universität
wien

MASTERARBEIT

Titel der Masterarbeit

„*Whom to dine with? Strategies of ravens (Corvus corax) in food monopolization experiments*“

Verfasserin

Miriam Jennifer Sima, Bakk. rer. nat.

angestrebter akademischer Grad

Master of Science (MSc)

Wien, 2012

Studienkennzahl lt. Studienblatt:	A 066 878
Studienrichtung lt. Studienblatt:	Verhaltens-, Neuro- und Kognitionsbiologie
Betreuer:	V.-Prof. Mag. Dr. Thomas Bugnyar

Contents

1 Introduction

1.1 Group-living

Social life can be cognitively challenging: individuals as intentional beings behave autonomously. Therefore their behavior is difficult to predict and difficult to manipulate (Jolly 1966; Humphrey 1976). The social brain hypothesis indicates that the more complex social groups are, the more challenging it is to deal with the problems of social life. Complexity can be reflected in group size (Byrne & Whiten 1989), types of relations (Dunbar 1998), and the degree of fission-fusion dynamics (Amici et al. 2008). Supporting this argument, brain size correlates with group size in mammals in general and primates in particular, with long-term relationships in mammals and birds, and with fission-fusion dynamics within primate groups (Dunbar 1992). According to Smith et al. (2008) fission-fusion societies are stable social units in which individual group members are often found alone or in small subgroups and in which subgroup size and composition change frequently over time.

Differences in group size come with different benefits and costs depending mainly on food availability and predation levels (Majolo et al. 2008). One of the costs is competition over resources – the more individuals are present in close proximity the fewer resources each one will get. Benefits of group-living are individual vigilance in a group (Pulliam 1973), collective defense against predators or other groups (Alexander 1974), confusion effects (Miller 1922), predator inspection phenomena (Pitcher et al. 1986), cooperative foraging (Packer & Ruttan 1988), cooperative breeding (Emlen 1982), grooming to reduce parasites (Richard C. 1995), information transfer (Ward & Zahavi 1973), and social thermoregulation (Armitage 1999). Another advantage of group living could be that cooperation, e.g. food sharing, may decrease stress levels, whereas resource competition and aggressive interactions between independent individuals may increase stress (Scott 2001; Krause & Ruxton 2002; Stöwe et al. 2008).

1.2 Food sharing

Food sharing represents a form of cooperation that is said to have played an important role in human evolution (Isaac 1978). As a consequence, studies on food sharing behavior in non-human animals, (e.g. Stanford 1999), are of particular interest, as they may provide insights into the evolutionary history of this behavior in humans (Brown et al. 2004).

A very concise definition of food sharing was given by Stevens & Gilby (2004): sharing is a joint use of monopolizable food. Hence, sharing occurs when an individual could defend a food item but allows another individual to consume part of the item. This can be passive sharing, also known as "tolerated theft" or active sharing e.g. facilitated transfer (Brown et al. 2004). The resource holder and the recipient have to make different decisions. The possessor of the food has to decide whether to defend a food item or to allow it to be taken. The food recipient has to decide if he should try to get a food item from another individual or if he should forage independently (Brown et al. 2004). The resource holder additionally has to make the decision with whom to share. Different factors of both social and ecological nature can be influencing this decision making process. One of the social factors is the relationship between the involved individuals which might be more likely to share with relatives, partners, or friends. Decisions can also be influenced by the sex and age of the interacting individuals, with factors such as same versus opposite sex and differences in age playing a crucial role. Examples of ecological factors are the accessibility and the divisibility of the food (Vahl & Kingma 2007). Additionally knowledge of the dominance hierarchies is crucial to understand the interference process during feeding (Vahl & Kingma 2007).

1.3 Biological market paradigm

Functionally, food sharing can be explained by kin selection, reciprocal altruism, costly signaling, or if there is an immediate benefit for all participants, byproduct mutualism (Stevens & Gilby 2004). Individuals can have immediate or delayed benefits from sharing. The challenge of delayed benefits is the trade of current for future fitness. This uncertainty could be the reason for discounting the value of delayed benefits (Stevens & Gilby 2004). Still, the evolution of food sharing in non-related individuals can be explained by reciprocity (Stevens & Gilby 2004). Another model explaining social relationships between non-kin, in which one individual has large investments over long series of interactions, is the biological market model (Noë et al. 1991). It assumes that individuals bring different resources and skills into the cooperation. These can be compared to the exchange of goods between traders in human markets. In the animal kingdom there could, for example, food be given in exchange for mating. Another possibility is that animals exchange food for grooming, or support in a dominance conflict (Noë & Hammerstein 1994).

