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„Partner choice in raven cooperation“

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Declaration

Contents of this master thesis were published on June 10th 2016 in the scientific journal PLOS ONE under the name of “Partner Choice in Raven (*Corvus corax*) Cooperation“ (Authors: Asakawa-Haas, K., Schiestl, M., Bugnyar, T. & Massen, J.J.M.). Author Kenji Asakawa-Haas is the first author of this publication, was significantly involved in conducting the experiments (data recording and analysis of the data) and wrote the article. Parts of the publication were used in this master thesis.

Literature:

Asakawa-Haas, K., Schiestl, M., Bugnyar, T., & Massen, J. J. (2016). Partner choice in raven (Corvus corax) cooperation. PloS one, 11(6), e0156962.

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I. Abstract

Although social animals typically cooperate with specific partners, the underlying mechanisms that promote such partner choice, in animal cooperation settings, have received little attention so far. Notably, previous studies compared the effectiveness of collaboration between different dyads but without allowing the subjects to actually choose among different partners. For this study, eleven ravens, *Corvus corax*, were tested by giving them the choice to collaborate with different partners in cooperative string pulling tasks.

In a first experiment subjects could choose to cooperate with either a highly familiar or a (rather) unfamiliar partner, while in a second experiment subjects could choose between a high-affiliated (friend) or low-affiliated (non-friend) partner. The ravens did not show any partner preference based on different levels of familiarity, but did show a preference based on relationship quality, as they did choose to cooperate more often with friends than with non-friends and also had a higher proficiency cooperating with them. In theory, individuals could cooperate two times within a trial if the second partner was able to inhibit pulling and wait for the test subject to arrive. Over the course of the experiments most partner birds learned to wait and inhibited pulling until test subjects arrived.

In order to further investigate the proximate mechanisms of the ravens partner choice in cooperation, a third (open choice) group experiment was designed that helped to identify whether the observed partner preference was a byproduct of a preference for close proximity or on an actual choice based on relationship quality. The setting was designed in such a way that closest proximity did not lead to cooperation and actual cooperation did not require close proximity. The results showed that friends preferred to stay close to each other over cooperating with one another which suggest that tolerance of spatial proximity and not relationship quality is the driving force underlying partner choice in raven cooperation.

Consequently, the results convey an important implication for the interpretation of past and current cooperation studies that did not include actual partner choice and demonstrates the need for future investigations of the proximate mechanisms in animal cooperation.

I.1 Zusammenfassung

Obwohl soziale Tiere regelmäßig kooperieren, sind die zugrunde liegenden Mechanismen der Partnerwahl im Kontext tierischer Kooperation bis jetzt nur wenig erforscht. Frühere Studien verglichen die Effektivität der Kooperation verschiedener Dyaden ohne jedoch den Testsubjekten die Wahl zwischen verschiedenen Partnern zu geben. Für diese Studie wurden elf Raben, *Corvus corax*, getestet. Dabei hatten diese die Möglichkeit zwischen verschiedenen Partnern zu wählen um eine Aufgabe zu lösen welche Kooperation erforderte.

Im ersten Experiment konnten die Testsubjekte zwischen einem bekannten und einem (relativ) unbekannten Individuum wählen, während die Testsubjekte im zweiten Experiment zwischen einem nahestehenden (Freund) und einem neutralen Individuum (Nicht-Freund) wählen konnten. Die Raben bevorzugten weder den bekannten noch den unbekannten Partner, doch bei der Wahl zwischen Freund und nicht-Freund kooperierten die Testsubjekte häufiger mit dem befreundeten Partner und hatten auch höhere Erfolgsquoten. Theoretisch konnten die Testsubjekte in jeder Runde zweimal kooperieren, solange der zweitgewählte Partner gelernt hatte auf das Testsubjekt zu warten. Im Laufe der Experimente lernten die meisten Individuen auf das Testsubjekt zu warten.

Um die proximaten Mechanismen von Partnerwahl im Kontext tierischer Kooperation weiter zu erforschen, wurde ein drittes Experiment durchgeführt. Ziel war es festzustellen ob die Vorliebe für befreundete Individuen aus der Präferenz für räumliche Nähe zu diesen entspringt oder tatsächlich durch aktive Partnerwahl aufgrund von höherer Bindungsqualität. Der Aufbau des Experiments wurde so konzipiert, dass räumliche Nähe nicht zu Kooperation führte und Kooperation keine räumliche Nähe erforderte. Die Ergebnisse zeigten, dass die Präferenz mit Freunden zu kooperieren durch die Neigung sich in deren räumlichen Nähe aufzuhalten entstand und nicht aufgrund höherer Bindungsqualität. Folglich lassen die Ergebnisse dieser Studie wichtige Rückschlüsse auf die Interpretation der Ergebnisse vorangegangener und aktueller Kooperationsstudien zu die keine aktive Partnerwahl ermöglichen und zeigt die Notwendigkeit in zukünftigen Studien auch die zugrunde liegenden proximaten Mechanismen tierischer Kooperation zu erforschen.

II. Introduction

II.1 Cooperation and cooperative behavior

It seems logical that Darwin´s “natural struggle for existence” (1859) should favor competition for the selfish benefit among all living organisms. In contrast to that, a keen observation of nature provides a vast array of examples from all kinds of organisms that cooperate for their mutual benefit (Dugatkin 2002, Bergmüller et al. 2007).

The instances range from billions of cells that cooperate together in a multicellular organism to many examples from cooperative breeding to cooperative hunting in fish (Wong & Balshine 2011, Arnegard & Carlson 2005), mammals (Jennions & Macdonald 1994, Boesch 1994) and birds (Bednarz 1988, Arnold & Owens 1998) to human cooperation that culminates in the formation of whole societies (Nowak 2006, Bergmüller et al. 2007, West et al. 2007, Boyd & Richerson 2009).

Cooperation does offer a lot of benefits in terms of increasing one´s own fitness regarding survival and reproduction. For example, cooperative mobbing of predators by meerkats (*Suricata suricatta*) chases off potential dangers and, therefore, increases survival of group members and offspring (Lima & Dill 1990, Graw & Manser 2006). Another famous example is cooperative hunting in African wild dogs (*Lycaon pictus*) that increases hunting success and, subsequently, breeding success in accordance to group size (Creel & Creel 1995).

Interestingly, cooperation is not limited to members of the same species but can also include members of different species. A well-known example can be found in collaborative hunting of the roving coralgrouper (*Plectropomus pessuliferus*) and giant moray eels (*Gymnothorax javanicus*) that cooperate together to flush out prey which hides in crevices (Bshary et al. 2006, Vail et al. 2014).

Animal cooperation is usually maintained by punishment for non-cooperative behavior as can be seen in chimpanzees and other species (de Waal 1982, Clutton-Brock & Parker 1995).

For my thesis, I am going to use the following definitions for cooperative behavior and cooperation, which are similar to those made by Bergmüller et al. (2007).

Cooperative behavior is defined as a costly action performed by a single individual that benefits another (as in kin selection and all forms of reciprocity), and cooperation is defined as an interaction performed by two or more individuals that results in net benefits for all participants (as in byproduct mutualism).

The following paragraphs cover five widely recognized causations for the evolution of cooperation and cooperative behavior namely kin selection, direct reciprocity, indirect reciprocity, general reciprocity and byproduct mutualism.

II.2 Kin selection

Related individuals often seem to behave altruistically. Hamilton (1964) developed a model that is able to explain the evolution of seemingly altruistic behavior between related individuals. It is called kin selection or inclusive fitness. According to the model an individual benefits another because of their shared genes. In this sense related genes benefit copies of themselves in others and therefore indirectly foster their own distribution within a population (Hamilton 1964, Sachs et al. 2004). Hamilton (1964) discovered that for cooperative behavior to appear the degree of relatedness between the interacting partners has to be higher than the cost to benefit ratio of the altruistic act – a principle that is now known as Hamilton´s rule:

$$\mathbf{r > c/b}$$

Accordingly, the highest probability to observe an altruistic act between two related individuals is when the cost (c) of the donor is low while the benefit (b) to the recipient is high and the relatedness (r) between donor and recipient is also high at the same time. By definition, this explanation is limited to cooperation between members of the same species. It has been argued that a prerequisite for this mechanism is at least associative learning, in the form of a simple rule like “everybody in my nest is kin” (Komdeur & Hatchwell 1999, Sachs et al.

2004) or more elaborate forms of kin recognition such as individual or class-level recognition (Tibbetts & Dale 2007).

One of the many examples for kin selection is found in chestnut-crowned babblers (*Pomatostomus ruficeps*), an obligate cooperatively breeding bird, where non-breeders help to raise offspring that are not their own. The helpers provide more help the closer they are related to the offspring (Browning et al. 2012).

II.3 Direct reciprocity

Remarkably, also unrelated individuals sometimes seem to behave altruistically since not always cooperative interactions result in an equal and immediate payoff for all participating partners. In these cases, the payoffs for one of the partners will be unequal or delayed in time. Trivers (1971) developed a model that may explain why cooperative behavior among unrelated individuals has evolved. It is called reciprocal altruism (Trivers 1971) or direct reciprocity (Nowak 2006, Clutton-Brock 2009). Unlike kin selection, the model of reciprocal altruism is able to explain cooperative behavior between members of the same species as well as between members of different species (Trivers 1971). In reciprocal altruism the donor performs a costly act to benefit the recipient and the latter returns the favor later by reciprocating a benefit back to the donor (Sachs et al. 2004). In this case, Axelrod and Hamilton (1981) demonstrated that for an altruistic act to arise the possibility for another encounter between the interacting partners has to be higher than the cost to benefit ratio of the altruistic act:

$$\mathbf{w > c/b}$$

Correspondingly, the highest probability for an altruistic act between two unrelated individuals to occur (same or different species) is when the cost (c) of the donor is low while the benefit (b) to the recipient is high and the probability (w) of an another encounter between the two individuals is also high at the same time. However, this model requires the interaction partners to have at least some rudimentary cognitive capacities like individual recognition and some form of memory of past interactions (Hammerstein 2003, Stevens & Hauser 2004, Clutton-Brock 2009, McAuliffe & Thornton 2014). A famous example for

reciprocal altruism is allogrooming in impalas. A typical grooming event involves around six to twelve reciprocal exchanges of grooming and is suggested to have evolved because these acts reduce ectoparasite load on body areas that a sole impala cannot reach on its own (Hart & Hart 1992).

II.3.1 Cooperative behavior that turns into reciprocal altruism

Per definition cooperative behavior refers to a costly action of one individual that benefits another hence it can be seen as an “altruistic interaction”. In the case of related individuals the action may not be truly “altruistic” because of the inclusive fitness benefits. In regard to unrelated individuals cooperative behavior always starts with an altruistic action and, once it has been reciprocated, it turns into reciprocal altruism (Noë 2006).

II.4 Indirect reciprocity

A later model on reciprocity points out how cooperation within groups can evolve without having the recipient return the favor directly. It is called indirect reciprocity. In indirect reciprocity the donor benefits the recipient even if the recipient is unlikely to be able to reciprocate the favor. In this case, the donor´s benefit is good reputation within the group. As a result the donor is more likely to be rewarded with cooperative acts by other members of the group (Nowak 2006). Especially, in human societies cooperative interactions are often asymmetric in the sense that the “altruistic” act of the donor is unlikely to be reciprocated by the recipient: “We help strangers who are in need. We donate to charities that do not donate to us.” (Nowak 2006). Experimental work shows that, in cooperation games, humans tend to give more often to individuals who had been generous to others before (Wedekind & Milinski 2000). An important prerequisite for this model is an assessment system like image scoring (Nowak & Sigmund 1998, Bergmüller et al. 2007) and, therefore, evolution should favor small, interacting groups for this behavior to occur in nature (Boyd 2002). An example for indirect reciprocity and image scoring between two animal species can be found in the longnose parrotfish (*Hipposcarus harid*) that chooses between different cleaner fish after observing the cleaner´s behavior with a previous client (Bshary 2002).

