose to lump the data over the different distances and rounds.

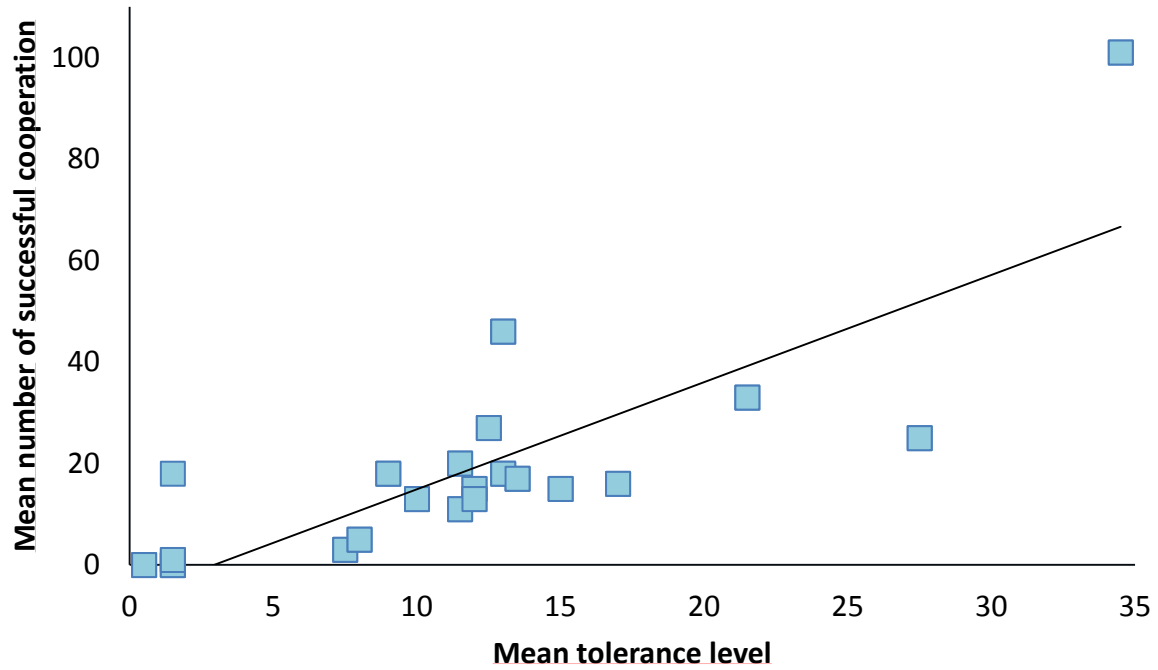
However, since during the group tests not all individuals were present, we choose to create a mean tolerance value per dyad over round 1 and 2, to include in tests about the group experiment, and a separate mean tolerance level over round 2 and 3, to include in tests about the dyadic experiments. After having established these singular tolerance variables, we proceeded to test which factor (s) affected successful cooperation in the group test. The best model (Table 6) only showed a significant positive effect of tolerance levels (GLMM;  $F_{1, 34} = 20.879$ ,  $\beta = 1.718$ ,  $p < 0.001$ ); i.e. pairs with higher inter-individual tolerance perform better than pairs with lower inter-individual tolerance (Figure 14). There was no significant influence of any other variable.

**Table 5:** Summary of the GLMM on our tolerance data, including the effect of distance and round, with F-values, the degrees of freedom and p-values.

Source	F	df1	df2	Sig.
Corrected Model	1.509	4	274	0.200
Distance	0.897	2	274	0.409
Session	2.121	2	274	0.122

**Table 6:** Summary of the best fitting GLMM on successful cooperation during the group test, showing all important fixed factors and their F-values, the degrees of freedom and p-values.

Source	F	df1	df2	Sig.
Corrected Model	11.022	7	34	0.000
Sex	0.479	1	34	0.494
Sex Combination	0.932	2	34	0.404
Rank	0.655	1	34	0.424
Rank Distance	0.138	1	34	0.713
Kinship	1.539	1	34	0.223
Tolerance 1	20.879	1	34	0.000



**Figure 14:** Relation between the mean number of successful cooperation and the mean tolerance level during the group test.