1.4 Social relationships and the quality of relationships

Social relationships are defined as the frequency, quality, and patterning of diverse interactions among the same individuals over time (Hinde 1979). Social relationships can consist of cooperation in form of affiliative behaviors but also of competition in form of agonistic behaviors, both defining the quality of the relationship (Cords & Aureli 2000). Social interactions between two individuals depend on their specific characteristics (e.g. age, sex, and dominance rank) but they also depend on the history of the interactions between the individuals (Cords & Aureli 2000).

Kummer (1978) saw relationships as social investments and interactions as ways of maximizing benefits from these investments. Relationships are not always equally valuable and each partner has a different value to those with whom they interact (McFarland & Majolo 2011b). Kummer (1978) differentiated between four components, namely value, availability, qualities of the partner, and behavioral tendencies. These components have recently been reclassified as value, compatibility, and security (Cords & Aureli 2000). Value describes the benefits afforded by the relationship. Compatibility represents the tolerance and affiliation between two individuals, which is based on their shared history of exchange of interactions. Security is determined by the consistency and predictability of the behavior of partners (Fraser et al. 2008). Individuals show preferences towards establishing social relationships with individuals from which they gain the most benefits (Cords 1997).

Hamilton’s famous kin selection theory (Hamilton 1964) refers to the strategy used by an individual to increase its inclusive fitness by maximizing the reproductive success of relatives. Silk et al. (2006) tested this theory and found that social relationships between relatives tend to be stronger than between non-kin.

Relationships can also result in coalitions, in which individuals support each other in agonistic conflicts (Cords & Aureli 2000). Coalitions can be formed between two individuals but larger coalitions also occasionally occur. Coalitions can improve access to a limited resource for both partners or at least for one of the partners at a time (Cords & Aureli 2000). There are two different types of competition for resources, contest and scramble (Krause & Ruxton 2002). In contest competition access to food sources depends on agonistic strength as resources are patchy and distributed in defensible clusters (Cords & Aureli 2000). When the resource is scrambled and the food cannot be monopolized the animals are forced to share. Thus, when the food resource is of the contest type, it makes sense for animals to team up and form coalitions as this improves their chances to access the limited resources. Dominant animals usually do not need allies. However, when they do form coalitions these are usually formed with individuals of medium rank as they do not receive enough benefits from pairing up with low-ranking individuals (Cords & Aureli 2000).

1.5 Grooming/Preening

Grooming or preening is a major indicator of social relationships. Allogrooming (interchangeably used with grooming) is defined as cleaning fur or feathers of others with hands, snout or beak (Lazaro-Perea et al. 2004). Social grooming occurs in many animal orders as for example primates (Dunbar 1991), carnivores (Kutsukake & Clutton-Brock 2010), rodents (Stopka & Macdonald 1999) and birds (Stöwe et al. 2008).

The function of grooming is both social and hygienic. One example of a hygienic function of grooming is removing parasites, which is beneficial for the groomed animal (hereafter the groomee) by reducing its parasite load (Hart et al. 1992; Hart & Hart 1992). Beside the hygienic function, grooming has several social functions and reflects the characteristics of the social relationship between groomer and groomee (Kutsukake & Clutton-Brock 2010). Grooming also has costs for the groomer including decreased resting time (Dunbar 2002) and decreased vigilance (Mooring & Hart 1995), although some authors consider grooming costs negligible (Schino et al. 2003; Schino & Aureli 2009).

Another function of grooming is to relax the groomee and groomer as it stimulates beta-endorphin release (Keverne et al. 1989) and also reduces the heart rate (Aureli et al. 1999). In social primates, for example, grooming occurs between related individuals, and has been suggested to represent nepotism or parental care (Schino 2001). There are two possibilities for which grooming can be exchanged, either for grooming itself (reciprocity; e.g. wild impala, *Aepyceros melampus*: (Hart & Hart 1992); chimpanzee, *Pan troglodytes*: (Watts 2002)) or for "social commodity" benefits other than grooming.