II.5 Generalized reciprocity

The model of generalized reciprocity may be able to explain the evolution of cooperative behavior in some species without the need for individual recognition and without advanced cognitive abilities. In generalized reciprocity an individual bases its decision, to cooperate or to defect, on the outcome of the last encounter independently of the interaction partner´s identity (Pfeiffer et al. 2005). An example for generalized reciprocity was found in female rats which were trained to pull down a lever in order to feed an unfamiliar individual. The rats were more likely to pull down the lever when they were helped previously by another unfamiliar individual (Rutte & Taborsky 2007).

II.6 Byproduct mutualism

For almost three decades the concept of reciprocal altruism has been the prime explanation for the evolution of cooperation among non-related individuals. But extensive scientific inquiry, during those years, revealed that definite examples for reciprocal altruism are, in fact, rare in nature (Hammerstein 2003, Frank 2003, Connor 2007, Leimar & Hammerstein 2010). Current research suggests that animals most often cooperate out of their common interest while the resulting benefits are distributed mutually among them (Brown 1983, Dugatkin 1997, Leimar & Connor 2003, Bergmüller et al. 2007, Connor 2007, Leimar & Hammerstein 2010).

In the model of byproduct mutualism an individual performs a self-serving act that benefits another individual as a byproduct of its selfish action (West 1975, Brown 1983, Bergmüller et al. 2007, Leimar & Hammerstein 2010). These byproducts can be directed one-way, the counterpart receives incidental benefits (as in cooperative behavior), or two-way, both or more partners receive benefits from another (Sachs et al. 2004). For example, consider two individuals that are more successful hunting large prey together - than each individual hunting alone - then the act of cooperation results in (two-way) byproduct benefits for both partners (Bergmüller et al. 2007, Connor 2007). Additionally, in the case of two-way byproduct mutualism animals suffer immediate costs or penalties for not behaving cooperatively. In other words, the immediate net benefits for cooperation outweigh the benefits of cheating (Dugatkin 1997).

A famous example for byproduct mutualism is group hunting in lions (*Panthera leo*). Lions hunt in groups when stalking large prey that a single lion cannot take down alone, while they hunt solely when they are stalking smaller prey (Scheel & Packer 1991, Dugatkin 1997). Another well-known example for mutualism in lions can be found in male coalitions for territory defense (Grinnell et al. 1995).

II.7 The prisoner´s dilemma

Behavioral research points out that cooperation (as in byproduct mutualism, where all partners get immediate benefits) and cooperative behavior (as in reciprocal altruism, where partners exchange altruistic behaviors over time without leaving all partners with immediate benefits) among animals are very similar to the prisoner's dilemma game of modern day economists (Trivers 1971, Noë 1990, Clutton-Brock 2009). In this game two individuals are constrained to interact with each other. Both partners can decide to either cooperate or to defect. The highest payoff (R = Reward), for the group, is gained when both partners cooperate, and the lowest payoff (P = Penalty), again for the group, is gained when both partners defect. Hence, from the group´s perspective, it seems logical to always cooperate. The dilemma is that from an individual perspective the absolute highest payoff (T = Temptation) is gained when oneself defects while the other party cooperates, and the absolute lowest payoff (S = Sucker´s payoff) is gained when the situation is vice versa. The payoffs are set up as follows (T > R > P > S). Both partners are confronted with the problem that, without any further knowledge about the partner´s action, it always seems more attractive to defect than to cooperate since T is better than R and P is better than S (Dugatkin 2002). It appears to be logical that natural selection would always favor defection but that leads to a suboptimal solution, payoff P, since mutual cooperation would have led to payoff R (Poundstone 1992).

II.7.1 The strategy of generous tit-for-tat

Although, it makes sense for an individual to always defect in one-time versions of the prisoner´s dilemma it does not so in iterated versions of the game. If the probability of meeting the other partner again is over a specific critical value, a strategy that is called generous tit-for-tat outcompetes all other strategies in iterated versions of the prisoner´s dilemma (Axelrod & Hamilton 1981, Dugatkin

1997, Riordan 2000, Rand et al. 2009). In this strategy one party starts with cooperation, then just mirrors the actions of the partner and forgives one-time defection to compensate for possible errors. Consequently, this strategy is able to (r)establish cooperation within and across populations.

II.7.2 The need for further investigation

Even though, generous tit-for-tat represents a powerful strategy that may enable humans and some animal species alike, to benefit from cooperative behavior and cooperation, while successfully preventing defectors from exploiting cooperators, it is questionable if all animal species fulfill the cognitive requirements to do so. Therefore, more proximate questions about the underlying mechanisms that promote cooperation need to be further addressed, especially how individuals choose their specific cooperation partners.

II.8 Ultimate and proximate mechanisms of cooperation

While the ultimate causations of cooperation and cooperative behavior have been the prime focus of past research, the proximate mechanisms that promote individuals to cooperate or to defect are still under-examined (Brosnan & de Waal 2002). According to Tinbergen, a phenomenon in nature can only be fully understood when analyzed on ultimate and proximate levels (Tinbergen 1963, Bateson & Laland 2013).

Social animals constantly decide with which individuals better to cooperate and with which not to (Conradt & Roper 2005). The spectrum of possible decision rules includes taking subsequent competition over rewards into account (de Waal & Davis 2003), deciding if cooperation is necessary at all or selecting the more effective collaborator among two cooperation partners (Melis et al. 2006b).

According to the famous rule $w > b/c$ by Axelrod & Hamilton (1981), a high probability of another encounter between two individuals facilitates the occurrence of cooperative interaction. Therefore, a preference to cooperate with familiar over unfamiliar individuals in social animal species is likely since the behavior of the collaboration partner can be foreseen from previous encounters and, maybe even more importantly, a potential loss can be compensated later (Trivers 1971). Such a preference may be an evolved strategy against cheating

(Hammerstein & Noë 2016) and represents a possible proximate mechanism for partner choice in cooperation. Examples for a preference to associate or to pair up with familiar individuals can be found in fish (Magurran et al. 1994) and birds (Bradshaw 1992, Choudhury & Black 1994). These ideas and findings led to the creation of the first experiment in which we gave one individual the choice to cooperate with either a familiar or unfamiliar partner.

As social animals live in groups, frequently occurring interactions between members lead to the formation of differential relationships. A close social relationship represents an ongoing chain of positive past interactions hence it is a strong indicator for positive future interactions and establishes some form of trust (Hinde 1976, van Schaik & Aureli 2000). Extensive research concludes that close social relationships result from continuous positive interactions stimulating partner-specific emotions, which are then memorized in a form of attitudinal/emotionally mediated bookkeeping (Brosnan & de Waal 2002, Schino & Aureli 2009). Regarding social behavior, humans and animals may base most of their decisions on the present partner specific emotional states (Aureli & Schaffner 2002, Aureli & Whiten 2003, Aureli et al. 2008) since it allows individuals to keep track of past interactions without the need for complex cognitive abilities (Schino et al. 2007, Schino et al. 2009 and Schino & Aureli 2009).

On the physiological level, oxytocin and endorphins have been proposed to mediate emotional bookkeeping. Oxytocin, a neuropeptide that strengthens mother-child bonding and other relationships in mammals, is sensitive to the quality of social relationships and, therefore, might help to keep track of past affiliative interactions (Berra 2014). In wild chimpanzees grooming elevates oxytocin levels only when the donor and the receiver have been bound previously (Crockford et al. 2013). Moreover, endogenous opioids like endorphins give feedback about how pleasant a social interaction between mother and child is (Panksepp et al. 1994).

The terms friendship (in humans) and close social association (in animals) refer to very similar phenomena, if not the same phenomenon. In particular, both terms relate to non-kin individuals that frequently interact with each other in an

affiliative manner (Massen et al. 2010). Human friendship and animal close social association are both unconditional, at least on the short term, which is a defining characteristic of this phenomenon (Davis & Todd 1985, Clark & Grote 2003, Massen et al. 2010).

Social psychology has delivered a considerable amount of evidence that humans do not carefully monitor the given and received benefits in close social relationships such as friendships, but they do the opposite when dealing with strangers (Fiske 1992, Fiske & Tetlock 1997, Silk 2003). In addition, humans help friends even when it is unlikely that they will be able to repay the favor (Tooby & Cosmides 1996). Experimental work showed that humans apply partner choice in cooperation games as they cooperate more often with, and donate higher amounts of money to, friends versus strangers in iterated prisoner´s dilemma games (Majolo et al. 2006).

Similar findings in social animals suggest differential preferences for friends and strangers in animals as well. A study in wild, male chimpanzees revealed a significant correlation between affiliation (such as association, grooming and proximity) and cooperation (such as alliances, meat sharing and boundary patrols). Importantly, the affiliation and cooperation patterns between most test subjects could not be explained by kin selection (Mitani et al. 2000).

Social tolerance, an integral part of relationship quality and hence an indicator for close social association (Massen et al. 2010), has been the predictor for cooperation in several animal species such as chimpanzees, *Pan troglodytes,* (Melis et al. 2006a), bonobos, *Pan paniscus*, (Hare et al. 2007), rooks, *Corvus frugilegus*, (Seed et al. 2008) and ravens, *Corvus corax*, (Massen et al. 2015). In particular, these results revealed that the higher the inter-individual tolerance within a dyad of two cooperators was, the more often both individuals cooperated.

However, these experiments tested the cooperation partners in dyads and did not allow subjects to choose among partners. Thus, the question remains if animals actually apply partner choice when given the possibility to cooperate with either a high or a low affiliated individual. A current study that allowed for partner choice in an open cooperation setting on chimpanzees identified a

preference based on social tolerance arising from kinship or low rank distance (Suchak et al. 2014). In addition, a similar preference has been found in another open choice experiment with wild Barbary macaques, *Macaca sylvanus*, where social tolerance was a prerequisite for cooperation to start at all, whereas a strong social bond helped to maintain cooperative interactions over time (Molesti & Majolo 2016). These thoughts led to the creation of the second experiment in which we gave an individual the choice to cooperate with either a friend or a non-friend.

Up to this point, the proximate mechanisms that drive partner choice in mutual cooperation settings still have not been identified since most of the experiments done so far did either not allow subjects an actual choice between at least two different partners or the settings did simply not allow to distinguish if partner choice was based on social tolerance or relationship quality as a whole. In order to clarify whether partner choice in ravens is a byproduct of a preference for close proximity or based on an actual choice between cooperation partners, due to relationship quality, we designed a third experiment.

II.9 The choice for ravens

Ravens are highly social and they usually form several affiliative bonds over the course of their lives (Heinrich & Bugnyar 2007). They develop differential relationships with their conspecifics which are even comparable to those of primates in complexity (Fraser & Bugnyar 2010b). Ravens are not only able to distinguish between individual group members, but remember them up to several years while even distinguishing between affiliates and non-affiliates (Boeckle & Bugnyar 2012, Bugnyar 2013). Furthermore, ravens frequently cooperate in various contexts (Kilham 1989, Heinrich 2011) such as foraging (Heinrich & Marzluff 1995, Marzluff et al. 1996) and hunting (Hendricks & Schlang 1998).

II.10 Research questions

I aimed to identify preferences in ravens regarding partner choice with the help of a cooperative string pulling task that allowed test subjects to choose between two distinct cooperation partners (Asakawa-Haas et al. 2016).

Research question 1

At first, I investigated whether ravens have a preference to cooperate with familiar over relatively unfamiliar individuals. As ravens are social animals, it was likely that they would show a tendency to cooperate with familiar individuals which they know for a longer period of time than newcomers to the group.

Research question 2

Next, I tested the individuals for a preference to cooperate with friends over non-friends. For the same reason as above, ravens should be likely to exert a preference for individuals with whom they have a close social relationship as a high relationship quality reflects consequent positive interactions over time.

Research question 3

In a third experiment, I gave all eleven individuals the possibility to cooperate freely with each other at two distinct string pulling apparatuses in order to identify the proximate mechanism on which a given partner choice preference might be based on i.e. tolerance for proximity or relationship quality.