Investigating what possible factors might explain the variance in cooperation in the dyadic test, we ran similar generalized linear mixed models, including all previous mentioned variables. As from previous analysis we knew that the session number had an effect, we also included this factor to control for that. The best fitting model showed that during the dyadic cooperation test tolerance level (GLMM;  $F_{1, 136} = 39.605$ ,  $\beta = 0.119$ ,  $p < 0.001$ ), sex-combination (GLMM;  $F_{1, 136} = 39.605$ ,  $\beta_{MM \text{ vs. } FF} = -1.869$ ;  $\beta_{MF \text{ vs. } FF} = -0.027$ ,  $p = 0.001$ ), kinship (GLMM;  $F_{1, 136} = 39.605$ ,  $\beta = 1.163$ ,  $p = 0.018$ ) and rank (GLMM;  $F_{1, 136} = 39.605$ ,  $\beta = -0.249$ ,  $p < 0.047$ ) had a significant effect on the performance of the individuals (Table 7).



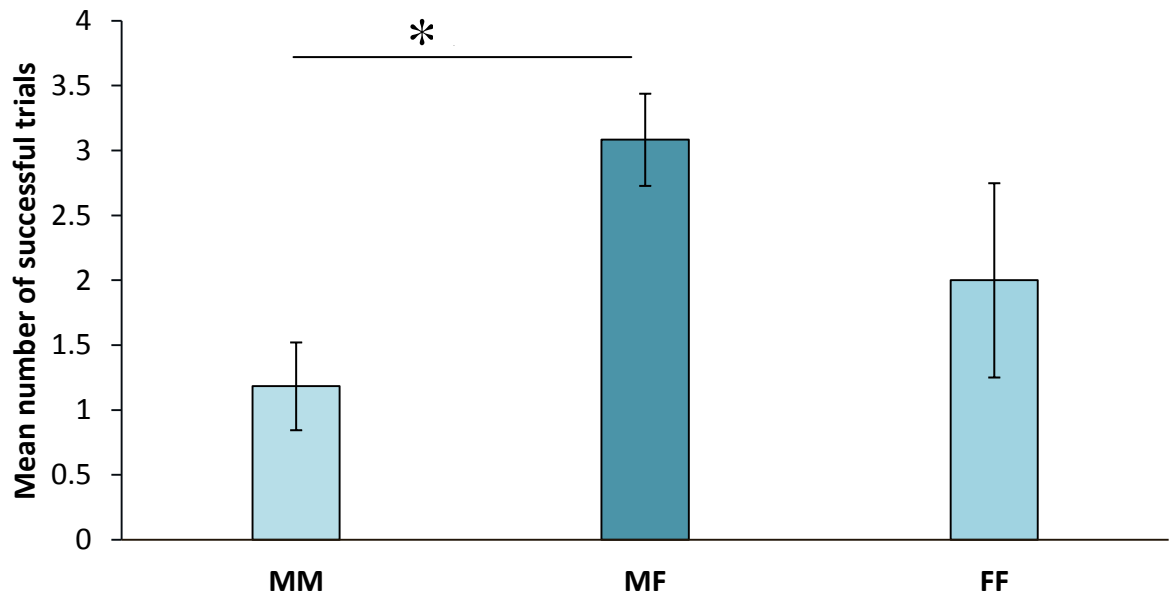
**Table 7:** Summary of the best fitting GLMM on successful cooperation during the dyadic test, showing all important fixed factors and their F-values, the degrees of freedom and p-values.