III. Material & Methods

III.1 Test subjects

I have tested eleven captive ravens that were born in the years 2010-2012 (age 3-5 years) and that were derived from different nests in Austria, Germany and Sweden (Tab 1). Nine of the male and female individuals arrived in their current aviary at the age of 3-5 weeks and were kept together ever since. Two of the birds, Joey (♀) and Rocky (♂), joined the group a 2-3 weeks before testing. Therefore, the two new birds were regarded as being new and relatively unfamiliar to the group. All of the ravens were hand-raised, used to frequent human contact and had participated in previous behavioral experiments except for the newcomer Rocky who had never participated in experiments before. Furthermore, all individuals were marked with different color rings to ease identification.

Table 1: List with names of all eleven birds and their characteristics such as name, sex, age, origin and kinship relations.

Name	Sex	Age	Origin	Kinship
Tom	♂	3 years	Bavaria (DE)	Family I
Laggie	♂	3 years	Bavaria (DE)	Family I
Adele	♀	3 years	Bavaria (DE)	Family I
Horst	♂	3 years	Stockholm (SE)	Family II
George	♂	3 years	Stockholm (SE)	Family II
Louise	♀	3 years	Stockholm (SE)	Family II
Nobel	♀	3 years	Stockholm (SE)	Family II
Paul	♂	3 years	Wels (AT)	Family III
Rufus	♂	3 years	Haag (AT)	Family IV
Joey	♀	5 years	Austria (AT)	Family V
Rocky	♂	4 years	Austria (AT)	Family VI

III.2 Housing conditions

The birds were kept together in an outdoor aviary (15 m x 15 m x 5 m) that consisted out of five compartments (Fig 1). Each compartment, the front, left, right and back compartment plus the Petrarium could be separated from each other by closing the sliding doors. The group had full access to all compartments when no experiments were being conducted. All individuals had ad libitum access to water. Their diet was composed out of a variety of meat, bones, eggs, yogurt, curd, bread and fruits. They were fed twice a day and were never food deprived for the experiments.

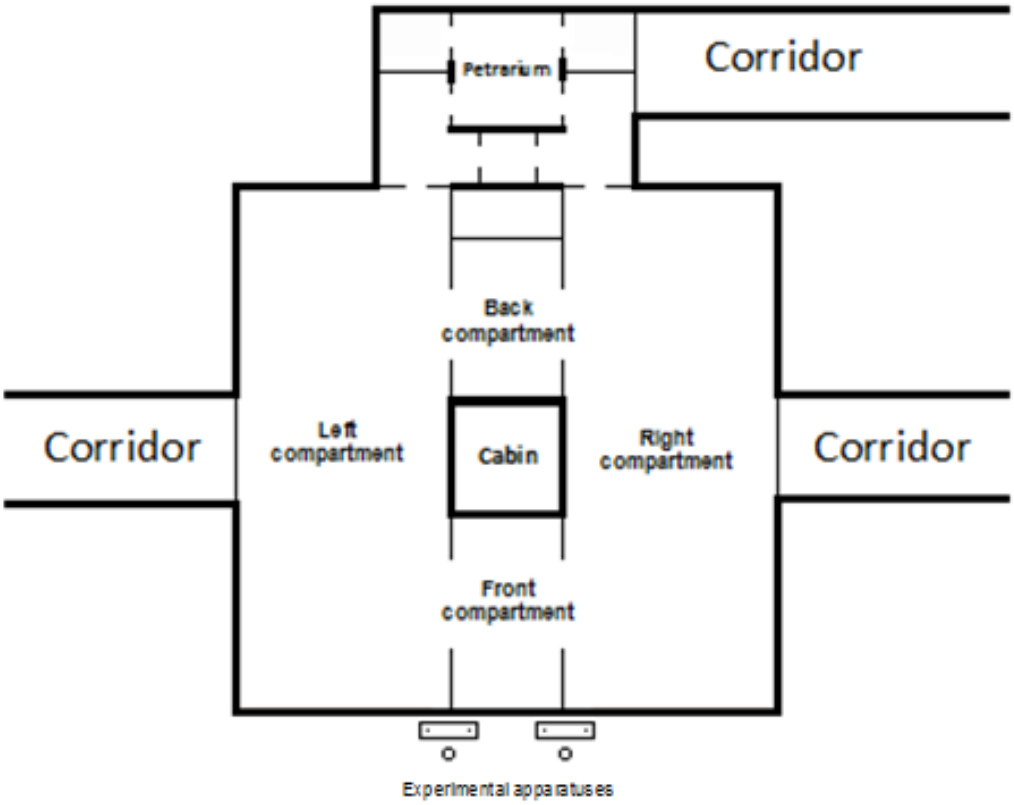


Figure 1: Blueprint of the outdoor aviary in which the ravens were housed. For the experiments the front, left and right compartments were used to separate the test subjects and partner birds. The two experimental apparatuses were placed in front of the aviary as indicated at the bottom of the sketch. The corridors led to the surrounding aviaries.

III.2.1 Ethical note:

This study was carried out according to Austrian law and followed the statutes of the University of Vienna regarding animal research. The experiments received authorization and supervision by the ethical board of the behavioral research group at the faculty of Life sciences, University of Vienna (case number: 2015-003). All behavioral experiments were non-invasive. The test subjects could choose to participate on a voluntary basis and could stop to participate at all times. After the study, the ravens remained in their enclosures at the Haidlhof Research Station.

III.3 Experimental apparatus

Two experimental apparatuses (Fig 2 & Pic 1), called the loose string paradigms (Hirata 2003), were fixed outside the aviary just next to the metal fence surrounding the aviary. The loose string paradigm has been used successfully in several studies e.g. in primates (Melis et al. 2006a, Hare et al. 2007), in elephants (Plotnik et al. 2011) and in corvids (Seed et al. 2008, Massen 2015). An apparatus consisted out of a big wooden board (200 cm x 40 cm x 2 cm) with two metal tracks on the top on which a small wooden board (100 cm x 20 cm x 2 cm) was fixated. The small board could move along the two metal tracks. Like a drawer, the small board could be pulled to the metal fence or away from it. Two cut nails, without a head, were attached onto the side of the small board facing the aviary. During the experiments little pieces of cheese were attached to them as rewards for the subjects. Two metal ring bolts were fixed on the top of the small board and a string was pulled through them. At the beginning of every training or experimental trial the small board was pulled away from the aviary and both ends of the string were placed inside the compartments. When two birds pulled simultaneously at each end of the string, the small board with the reward was pulled into their reach. When only one bird pulled or when both birds pulled asynchronous, the string was pulled through the ring bolts and the subjects could no longer retrieve any rewards.

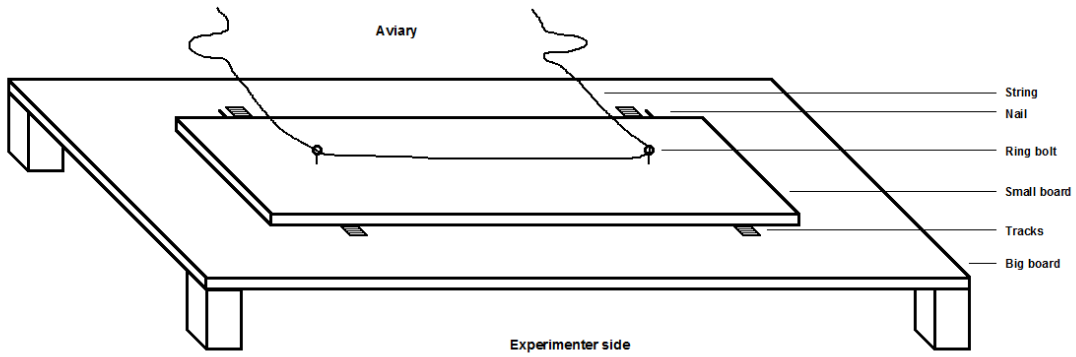
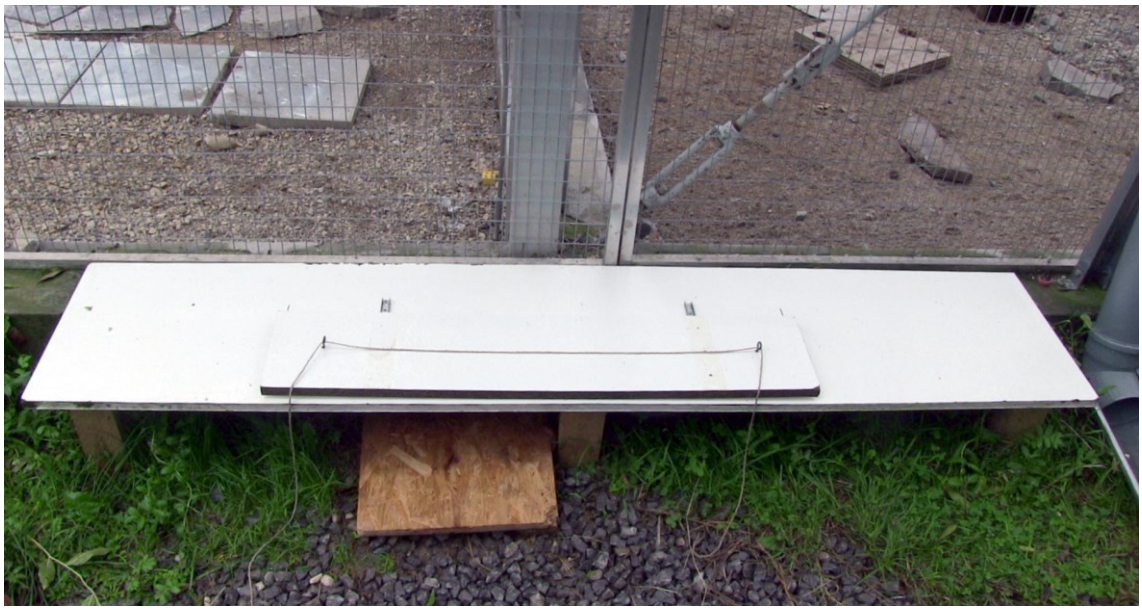


Figure 2: Blueprint of the experimental apparatus (front view). The tracks kept the small board in line when it was pulled towards the aviary by the subjects or when pulled away by the experimenters (Asakawa-Haas et al. 2016).



Picture 1: The picture shows the left experimental apparatus from the front view. The left compartment is located on the upper left, and the middle compartment is located on the upper right corner of the picture. The wooden panel, in front of the apparatus, was used as a seat by the experimenters.

III.4 Habituation phases

III.4.1 Habituation to experimenters and apparatuses

Six weeks before habituation for experiment No. 1 and No. 2, the ravens were habituated to the presence of experimenter K.H. for two times per week. This phase lasted from June to July 2014. The birds were already used to experimenter M.S. hence they did not receive any habituation on this matter. The nine original group members already had previous experience with the loose string paradigm. Thus, after the third week, the two experimental apparatuses were installed in front of the aviary in order to get the whole group accustomed to them. Except for the newcomer Rocky, all subjects were used to being separated due to previous behavioral experiments. At the end of this habituation phase, the individuals did not show any obvious signs of stress to the presence of experimenter K.H., experimenter M.S., the separation process or the experimental apparatuses.

III.4.2 Habituation for experiment No. 1 and No. 2

Before the experiments No. 1 and No. 2 started, each test subject received 40 trials were it could pull cooperatively with one partner bird at one of the apparatuses. Out of those 40 trials each bird got 20 trials in the middle compartment (position of the test subject) as well as 10 trials in the left and 10 trials in the right compartment (position of the partner bird) to get them accustomed to the situation. The order in which the birds were put into the compartments was counterbalanced over the individual. Importantly, individuals that were put together in the training as partners were not put together later in the experiments to eliminate any bias that could result from previous experience with a given partner at hand. This habituation phase lasted from July to August 2014.

III.4.3 Habituation for experiment No. 3

The second habituation phase was conducted subsequently to the experiments No. 1 and No. 2 to get the birds accustomed to the situation in experiment No. 3 (open choice experiment). Here, one of the sliding doors between the middle compartment and either the left or the right compartment was opened. This allowed a group of ravens to access one of the apparatuses and to choose

freely with whom to pull. To ensure that every bird received a chance to pull, the group was separated into a dominant group (Tom, Laggie, Horst, George, Louise and Nobel) and a subdominant group (Adele, Paul, Rufus, Joey and Rocky). Each group received 50 trials and was allowed to pull at one of the apparatuses. This phase was conducted in October 2014.

III.5 Experiments

III.5.1 Experiment No. 1: Familiar vs. Stranger

In the first experiment, I wanted to investigate whether the test subjects had a preference to cooperate with either a familiar bird or a relatively unfamiliar bird (stranger). Hence, triads were formed that incorporated one test subject, one familiar bird and one stranger. For the role of the familiar bird I chose individuals that were intermediately affiliated to the test subjects in order to avoid a possible bias that could result from differential intensities of their bonding. For the role of the stranger I chose one of the new individuals (5 x Joey and 4 x Rocky). As a result, only the nine initial group members were used either as test subjects or familiar birds. The newcomers always had to take the role of the stranger (Tab 2). Therefore, the sample size was nine test subjects (n=9). Every triad was tested for 1 session with 20 trials resulting in 9 sessions with 180 trials in total. This experiment was conducted in August 2014.

Table 2: List showing all eleven birds and their roles in the Familiar vs. Stranger experiment.

Test subject	Familiar	Stranger	Sex
Tom	Horst	Rocky	♂+♂+♂
Laggie	Nobel	Joey	♂+♀+♀
Adele	Louise	Joey	♀+♀+♀
Horst	Rufus	Rocky	♂+♂+♂
George	Laggie	Rocky	♂+♂+♂
Louise	Adele	Joey	♀+♀+♀
Nobel	Paul	Rocky	♀+♂+♂
Paul	Nobel	Joey	♂+♀+♀
Rufus	Nobel	Joey	♂+♀+♀

III.5.2 Setting

Three subjects were separated for a test session. The test subject was put into the middle compartment and each of the remaining partner birds was put in the left or right compartment (Fig 3). Both experimenters positioned themselves in front of the experimental apparatuses.

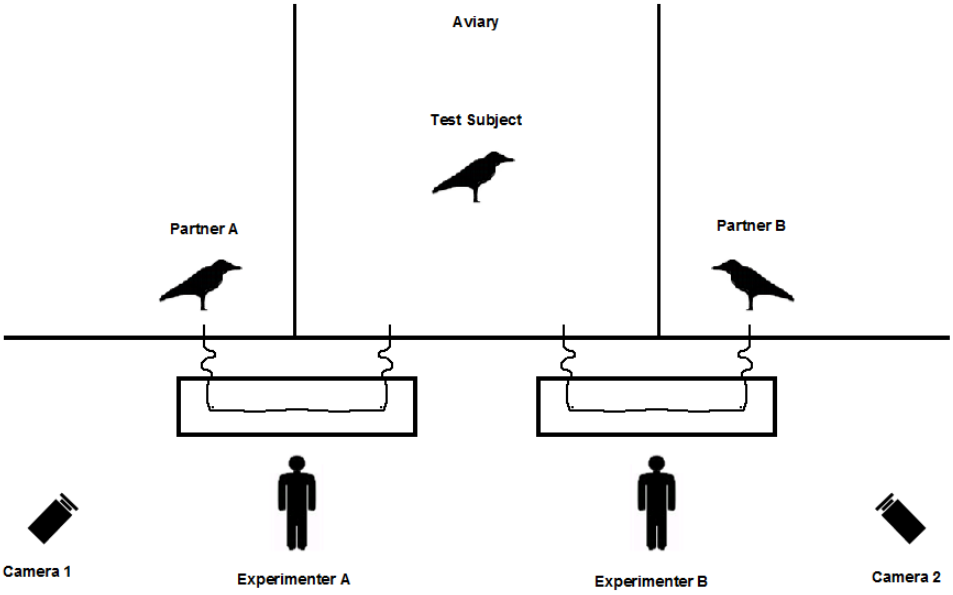


Figure 3: Scheme of the setting for experiments No. 1 and No. 2. The test subject had the choice to either cooperate with the left or right partner bird (Asakawa-Haas et al. 2016).

III.5.3 Procedure

To prepare a trial both experimenters stuck the rewards, small pieces of cheese (Edamer), on the cut nails that were attached to the experimental apparatus (Fig 2). Subsequently, the experimenters made sure that both partner birds were waiting in front of the boards and that the test subject was standing in the center of the middle compartment, with the use of some cheese as bait, before a test trial started. On a vocal command both experimenters simultaneously put the ends of the strings into the compartments (Pic 2). Both experimenters coordinated their actions with these short, spoken commands since they had to act simultaneously during the experiments. The role of the speaker alternated after each trial to counterbalance for any bias by the experimenter´s vocalized commands. Additionally, the experimenter´s positions alternated every 5 trials

and every 10 trials the positions of the partner birds were changed i.e. partner A was placed in the position of Partner B and vice versa to avoid any possible side bias (Fig 3).

Picture 2: The picture shows both experimenters and three subjects during the experiment. The test subject (in the middle) had already decided to go over to the left partner bird before the strings were completely put into the aviary.

III.5.4 Conditions

In order to get the reward, the test subject had to approach either Partner A or Partner B and to cooperatively pull the ends of the string together with the chosen partner (Pic 3). When only one bird pulled or when the test subject and the partner bird pulled asynchronous, the string was pulled through the ring bolts and the reward could not be retrieved anymore (Pic 4). Theoretically, the test subject could cooperate with both partner birds if they waited long enough for the test subject to arrive.

Picture 3: The picture shows a successful cooperation pull. The test subject and one of the partner birds pulled the strings simultaneously therefore they were successful in retrieving the reward.

Picture 4: The picture shows an unsuccessful cooperation pull. The test subject and one of the partner birds pulled the strings asynchronous therefore they were unsuccessful in retrieving the reward.

III.5.5 End criteria

The trial could end when the test subject successfully retrieved both rewards (end criteria 1), one reward but with no possibility to retrieve the other (end

criteria 2) or when he was not successful in retrieving any reward and without the possibility to pull further (end criteria 3). Additionally, a maximum time period of two minutes per trial was set for the case nothing happened (end criteria 4).

III.5.6 Experiment No. 2: Friend vs Non-friend

In the second experiment, I wanted to investigate whether the test subjects had a preference to cooperate with either a friend (a high affiliated individual) or a non-friend (low affiliated individual). Setting, procedure, conditions and end criteria for experiment No. 2 were similar to experiment No. 1 only the familiar and the stranger were exchanged with a friend and a non-friend. Notably, at the time of experiment No. 2 the two unfamiliar individuals (Joey and Rocky) had 5-6 weeks to be integrated into the group thus I used them as test subjects as well. As a result, all eleven group members (n=11) could be used as test subjects as well as friends and non-friends (Tab 3). Every triad was tested for 1 session with 20 trials resulting in 11 sessions with 220 trials in total. This experiment was conducted in August to September 2014.

Table 3: This list shows all eleven birds and their roles in the Friend vs. Non-friend experiment.

Test subject	Friend	Non-friend	Sex
Tom	Laggie	George	♂+♂+♂
Laggie	Adele	Louise	♂+♀+♀
Adele	Tom	Paul	♀+♂+♂
Horst	Louise	Adele	♂+♀+♀
George	Nobel	Adele	♂+♀+♀
Louise	George	Paul	♀+♂+♂
Nobel	Horst	Rufus	♀+♂+♂
Paul	Rufus	Horst	♂+♂+♂
Rufus	Adele	Louise	♂+♀+♀
Joey	Rocky	Nobel	♀+♂+♀
Rocky	Adele	Horst	♂+♀+♂

III.5.7 Experiment No. 3: Open choice

In the third experiment, I investigated how the birds would position themselves when they, as a group, had free access to all three compartments and both experimental apparatuses. Hence, all eleven birds were tested at once and the sliding doors between left, middle and right compartment were opened. Notably, every bird could choose freely where and with whom to cooperate (Fig 4). As a result, the sample size was eleven test subjects (n=11). In particular, I investigated if friends preferred to cooperate together at an apparatus (i.e. if they applied actual partner choice based on relationship quality as a whole) or if they preferred to just stay close to each other in the middle compartment (i.e. if they chose tolerance of spatial proximity over cooperation). The group was tested for 7 sessions with 100 trials per session resulting in 700 trials in total in order to give all birds the possibility of pulling. The setting for experiment No. 3 differed from the previous experiments regarding the number of simultaneously tested individuals and, regarding the procedure, the experimenters changed positions every 10 trials. The conditions and end criteria stayed the same. This experiment was conducted in October to November 2014.

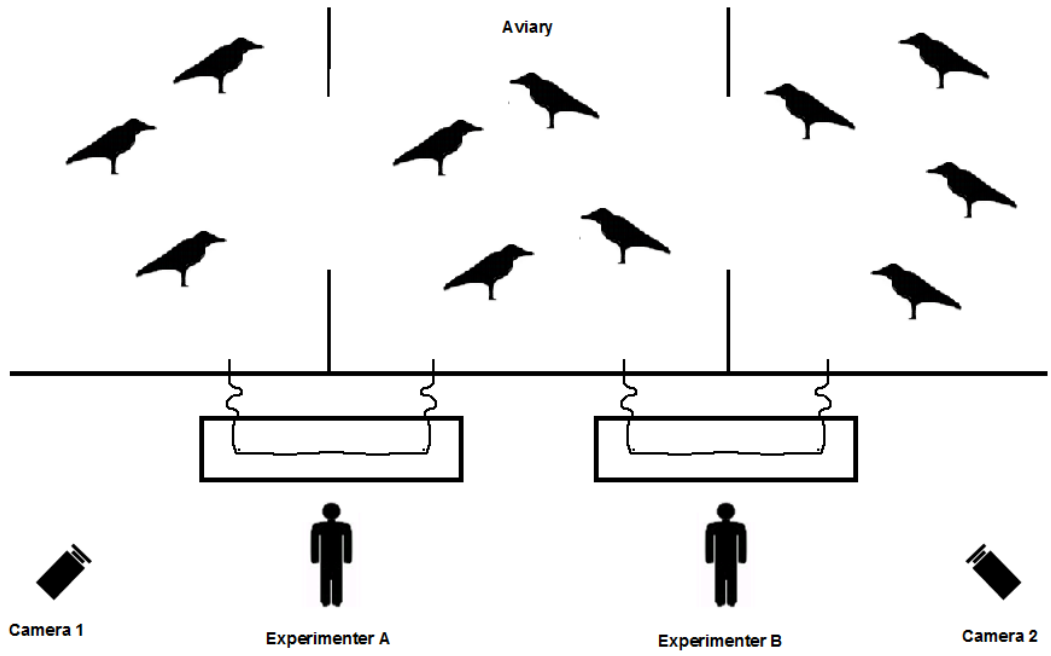


Figure 4: Scheme of the setting for experiment No. 3. The birds could freely position themselves in the left, middle or right compartment (Asakawa-Haas et al. 2016).

III.6 Measurements

The focal animal samplings were recorded with a HD camera (Canon LEGRIA HF G10) while the experiments were recorded with two HD cameras of the same model and were positioned next to the experimental apparatuses (Fig 3 & Fig 4).

III.6.1 Measurements in experiment No. 1 and No. 2

I scored the test subject´s first and, if applicable, second partner choice within each trial i.e. which partner bird the test subject approached first or second within a trial. When the test subject positioned itself, in a distance of at least 20 cm in front of either the left or the right experimental apparatus, the approach was counted as such.

In addition, I scored with which partner bird the test subject succeeded in a cooperation pull. If a test subject and the chosen partner succeeded in pulling the rewards into their reach the successful cooperation pull was counted as such. Both variables were investigated since they could, at least in theory, differ from each other.