Source	F	df1	df2	Sig.
Corrected Model	21.981	7	136	0.000
Session	20.631	1	136	0.000
Sex	1.187	1	136	0.278
Sex Combination	7.776	2	136	0.001
Rank	4.004	1	136	0.047
Kinship	5.719	1	136	0.018
Tolerance	39.605	1	136	0.000

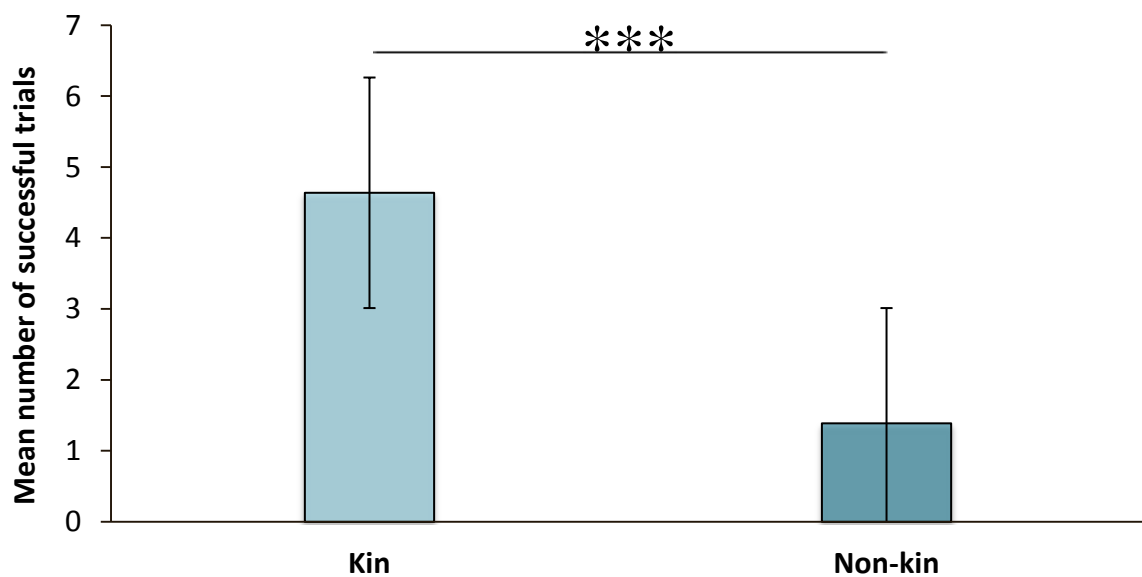
Post-hoc analyses show that, when looking at the sex-combination, mixed-sex dyads perform significantly better than male-male dyads but not significantly better than female-female dyads (Wilcoxon Signed Rank; MM/MF,  $T^+ = 759.50$ ,  $N = 9$ ,  $p < 0.01^1$ ; MF/FF,  $T^+ = 11.00$ ,  $N = 9$ ,  $p = 0.916^1$ , Figure 15). Additionally, the results also show a marginal, non-significant, difference between female-female and male-male dyads (Mann Whitney U; MM/FF,  $T^+ = 531.00$ ,  $N = 9$ ,  $p = 0.118^1$ , Figure 15), i.e., it seems that female-female dyads perform better than male-male dyads. When looking at the different performance of kin and non-kin, kin have a significant higher number of successful cooperation than non-kin (Wilcoxon Signed Rank;  $T^+ = 65.50$ ,  $N = 9$ ,  $p < 0.001$ , Figure 16). Regarding the effect of rank, we found a significantly positive, yet very small relationship between the total number of successful cooperation and the dominance rank an individual has (Figure 17).