III.6.2 Measurements in experiment No. 3

I scored which birds engaged successfully in a cooperation pull at the apparatuses (choice to cooperate) and which birds stayed close to each other in the middle compartment while pulling with another partner (tolerance of spatial proximity without cooperation).

III.6.3 Relationship quality - familiars, friends and non-friends

Before the start of the experiments it was necessary to assess the relationship qualities among all subjects. Therefore, the birds affiliative (socio-positive) and agonistic (socio-negative) interactions were scored by the use of focal animal samplings taken in April-Mai, right before experiments No. 1 and 2, as well as taken in August-September, right before experiment No. 3. The samplings recorded 5 min per animal about 2-3 times per week on video. In sum 36.75 h (M = 3.33 ± S.E. = 0.25 h/bird) of observations were used for this study and were subsequently analyzed by a research assistant from the Department of Cognitive Biology at the University of Vienna.

Actual research favors two important factors in order to assess relationship quality among animals. First, proximity i.e. contact sitting in all animals and, second, affiliative body contact i.e. preening in birds (de Waal 1997, Silk 2002, Fraser & Bugnyar 2010a, Massen et al. 2010). Proximity refers to either the number of times or the amount of time two individuals spend close to one another (in animals: Smuts 1985, Cords 2002, in humans: Hill & Dunbar 2003). Affiliative body contact refers to either the number of occasions or the time spent for activities like grooming (in primates: Dunbar 1996), preening (in birds: Fraser & Bugnyar 2010a) or cuddling and hugging each other (in humans: Newcomb & Bagwell 1995, Dunbar 2010). Currently, the frequency of both pro-social behaviors is regularly used to determine relationship quality (Smuts 1985, Silk 2002, Massen 2010, Seyfarth & Cheney 2012).

Therefore, the relationship qualities between subjects were calculated according to the frequency of contact sitting and preening for each individual (number of times/total observation time for both individuals). Bouts of contact sitting and preening are defined as not being interrupted by > 3s. Preening is observed rarely but unidirectional and therefore represents a more relative measure for the importance of the relationship for each individual dyad. Contact sitting can be regularly observed among ravens but is always bidirectional and hence does not allow such a sophisticated insight.

For this study the frequencies of both socio-positive behaviors were lumped since it is difficult to determine their relative importance against each other. For the purpose of determining the quality of relationships, all social partners for each individual were ordered from most affiliative (1) to least affiliative (10) using the data from the focal animal samplings. Intermediately affiliated individuals were chosen to be familiars (exp. 1, Tab 4) while friends and non-friends (exp. 2, Tab 5) were chosen according to the relative extremes of the calculated order. Moreover, it was ensured that all dyads (training) and triads (exp. 1 & 2) were novel to avoid reciprocation. For the sake of completeness, I also took socio-negative behavior, respectively displacement, into account yet in a conversed way.

Dominance relationship between subjects was calculated with data on unidirectional agonistic behavior (displacement) using MatMan 1.1 (de Vries et al. 1993) to calculate Landau´s linearity indices and the resulting fitted hierarchy was significantly linear (h' = 0.581, n = 11, $p<0.01$). Friends and non-friends of test subjects were chosen in such a way that they were similar in rank (M = 2.9 ± S.E. 0.59) and there was no significant difference in rank distance of test subjects with their friends or non-friends (Wilcoxon: T+ = 30.5, N = 11, p = 0.823). These calculations were also used to test for the influence of rank relation and rank distance in the open choice experiment.

Table 4: The table shows the relationship qualities between test subjects, familiars and strangers. Since I tested the test subject´s partner choices for either the known or the unknown partners I made sure that the relationship qualities between familiars and strangers did not differ much.

Test subject	Familiar	R. Q.	Stranger	R. Q.
Tom	Horst	8,5	Rocky	8,5
Laggie	Nobel	4,5	Joey	8
Adele	Louise	8	Joey	8
Horst	Rufus	6,5	Rocky	6,5
George	Laggie	8	Rocky	8
Louise	Adele	8,5	Joey	8,5
Nobel	Paul	9	Rocky	9
Paul	Nobel	6,5	Joey	6,5
Rufus	Nobel	7,5	Joey	7,5

Table 5: The table shows relationship qualities between test subjects, friends and non-friends. This time, I tested the test subject´s partner choices for either the high affiliated or the low affiliated individuals so I made sure that the relationship qualities between friends and non-friend was high.

Test subject	Friend	R. Q.	Non-friend	R. Q.
Tom	Laggie	1	George	8,5
Laggie	Adele	2	Louise	4,5
Adele	Tom	2	Paul	8
Horst	Louise	1	Adele	6,5
George	Nobel	1	Adele	3,5
Louise	George	4	Paul	8,5
Nobel	Horst	4,5	Rufus	6,5
Paul	Rufus	6,5	Horst	6,5
Rufus	Adele	1	Louise	7,5
Joey	Rocky	5,5	Nobel	5,5
Rocky	Adele	5,5	Horst	5,5

III.7 Statistical Analysis

Data from all experiments were coded by me using the Solomon Coder (Péter 2014). J.J.M.M, recoded 25% of the data from experiments 1 & 2 and the inter-observer reliability was perfect (Cohen´s kappa: 1.0). Data from experiment 3 was coded live with pencil and paper by both experimenters. I recoded 15% of the video tapes from experiment 3 and inter-observer reliability was again perfect (Cohen´s kappa: 1.0). Data from the focal animal samplings were coded by a research assistant from the Department of Cognitive Biology of the University of Vienna whose coding is usually compared that of the main coding research assistant. Their inter-observer reliability is almost excellent (Cohen´s kappa: 0.84). Subsequent statistical tests were conducted with IBM SPSS Statistics 20.0. Experimental data was not normally distributed so nonparametric tests were used for analysis. All statistical tests were two-tailed and α was set to 0,05.

III.7.1 Experiments No. 1 & 2

The number of the test subjects first partner choices (in the whole 20 trials for each test subject) and the number of successful cooperation pulls were compared to a random distribution using Wilcoxon signed-rank tests. Moreover, for each test subject the success rates (number of successful cooperation trials/ total number of opportunities) were calculated. Test subjects success rates with familiar and unfamiliar partners were then compared using Wilcoxon signed-rank tests as well as the success rates with friends and strangers.

III.7.2 Waiting behavior in experiment No. 1 & 2

A possible learning effect on the partner birds regarding waiting behavior within and across sessions was investigated using two separate binomial generalized linear mixed models (GLMM) for dependent variables. First, it was analyzed whether the frequency of waiting behavior increased over time i.e. does the partner bird wait (yes/no) and, second, whether the waiting behavior got more successful over time i.e. does the waiting behavior lead to a subsequent success (yes/no). The trial number per session and the total trial number across sessions for each specific individual were fixed factors while the partner and actor identity were random factors. For the purpose of finding the best fitting model reduced models were also calculated and all models were compared based on the corrected Akaike Information Criteria cAIC. Models with a smaller cAIC (difference > 2) were considered to be the best fitting models. Finally, the data from all experiments was checked for influences of variables like sex combination.

III.7.3 Experiment No. 3

First, a relationship quality matrix including socio-positive interactions (contact sitting and preening combined) with actors in rows and recipients in columns was created. Second, two other matrices were created including either (1) the number of successful cooperation pulls of individuals pulling together at the experimental apparatuses or (2) the number of times individuals pulling next to each other in the middle compartment again with subjects in rows and partners in columns. Next, partial row-wise matrix correlations (Hemelrijk 1990) with 10000 permutations were conducted by correlating the relationship quality matrix with either the (1) matrix or the (2) matrix in order to determine if

relationship quality correlates with successful cooperation or close proximity in the middle compartment. Additionally, the effect of rank distance was controlled for by partialling it out. Row-wise matrix correlations are robust against zeros and control for the dependency of given data i.e. they take the relative frequency of interactions with each subject per subject into account instead of correlating overall frequencies. Therefore, a bias that results from an over- or underrepresentation of specific individuals can be avoided e.g. dominant individuals pulling much more often than subdominant individuals (de Vries et al. 1993, Hemelrijk 1990).

IV. Results

IV.1 Experiment No. 1: Familiar vs. stranger

IV.1.1 First choice approaches exp. 1 (group level)

Out of a total of 180, trials test subjects chose to approach the familiar bird in 100 trials (55.56%) and approached the stranger in 79 trials (43.89%) on first choice within a trial. In 1 trial (0.56%) subject Rufus did not choose to approach any bird.

Test subjects did not show a preference to approach a specific partner based on the degree of familiarity. There was no significant difference in the number of times (out of 20 per bird) a test subject chose to approach either the familiar partner or the stranger on first choice (Wilcoxon: T^{+} = 26.5, N = 9, p = 0.631; Fig 5; Asakawa-Haas et al. 2016).

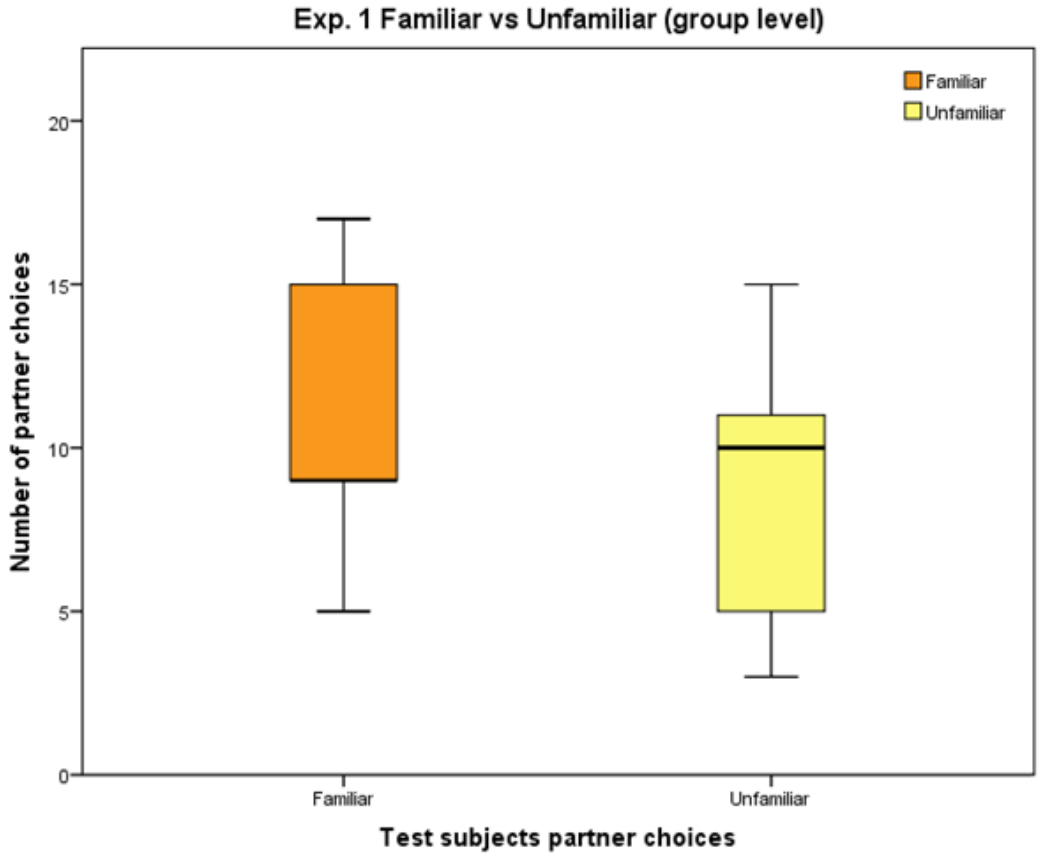


Figure 5: Boxplot (median, inter-quartile range and range) showing test subjects partner choices in exp. 1 (Asakawa-Haas et al. 2016).

IV.1.2 Successful cooperation pulls exp. 1 (group level)

Out of 180 trials, test subjects successfully cooperated with the familiar bird in 80 trials (44.44%) and with the stranger in 56 trials (31.11%) on the first cooperation pull per trial. In 44 trials (24.44%) subjects were not able to cooperate successfully.

Similar to the first choice approaches, there was no significant difference comparing the numbers of successful trials with respect to test subjects pulling with the familiar bird or the stranger (Wilcoxon: T^{+} = 30.5, N = 9, p = 0,341; Fig 6; Asakawa-Haas et al. 2016).

Additionally, no significant difference in success rates (number of successes/total number of opportunities) of test subjects cooperating with familiars or strangers could be found (Wilcoxon: T^{+} = 32.5, N = 9, p = 0.236; Asakawa-Haas et al. 2016).

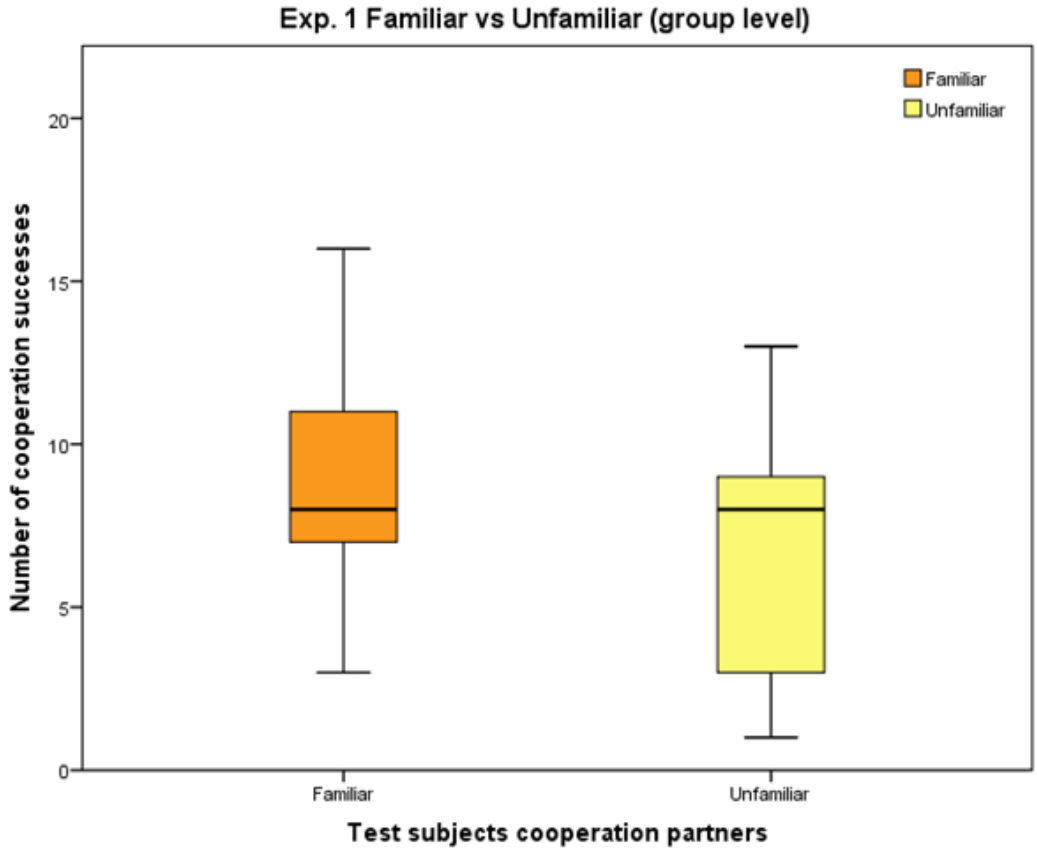


Figure 6: Boxplot (median, inter-quartile range and range) showing test subjects cooperation successes in exp. 1.

IV.1.3 First choice approaches exp. 1 (individual level)

Five of the nine test subjects showed no preference in approaching either the familiar bird or the stranger on first choice, whereas three subjects (Laggie, Adele and Louise) had a preference to approach the familiar bird while one subject (George) had a preference to approach the stranger (Fig 7, Tab 6).

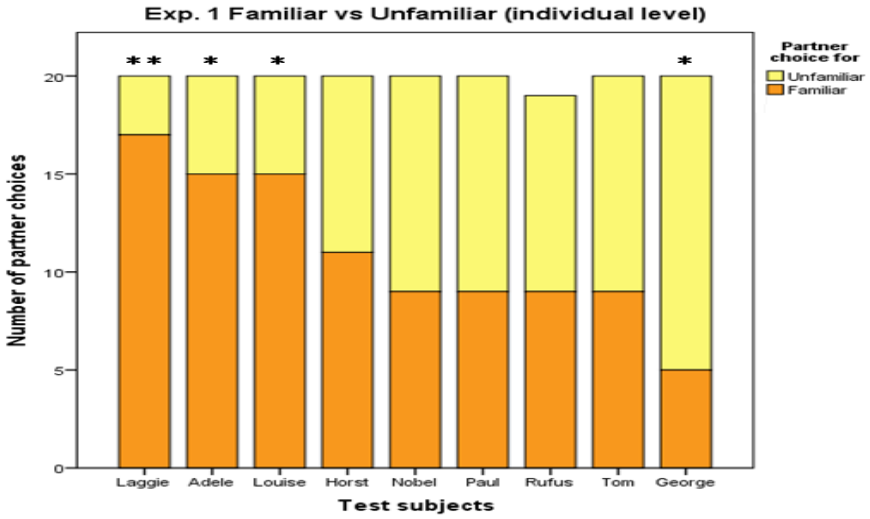


Figure 7: Staked graph illustrating each individual test subject and the frequency of partner choices (*p ≤ 0.05; **p ≤ 0.01) for either the familiar or the stranger.

Table 6: Test subject´s first choice approaches and the results from Pearson´s x^2 tests.

Subject	For Familiar	For Stranger	Pearson´s x^2
Tom	9	11	x^2=0,200; p=0,655
Laggie	17	3	x^2=9,800; **p=0,002**
Adele	15	5	x^2=5,000; **p=0,025**
Horst	11	9	x^2=0,200; p=0,655
George	5	15	x^2=5,000; **p=0,025**
Louise	15	5	x^2=5,000; **p=0,025**
Nobel	9	11	x^2=0,200; p=0,655
Paul	9	11	x^2=0,200; p=0,655
Rufus	10	9	x^2=0,053; p=0,819

IV.1.4 Successful cooperation pulls exp. 1 (individual level)

Correspondingly, the five test subjects who did not show a preference on the individual level did not have higher success cooperating with either the familiar bird or the stranger. Moreover, the same three subjects who had a preference to approach the familiar (Laggie, Adele and Louise) had higher success cooperating with the familiar while the same subject (George) who had a preference to approach the stranger had higher success cooperating with the stranger (Fig 8, Tab 7).

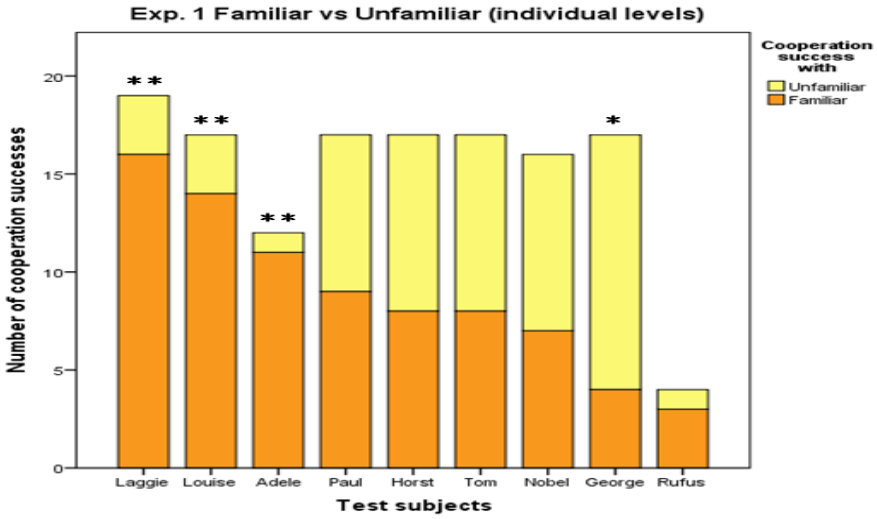


Figure 8: Staked graph illustrating each individual test subject and the frequency of cooperation successes (*p ≤ 0.05; **p ≤ 0.01) with either the familiar or the stranger.

Table 7: Test subject´s first cooperation pulls and the results from Pearson´s x^2 tests.

Subject	For Familiar	For Stranger	Pearson´s x^2
Tom	8	9	x^2=0,059; p=0,808
Laggie	16	3	x^2=8,895; **p=0,003**
Adele	11	1	x^2=8,333**; p=0,004**
Horst	8	9	x^2=0,059; p=0,808
George	4	13	x^2=4,765; **p=0,029**
Louise	14	3	x^2=7,118; **p=0,008**
Nobel	7	9	x^2=0,250; p=0,617
Paul	9	8	x^2=0,059; p=0,808
Rufus	3	1	x^2=1,000; p=0,317

IV.2 Experiment No. 2: Friend vs. non-friend

IV.2.1 First choice approaches exp. 2 (group level)

Out of a total of 220 trials test subjects chose to approach the friend in 118 trials (53.64%) and approached the non-friend in 79 trials (35.91%) on first choice per trial. In all 20 trials (9.09%) test subject Rocky and in 3 trials (1.36%) test subject Joey did not choose to approach any bird.

In contrast to the previous experiment, test subjects did show a preference to approach a specific partner based on the degree of relationship quality. There was a significant difference in the number of times (out of 20 per bird) a test subject chose to approach the friend over the non-friend on first choice (Wilcoxon: T^{+} = 39.5, N = 11, p = 0.043; Fig 9; Asakawa-Haas et al. 2016).

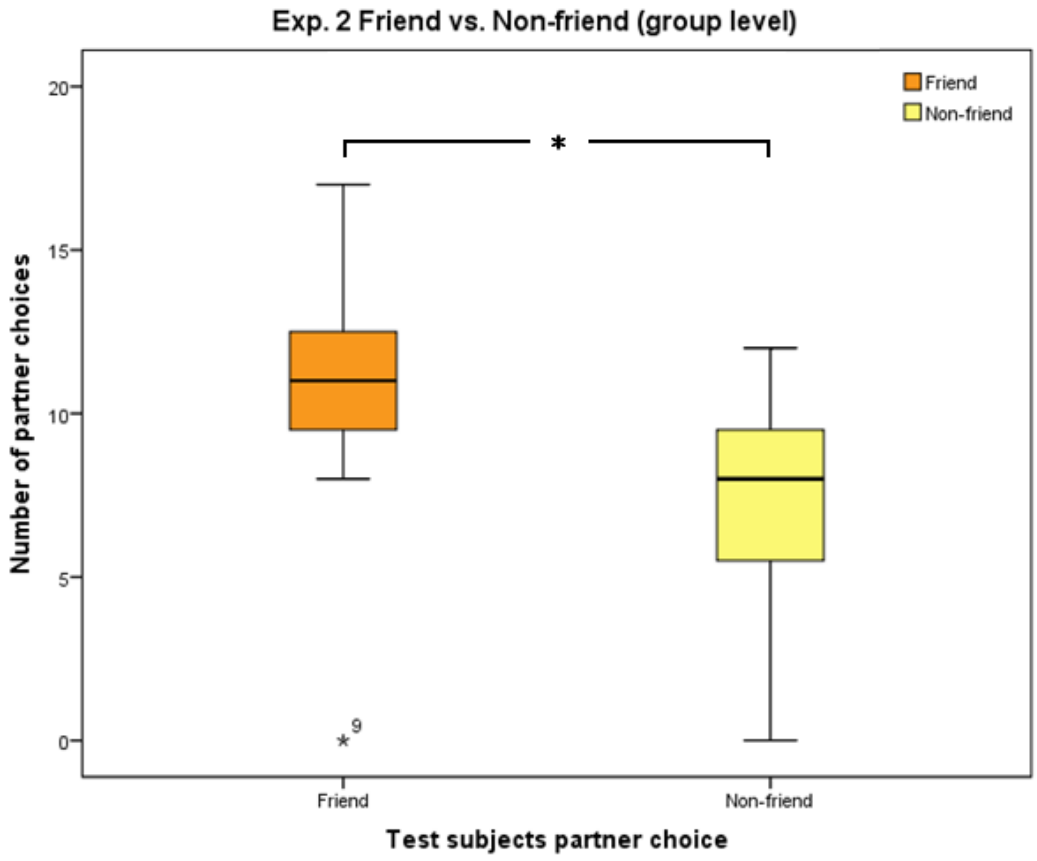


Figure 9: Boxplot (median, inter-quartile range and range) showing test subjects partner choices (*p ≤ 0.05) in exp. 2 (Asakawa-Haas et al. 2016).