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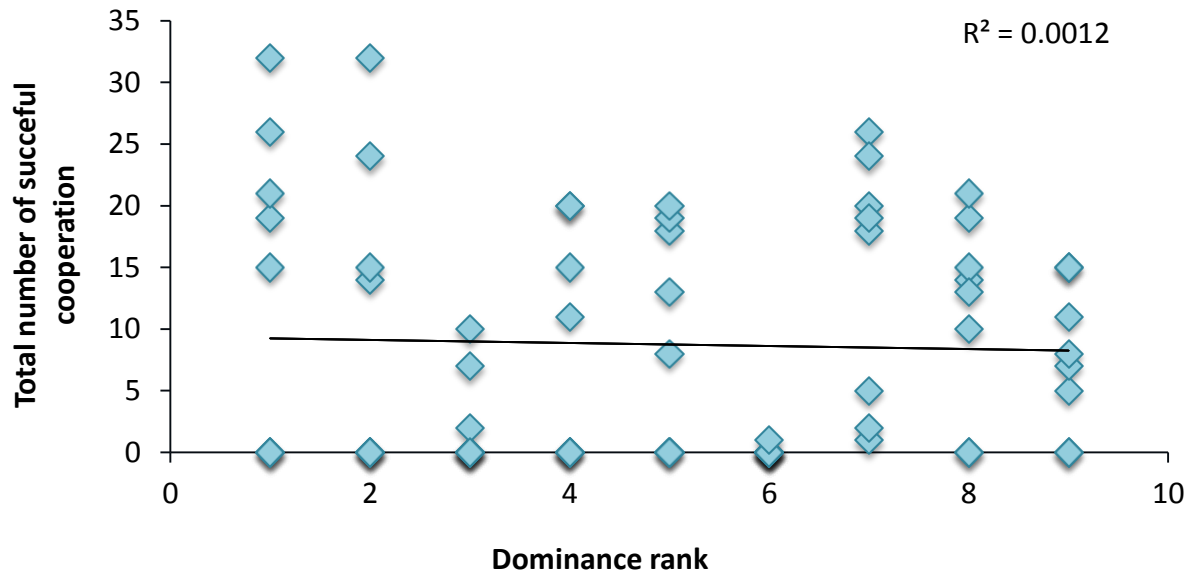
<sup>1</sup> After Bonferroni - correction



**Figure 15:** Mean  $\pm$  S.E.M. number of successful trials during the dyadic test of male-male dyads (MM), male-female dyads (MF) and female-female dyads (FF), MM/MF: \*\* $p < 0.01$ , MM/FF:  $p = 0.059$ .

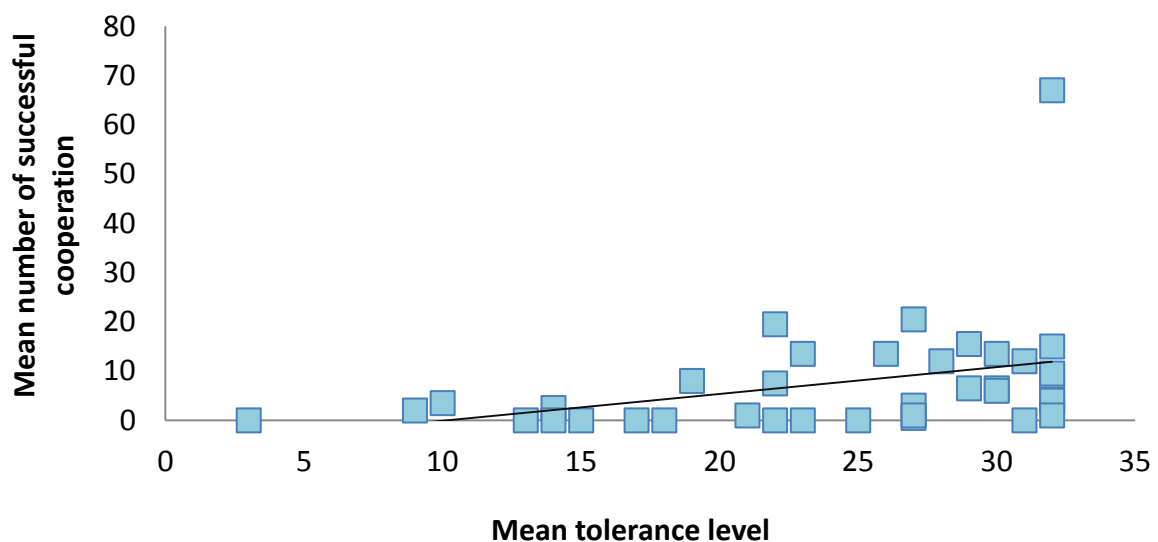


**Figure 16:** Mean  $\pm$  S.E.M. number of successful trials of kin and non-kin, \*\*\* $p < 0.001$ .



**Figure 17:** Relationship between the total number of successful cooperation and the dominance rank each individual has, note that rank 1 is the highest rank.