IV.2.2 Successful cooperation pulls exp. 2 (group level)

Out of 220 trials test subjects successfully cooperated with the friend in 106 trials (48.18%) and with the non-friend in 65 trials (29.55%) on the first cooperation pull per trial. In 49 trials (22.27%) subjects were not able to cooperate successfully.

Similar to the first choice approaches, there were significantly higher numbers of successful trials with respect to test subjects pulling with the friend over the non-friend (Wilcoxon: $T^+ = 42.5$, N = 11, p = 0.018; Fig 10; Asakawa-Haas et al. 2016).

Additionally, success rates (number of successes/total number of opportunities) of test subjects cooperating with the friends were significantly higher than with the non-friends (Wilcoxon: $T^+ = 27$, N = 11, p = 0.028; Asakawa-Haas et al. 2016).

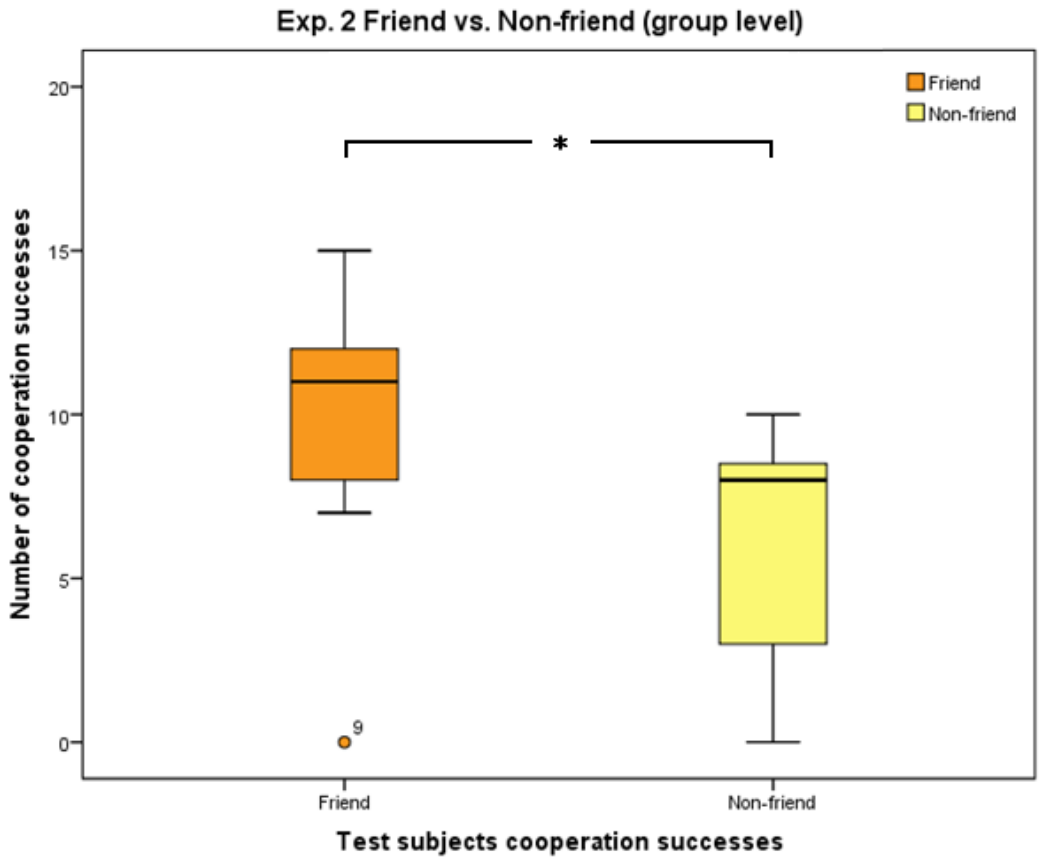


Figure 10: Boxplot (median, inter-quartile range and range) showing test subjects cooperation successes (*p ≤ 0.05) in exp. 2.

IV.2.3 First choice approaches exp. 2 (individual level)

Seven of the nine test subjects showed no preference in approaching either the friend or the non-friend on first choice, whereas two subjects (Paul and Louise) had a preference to approach the friend (Fig 11, Tab 8).

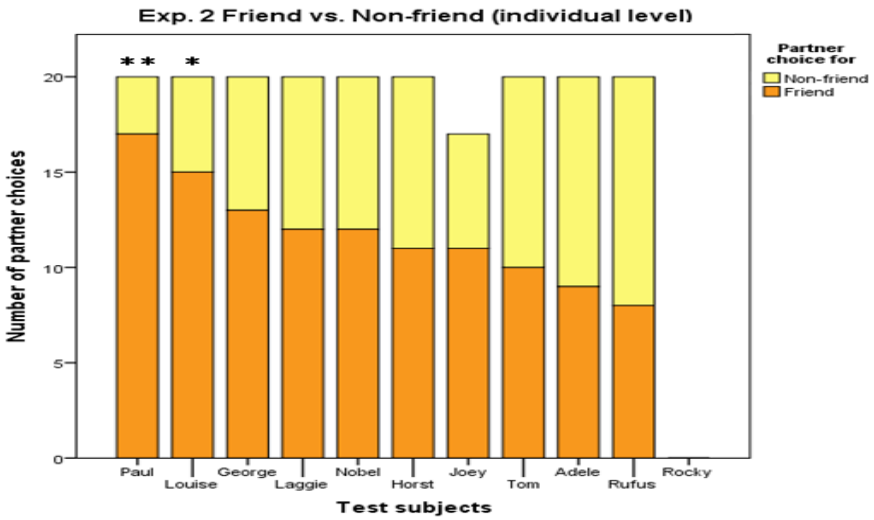


Figure 11: Staked graph illustrating each individual test subject and the frequency of partner choices (*p ≤ 0.05; **p ≤ 0.01) for either the friend or the non-friend.

Table 8: Test subject´s first partner choices and the results from Pearson´s x^2 tests.

Subject	For Friend	For Non-Friend	Pearson´s x^2
Tom	10	10	x^2= 0,000; p=1,000
Laggie	12	8	x^2= 0,800; p=0,371
Adele	9	11	x^2= 0,200; p=0,655
Horst	11	9	x^2= 0,200; p=0,655
George	13	7	x^2= 1,800; p=0,180
Louise	15	5	**x^2= 5,000; p=0,025**
Nobel	12	8	x^2= 0,800; p=0,371
Paul	17	3	**x^2= 9,800; p=0,002**
Rufus	8	12	x^2= 0,800; p=0,371
Joey	11	6	x^2= 1,471; p=0,225
Rocky	0	0	No choice

IV.2.4 Successful cooperation pulls exp. 2 (individual level)

Correspondingly, the seven test subjects who did not show a preference on the individual level did not have higher success cooperating with either the friend or the non-friend. Moreover, the same two subjects who had a preference to approach the friend (Paul and Louise) had higher success cooperating with the friend (Fig 12, Tab 9).

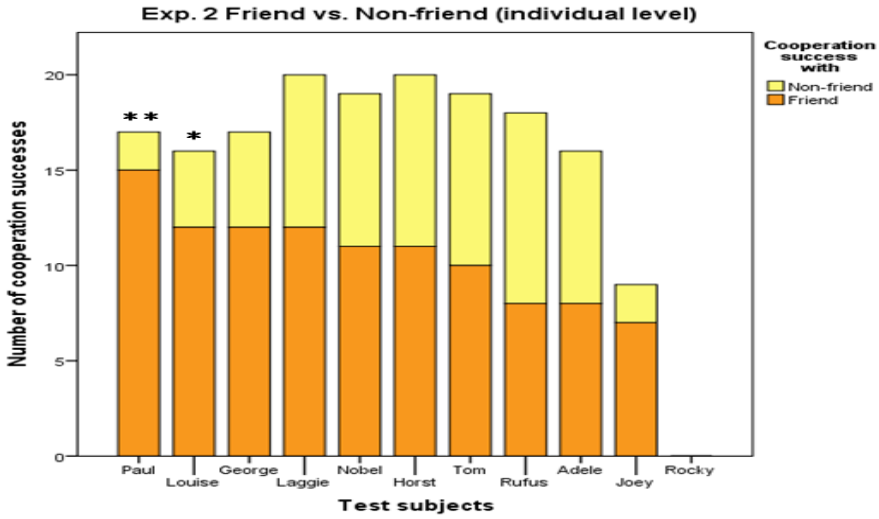


Figure 12: Staked graph illustrating each individual test subject and the frequency of cooperation successes (*p ≤ 0.05; **p ≤ 0.01) with either the friend or the non-friend.

Table 9: Test subject´s first cooperation pulls and the results from Pearson´s x^2 tests.

Subject	For Familiar	For Stranger	Pearson´s x^2
Tom	10	9	x^2=0,053; p=0,819
Laggie	12	8	x^2=0,800; p=0,371
Adele	8	8	x^2=0,000; p=1,000
Horst	11	9	x^2=0,200; p=0,655
George	12	5	x^2=2,882; p=0,090
Louise	12	4	**x^2=4,000; p=0,046**
Nobel	11	8	x^2=0,474; p=0,491
Paul	15	2	**x^2=9,941; p=0,002**
Rufus	8	10	x^2=0,222; p=0,637
Joey	7	2	x^2=2,778; p=0,096
Rocky	0	0	No pull

IV.3 Experiment 3: Open choice

Out of 700 trials, test subjects successfully cooperated in 585 trials at the left apparatus, whereas in 568 trials at the right apparatus.

There was no significant correlation between relationship quality and the number of times two individuals cooperated at each of the apparatuses while taking dominance hierarchy into account (Partial Kendall row-wise correlation: $tau_{rw;XY.Z}$ = 0.047, N = 11, p = 0.336; Asakawa-Haas et al. 2016).

In contrast, there was a significant correlation between relationship quality and the number of times two individuals pulled next to each other in the middle compartment although cooperating with another bird (Partial Kendall row-wise correlation: $tau_{rw;XY.Z}$ = 0.349 , N = 11, p = 0.0037; Fig 13; Asakawa-Haas et al. 2016).