As in the group test, there is a significantly positive correlation between the number of successful cooperation and tolerance levels, indicating that dyads that are able to tolerate each other on a higher rate also succeed more often during the task (GLMM;  $F_{1, 136} = 39.605$ ,  $\beta = 0.119$ ,  $p < 0.001$ , Figure 18).



**Figure 18:** Positive correlation between the mean number of successful cooperation and the mean tolerance level during the dyadic test. There is a significant positive relationship between both patterns indicating that tolerance levels influence the performance of dyads in the dyadic test set up.

## **6. Discussion**

### **6.1 Summary of the results**

The aim of this study was to investigate whether ravens are capable of solving a loose string paradigm by cooperating with different group members when given the choice with whom to cooperate with as well as when placed in a dyadic set up. Additionally we tried to examine if they did understand that a partner was needed to solve the task successfully. Therefore, we investigated if ravens considered the role of the partner or not. Finally, we aimed to test for the effect of several factors on cooperative behavior and performance of individuals with the task, including tolerance, sex, sex combination, kinship, rank distance and hierarchy. Overall our results indicate that ravens in fact are able to cooperate with a number of group members when confronted with a loose string paradigm. They performed very successfully in solving the task, with a 66.17 % success-rate during the group test and a 27.34 % success-rate during the dyadic set up. When analyzing the data of both control tests (delay and alone) we found no evidence that ravens considered the presence, and possibly, understand the need of a partner in this set up. All individuals performed poorly during both control phases; i.e. they went on pulling when tested alone and did not inhibit their pulling action while waiting for the partners' arrival. Finally, with regard to different factors that might influence their performance, we found that neither sex nor rank distance apparently had any influence on cooperative success. Tolerance, kinship and sex-combination had a clear influence on their performance, however. Additionally we also found that hierarchy had a small effect on how individuals succeeded. With this, tolerant individuals had a higher success in solving the problem than non-tolerant individuals; kin cooperated better than non-kin, mixed dyads performed significant better than male-male dyads but not better than female-female dyads and higher ranked individuals performed slightly better than lower ranked individuals. Interestingly these effects could only be found during the dyadic cooperation set up but not during the group test, in which only tolerance levels acted as constraints on the individual ability to cooperate. This may indicate that ravens do care who is around but not so much when this one is pulling.

## **6.2 Are ravens able to solve a cooperative string pulling task?**

The results show that all individuals were able to solve the loose-string paradigm at least once with different but not all partners. This result matches most previous studies in which different species were able to solve a similar cooperative task; i.e. chimpanzees (Chalmeau and Gallo 1996, Melis et al. 2006a, Hare et al. 2007, Hirata and Fuwa 2007), capuchins (Mendres and de Waal 2000, de Waal and Davis 2003), hyenas (Drea and Carter 2009), elephants (Plotnik et al. 2011), orangutans (Chalmeau et al. 1997b), cottontop tamarins (Cronin et al. 2005) parrots (*Psittacus erithacus*) (Peron et al. 2011) and rooks (Seed et al. 2008). Still, in contrast to most of these studies individuals in our task did solve the problem without any previous training, spontaneously and repeatedly. Apes, and particularly chimpanzees, showed only limited tendencies to cooperate spontaneously and individuals needed at least some training or many repetitions to be successful (Chalmeau and Gallo 1996, Hirata and Fuwa 2007). The only two studies on corvids; i.e. rooks showed similar results in performance in which individuals solved the problem without previous training (Seed et al. 2008, Scheid and Noe 2010). Rooks as well as the ravens in our study were repeatedly able to cooperate within the loose-string paradigm without going through any previous acquisition phase. Moreover, we found that individuals performed significantly better over time. This was true when comparing the first and second round of the dyadic test but also across all sessions. This result might indicate a possible learning effect over time in which each individual increased its mean number of successful trials across all sessions, regardless, of which partner they were paired with. However we also found that not only the mean number of successful trials increased but also the mean number of pulls in general, including both successful and unsuccessful trials, suggesting the increase in success over time can also be explained by motivational factors. Therefore, it remains unclear whether ravens reached a better synchronization, just habituated to the apparatus, or became more motivated and, with this, increased in performance. Still, when considering that individuals participated in at least 30 group sessions before the dyadic test, it is likely that they already were fully habituated to the apparatus. A recent study on chimpanzees examined similar tendencies in performance (Suchak et al. 2014). Here chimpanzees were tested in both a dyadic and triadic set up while having access to all members of the group. As with our ravens, individuals increased their level of success during the second test phase in both dyadic and triadic trials.