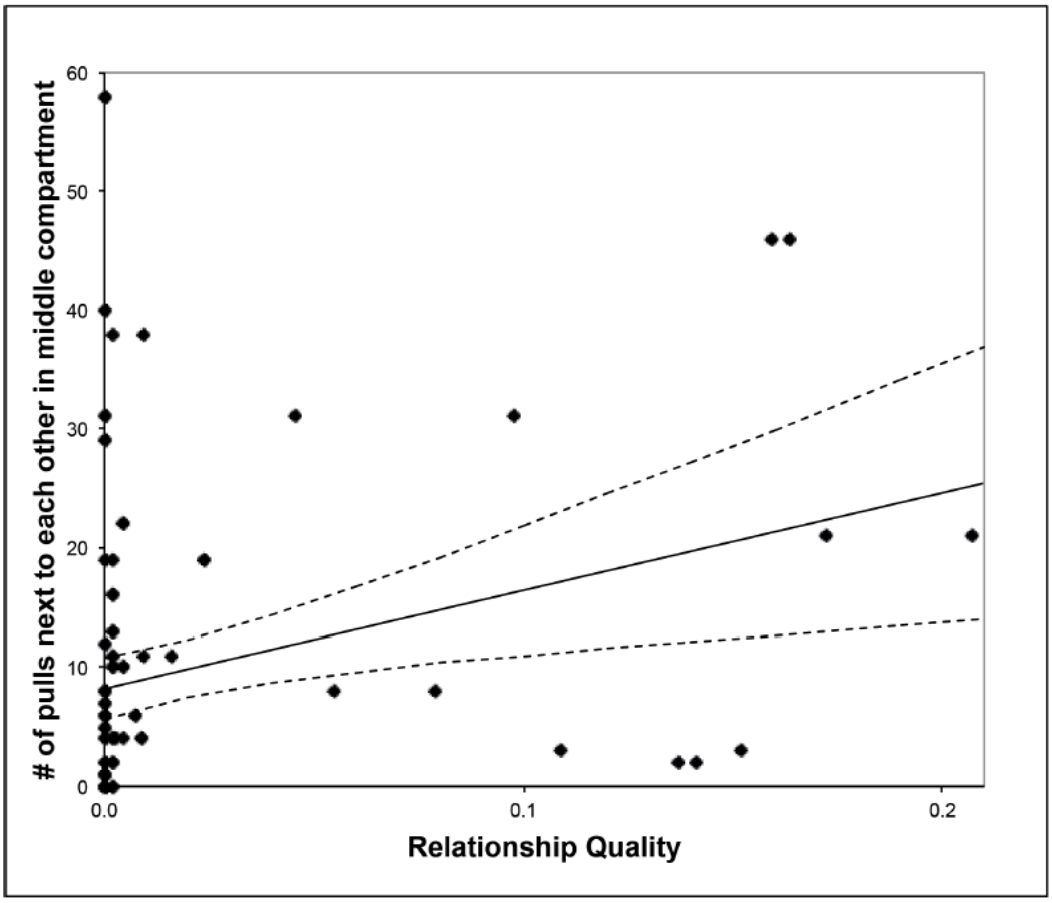


Figure 13: Correlation between relationship quality and how often two subjects preferred to stay close while cooperating with another bird (Asakawa-Haas et al. 2016).

IV.4 Waiting behavior

Taking experiments No. 1 & 2 together, partner birds, who had to wait for the test subject, showed a significant learning effect regarding the frequency of waiting behavior in relation to total trial number across sessions (GLMM: $F_{1,420} = 7.72$, $\beta = 0.018$, $p = 0.006$; Fig 14; Asakawa-Haas et al. 2016).

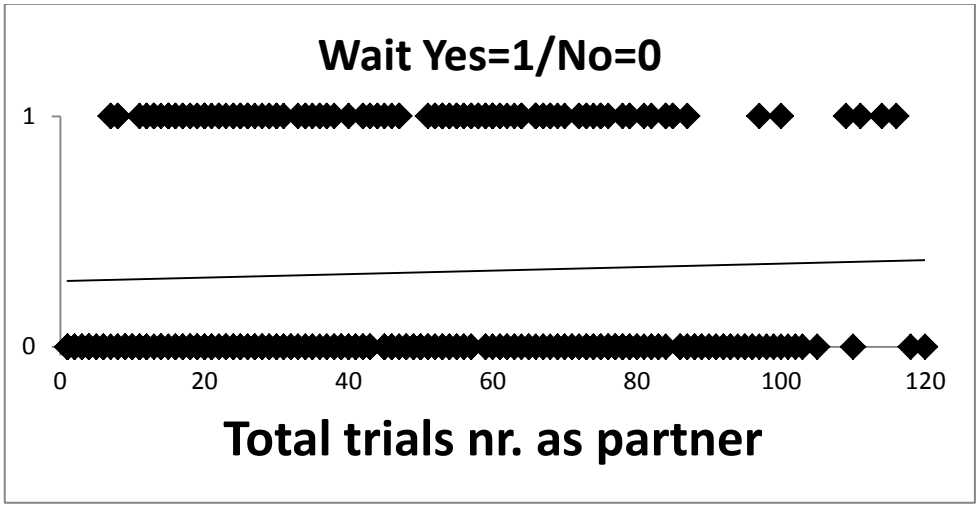


Figure 14: Graph showing the increase in waiting behavior in relation to total trial number across sessions.

There was also a trend but no significant correlation between waiting success and total trial number across sessions (GLMM: $F_{1,133} = 3.443$, $\beta = 0.020$, $p = 0.066$; Fig 15; Asakawa-Haas et al. 2016).

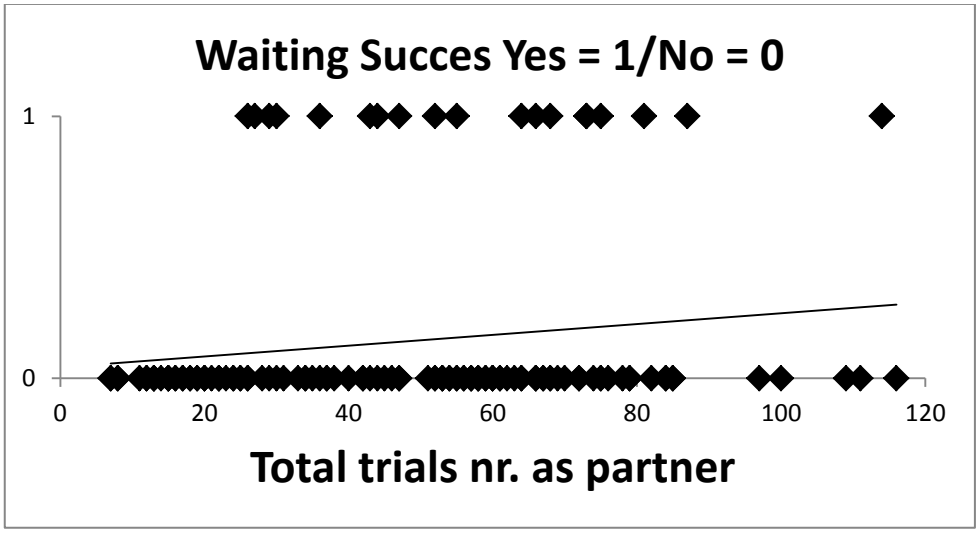


Figure 15: Graph showing the increase in waiting success in relation to total trial number across sessions.

V. Discussion

For this study, a modified version of the loose string paradigm (Hirata 2003) was used by applying two apparatuses at the same time and this allowed, unlike previous studies (Werdenich & Huber 2002, Melis et al. 2006a/b, Hare et al. 2007, Seed et al. 2008, Drea & Carter 2009, Massen et al. 2015), to test subjects that could actually choose among two possible cooperation partners in relation to familiarity or relationship quality. Therefore, animal partner choice in a real time cooperation setting was assessed which closer resembles natural conditions (cf. Suchak et al. 2014, Molesti & Majolo 2016).

In experiment No. 1, the ravens did not show a preference to approach either the familiar partner or the stranger, nor were subjects more successful in cooperating with either one of them (Asakawa-Haas et al. 2016). These findings coincide with the characteristics of the raven´s social system. After leaving their nests, ravens usually join large groups which are characterized by a high degree of fission-fusion dynamics and only later in life they form monogamous pair bonds while settling for a territory (Heinrich 1989, Boarman & Heinrich 1999). Unfamiliar individuals frequently fuse into these groups and familiar individuals might leave them. Hence, in such variable environments it may be beneficial to not have preset preferences for cooperation partners, based on degrees of familiarity, in order for individuals to quickly assess a newcomer´s willingness and efficiency in cooperation by trying them out (Bugnyar 2013).

In experiment No. 2, the ravens did have a preference to approach the friend rather than the non-friend and, additionally, also had higher success rates in retrieving the rewards together (Asakawa-Haas et al. 2016). These results support observations in the wild (Heinrich 1989) as well as in captivity (Fraser & Bugnyar 2012) and show that ravens apply actual partner choice in the context of a cooperative string pulling task. Moreover, these outcomes are congruent with the observations of previous studies that identified social tolerance, a prerequisite for close social association (friendship), as an important factor for cooperation and either used the same group of ravens (Massen et al. 2015) or other species such as apes (Werdenich & Huber 2002, Melis et al. 2006a, Hare

et al. 2007), rooks (Seed et al. 2008) and spotted hyenas, Crocuta crocuta, (Drea & Carter 2009).

Although, it needs to be mentioned that these previous studies have only used dyadic settings in which the test subjects could not choose between different partners.

The question remains, whether ravens base their partner choice on relationship quality as a whole or if the choice arises from a more simple mechanism such as tolerance for spatial proximity i.e. the preference to stay close to friends or the avoidance of proximity to non-friends. In order to clarify the proximate mechanism of partner choice in cooperation settings, a third experiment was designed were, on the one hand, cooperation did not require close proximity and, on the other hand, closest proximity did not lead to cooperation.

In the third experiment, were all subjects could freely choose with whom to cooperate, the individuals that shared a close social relationship preferred to stay close to each other over actually cooperating with one another (Asakawa-Haas et al. 2016).

Altogether, these findings suggest that partner choice in raven cooperation may not be driven by relationship quality as a whole, but derives from a more simple mechanism such as the preference to stay close to close social associates i.e. tolerance of spatial proximity. Similar to these results, a different open choice experiment, with captive chimpanzees, did not find any effect of affiliation on partner choice for cooperation but rather social tolerance arising from kinship and close rank distance (Suchak 2014). Notably, an open choice experiment with wild Barbary macaques showed that social tolerance was necessary for cooperation to start at all whereas a close social relationship was necessary to maintain cooperation over time (Molesti & Majolo 2016). Both studies, however, used only one apparatus hence subjects were limited in their partner choices i.e. subjects only had the choice to either cooperate with a dominant individual already occupying the apparatus or not to cooperate at all.

It has to be mentioned that the setup for this study had wire-mesh separating cooperation partners which differs from the buildup of most other loose string

paradigm studies (Werdenich & Huber 2002, Melis et al. 2006a, Hare et al. 2007, Seed et al. 2008, Drea & Carter 2009, Suchak 2014, Molesti & Majolo 2016) making direct comparisons difficult. It is also possible that ravens may 'actively' choose not to cooperate with their non-friends in more unrestricted environments, e.g. in the wild, as cooperation partners are able to steal rewards more easily when no wire mesh is separating them.

Though the results shown do not require subjects to have a cognitive understanding of the paradigm's inner working mechanisms, it is interesting to contemplate whether the ravens did understand the necessity of a partner to retrieve the reward or not. In a previous experiment, with the same group of ravens, the individuals failed to inhibit pulling the string when they were either alone or had to wait for the partner (Massen et al. 2015). During the first two experiments, the second partner bird, i.e. the one who was not chosen first, could wait until the test subjects arrives and then pull together in order to receive the reward. In case of an understanding the second partner would have inhibit pulling until the test subjects pulls at the other end. While at first that did not happen, the birds learned to wait over time and at the end of the second experiment 7 out of 11 birds were successful at least once. This shows the crucial effects of learning within the loose-string paradigm (Bugnyar 2008). Whether the subjects understood the need of a partner or if they just waited until they felt tension on the string remains to be clarified in future experiments.

In summary, the ravens showed preferences with whom to cooperate and with whom not to. Additionally, subjects were also more proficient in retrieving rewards while cooperating with the chosen partners. However, the results indicate that the raven's partner choice, at least in the setting used here, was based on tolerance of spatial proximity rather than on relationship quality as a whole. The findings give rise to the question if preferences and different success rates in other non-open choice experiments might not also be a direct result from different degrees of social tolerance. Notice that for the outside observer the result is the same: animals prefer to cooperate with their friends over non-friends. Consequently, it should be profitable to further investigate proximate mechanisms of partner choice in cooperation settings in other species as well, while also controlling for the effects of tolerance of spatial

proximity, in order to deepen our understanding regarding the basics of animal cooperation. Future studies should allow subjects to make free choices regarding their cooperation partners and, furthermore, use experimental apparatuses that do not require spatial closeness as this closer resembles naturally occurring cooperation in the wild (cf. Bednarz 1988, Stander 1992, Hendricks & Schlang 1998, Boesch 2002).

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