However they also showed that, chimpanzees decreased their pulling rate when tested alone, suggesting that the chimpanzees learned about the characteristics of the task. As this was not the case in our study, we suggest that there is no similar learning effect for ravens in this respect.

### 6.3 Do ravens understand the need of a partner to solve the task?

Even though ravens did solve the problem successfully we found no evidence that they also understood the need and importance of the partner. In contrast to chimpanzees (Melis et al. 2006a, b), elephants (Plotnik et al. 2011) and capuchins (Mendres and de Waal 2000), they neither reduced pulling when tested alone nor did they inhibit their pulling action in order to wait for the partners' arrival when confronted with a delay test. Consequently, all individuals performed poorly during both control phases. Their low numbers of successful trials may suggest that ravens within our test set up did not understand that a partner was needed to get the reward. Alternatively, it could be that the birds had problems with inhibiting their behavior. We therefore compared the mean number of pulls when tested alone during the dyadic set up in order to see whether individuals at least decreased their pulling rate when no partner was present over time. Surprisingly, we found that the mean number of pulls when alone did not just stay the same but increased significantly from the first to the second round. This could either be explained through motivational factors in which the individuals got reinforced for pulling (considered to be a self-rewarding behavior) but did not come to relate their own pulling action to that of their partner. Or, it might suggest that the ravens truly did not consider the need of the partner or understand the basic patterns of the task.

Considering a possible self-rewarding behavior, pulling and handling the string might be such a pattern in which the string itself functions as reward, and therefore, would increase the pulling behavior regardless of any understanding of the task. Another explanation might be that the visual presence of the partner might be enough to trigger the pulling behavior. Even though the partner was never able to reach the apparatus the focal individual could hear and see the partner at every point waiting in the other compartment. Therefore further tests might be necessary in which the partner is completely out of sight during the delay phase and alone trials.

Using a delay test and alone trials might be of advantage in order to see whether a species truly understands the need of a partner, however, control trials only make sense when integrated randomly and repeatedly into cooperative trials. Still, most studies in which dyads did show a high success-rate during these control trials, either carried out a previous training or control trials only appeared at the end of all cooperative trials (Mendres and de Waal 2000, Melis et al. 2006a, b, Plotnik et al. 2011). This might lead to a greater learning effect or habituation to this specific situation and takes away any possible flexibility in reacting to different trials in a row, which should be cognitively more demanding. Therefore when repeatedly confronted with the same sequence of trials individuals do get a greater chance to learn to show the right behavior as they do not need to spontaneously adjust their behavior to alternating trials. This could hint towards their ability to learn specific attributes, possibly through try and error, but doesn't tell us much about their understanding of the partner.

Despite all these methodological arguments we need to bear in mind that the ravens' performance compares perfectly to the findings of the study in rooks (Seed et al. 2008, Scheid and Noe 2010). Both corvid species did not respond to the absence of a partner, which stands in contrast to findings in chimpanzees and other primate species such as capuchins or cottontop tamarins as well as elephants (Chalmeau and Gallo 1996, Mendres and de Waal 2000, Cronin et al. 2005, Hirata and Fuwa 2007, Plotnik et al. 2011). This difference is surprising as it has been suggested that corvid species might share the same or similar cognitive abilities as certain primate species. Yet, there are also studies on primates as well as hyenas that reported their difficulties or even failure in waiting for a partner (Chalmeau et al. 1997a, Drea and Carter 2009). Hence, it seems too early to draw conclusions about cognitive mechanisms and taxonomic differences.

#### **6.4 Constraining factors and their influence on partner choice**

Although the ravens did not consider the importance of a partner, they nonetheless succeeded relatively often in cooperating in this paradigm. However, there was a lot of variation in success across the group and dyadic experiment. Therefore, we investigated which factors might explain this variance. First we found no influence of an individual's own sex on cooperative success. However, we found that mixed dyads perform significantly better than male-male dyads but not female-female dyads.

This might be explained due to a clearly defined hierarchy between male and female partners (Braun and Bugnyar 2012), which can lead to less competition of different sex partners compared to same sex partners, causing a higher success rate in solving the problem. Interestingly, when looking at the individual data, the dyad with the highest success in all test parts including tolerance tests, group tests and dyadic cooperation tests, consisted of the two highest ranked males. These males, Laggie and Tom, are brothers who showed a 100 % success rate during both rounds of dyadic cooperation test. This effect might be explained by the fact that both males are not just highly tolerant to each other but actually form a stable alliance, helping each other in conflicts. Furthermore, they are closely related and we generally found that kin did cooperate better than non-kin. Previous studies found such a tendency in other species as well; i.e. chimpanzees (Langergraber et al. 2007, Suchak et al. 2014) and rooks (Seed et al. 2008). Ultimately, better cooperation between kin might also reflect kin-selection (Hamilton 1964a, b).

The fact that the two highest ranked males performed best during all tasks also can be explained through our findings according to the relationship between dominance rank and cooperative success. We found that individuals with higher ranks performed slightly better than individuals with lower ranks. This result also matches with findings on chimpanzee tolerance in which higher ranked individuals tended to approach higher ranked partners more often than others (Suchak et al. 2014). However, in contrast to the chimp study we could not find that dyads with similar ranks had more success than dyads with different ranks, as rank distance appeared to have no influence on cooperative success in our experiment at all. Finally, we found that tolerance acts as a constraint on the individual ability to cooperate. Dyads that tolerated each other more during the tolerance tests also performed better compared to less tolerant dyads and it furthermore might seem that individuals actively choose to cooperate more often with partners they tolerate more. This finding supports the argument that less competition and a higher degree of affiliation does support cooperative success and increases a certain synchronization level also in ravens. It therefore matches findings in other species in which tolerant individuals reached a better performance (de Waal and Davis 2003, Melis et al. 2006a, Hare et al. 2007, Seed et al. 2008, Suchak et al. 2014). In contrast to these studies, all, except the most recent study on chimpanzees (Suchak et al. 2014), presented the apparatus to only a few certain dyads of which individuals were known to be highly or at least to a certain amount, tolerant to each other.



This can be seen as a problem as our results indicate that especially tolerance levels play an important role in providing the possibility to develop cooperative behavior. Although in our study individuals were successful during both the group test and the dyadic set up, there was a significant difference between both test phases. Ravens performed better during the group test than during the dyadic test. This and the fact that not all dyads performed with the same success throughout the test phases suggests that ravens do actively choose with whom to cooperate. A study on chimpanzees examined the possible active choice of certain partners over others, showing that individuals distinguished between partners with whom they had previous success with or not (Melis et al. 2006a, b). Here our results indicate that ravens just as chimpanzees also develop a clear preference with whom to cooperate with after only a few initial trials. Furthermore the difference between both test phases also shows once more that ravens do distinguish between different group members and do understand their relationship to others, as they do not react the same way to every partner during the dyadic tests but show differences in performance (Boeckle and Bugnyar 2012).

## **6.6 Conclusion**

We could show that ravens just as rooks, chimpanzees, capuchin monkeys, hyenas and elephants are able to solve the loose-string paradigm. With regard to the definition we used, in which cooperation is the "... the voluntary 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), ravens are able to cooperate in this task. Taking their poor performance during both control phases, they do not seem to take the role of the cooperation partner into account. However, given the difference in performance during the group test and the dyadic test, ravens seem to care with who they want to be close to the apparatus. Finally, regarding influential factors, we found no effect of kinship, sex-combination or rank on the number of successful trials during the group test but only during the dyadic set up. However tolerance levels appeared to influence their behavior during both test phases. This would suggest that ravens mainly base their decision with whom to cooperate on tolerance levels of the partner. When forced in dyads, other factors seem to play a role on decision making. Finally when comparing all studies on cooperation which use the loose-string paradigm, highly conflicting results were described even sometimes on the same species.

With consideration of all these discussed arguments one should question not only the method; i.e. using pre-training, testing only certain dyads, the sequence of test and control trials etc., but also the paradigm itself. A cooperative string-pulling task might be one among many different tasks to test a certain ability to show cooperative behaviors, but might not be one to use to make big claims on how cooperation works. We therefore suggest testing individuals in different tasks and paradigms, which allow the subjects the possibility to react spontaneously and adjust their behavior in a flexible way to a variation of other individuals, such as in triadic or group settings.

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## Curriculum Vitae

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### Personal Data

Name: Caroline Ritter B.Sc.  
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### Education:

Since March 2012	Master studies of Behavioral-, Cognitive- and Neurobiology at the University of Vienna, Austria
October 2007 – August 2011	Bachelor studies of Biology at the Martin-Luther-University Halle-Wittenberg, Germany Topic of the Bachelor thesis: “Untersuchungen nicht - photischer Zeitgeber auf das Synchronisationsverhalten des Dsungarischen Zwerghamster ( <i>Phodopus sungorus</i> )”
2004 – 2007	Grammar school Johann-Gottfried-Herder at Halle/Saale, Germany
2000 – 2004	Grammar school Europaschule Torgymnasium at Halle/Saale, Deutschland

**Practical courses**

March – October 2011	Internship at the Department of cognitive Biology, Clever Dog Lab in Vienna about “Size discrimination and age effect in domestic dogs ( <i>Canis lupus familiaris</i> )”
June – August 2011	Internship at Max-Planck-Institute for evolutionary Anthropology in the field of great ape research, Wolfgang-Köhler Primate research centre at the zoo of Leipzig, Germany
March – June 2011	Internship at the Wolf Science Centre, Ernstbrunn, Austria about tolerance in dogs and wolves, Range F., Ritter C., Virányi Z., Testing the myth: tolerant dogs and aggressive wolves - in prep.
September – November 2007	Internship at the animal shelter, Bernburg, Germany with focus on dog keeping
April 2005	Internship as animal keeper and veterinarian assistant at the Medical animal centre for pigs, ruminant animals and ungulates, Leipzig, Germany

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**Work experience**

Since December 2011	<u>Wolf Science Centre, Ernstbrunn</u> Employed as trainer assistant in working with dogs and wolves, including hand-raising of both species and in the field of tourism
April – June 2014	
August – November 2014	Department of cognitive Biology, University Vienna Employed as research assistant with coding videos of raven behavioral patterns

**Language skills and IT skills**

Language:	German, first language  English, advanced skills in reading, writing and speaking
IT:	Very good command about Microsoft Office TM tools (Word TM, PowerPoint TM, Excel TM)  Very good command about behavioral biological programs such as, Chronobiological Kit, Fragment Profiler, Observer XT 10 und Solomon Coder  Good knowledge about statistical programs such as, Win stat for Excel, R und SPSS 18.0  Basic knowledge about Origin 50 – data analysis and technical graphics
Drivers License:	European computer drivers license (ECDL)

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**International experience**

November 2006	Study trip, English language course to Bournemouth, England
February 2004 – March 2004	Student exchange with Foothill High-School Pleasanton, California, GAPP – German – American – Partnership Program

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Contribution to meetings:	Ritter C., Virányi Z., Range F., (2012) “Who is more tolerant? Co-feeding in pack living dogs ( <i>Canis lupus familiaris</i> ) and wolves ( <i>Canis lupus</i> )”, poster presentation at the Canine Science Forum 2012 in Barcelona, Spain
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