1.6 Conflicts and conflict management

Conflicts can occur in a variety of contexts when two or more individuals are interested in the same resource. This could be among potential mating partners (Parker 1979), between parents and offspring (Trivers 1974), or because of a competition for access to a limited resource, e.g. mates (Trivers 1972, Clutton-Brock 1989) or food (Van Schaik 1989). This may be detrimental to social relationships, particularly when close affiliates are involved (Aureli & Waal 2000). Hence, species living in complex societies have evolved mechanisms to manage social relations and to puffer costly consequences of conflicts (Preuschoft & Van Schaik 2000).

De Waal (1985) introduced the term "relational model", which explains the function of aggressive behavior within social relationships. In this model social partners are seen as commodities of variable values. If animals compete for a limited resource, the opponents have to compare the value of the limited resource with the risk of injury. They also have to weigh the damage the fight may cause against the relationship and the value and advantages of this relationship. This predicts that if a social relationship is easy to repair after damage, the chance of a conflict is higher (Preuschoft & Van Schaik 2000). The likelihood of conflicts decreases with a high possibility of injury and a high value of the relationship, however, with a higher likelihood of reparability of the relationship afterwards and a high resource value, the chance of conflict increases (Preuschoft & Van Schaik 2000).

Negative results of a conflict are not necessarily only temporary but lead to a higher possibility of further attacks from the same aggressor in the period immediately following the initial attack (Aureli & Schaik 1991a; Aureli 1992; Schino 1998). Additionally the likelihood that other group members attack the receiver of the previous attack after the original conflict rises (Aureli et al. 2002). Spotted hyenas seem to, additionally, recognize third-party relationships and attack the relatives of their opponents after a fight more often than other low ranking individuals (Engh et al. 2005). If conflicts between the same individuals occur more often a dominance-subordination relationship is established to lower the costs and reduce the need for fights between these individuals in the future (Preuschoft & Van Schaik 2000).

After a conflict the opponents can reconcile their differences (Cords & Aureli 2000). Reconciliation does not occur after all conflicts but mainly when the partners share a valuable relationship and the benefits of this relationship outweigh the cost of renewed aggression directed towards the previous conflict partner (Fraser & Bugnyar 2011). Reconciliation was observed in many different group-living species: primates (Watts 2002, 2006), wolves (Cordoni & Palagi 2008), dolphins (Weaver 2003), and ravens (Fraser & Bugnyar 2011). Reasons for animals to reconcile are not only to repair the relationship between former opponents (Koyama 2001) but also to reduce post conflict stress (Aureli & Schaik 1991b) and to reduce the chances of renewed aggression (Silk et al. 1996). Reconciliation can also be risky: "false reconciliation" has been reported when one opponent only pretends to reconcile, approaches, and then makes a surprise attack (de Waal 1985). Also, if one of the opponents is approached before being ready to reconcile this could lead to renewed aggression (de Waal 1985).

Reconciliation can be shown in different ways, and different behaviors and gestures have been interpreted as reconciliation after a conflict. The most common form observed as post conflict contact is affiliation such as grooming, preening, or body contact. These are behaviors which also occur regularly in daily social contexts (Aureli & Schaik 1991b).

Another behavior pattern in addition to reconciliation is post-conflict bystander affiliation. Bystander affiliation describes friendly actions of individuals who were not involved in a conflict towards one of those who were. When individuals offer post-conflict affiliation to the recipient of recent aggression they reduce the stress of the comforted individual, but, at the same, they risk receiving aggression from the previous opponent themselves (Fraser et al. 2009). Like reconciliation, bystander affiliation can have different functions, e.g. stress reduction, self-protection, and opponent relationship repair (Fraser et al. 2009).

The best strategy to lower the risk of conflicts and escalated aggression is to prevent conflicts in the first place. Interestingly, most studies have focused on post-conflict behavior whereas only a few have paid attention to anticipatory aspects of conflict management (Koyama 2000). Pre-conflict strategies are more demanding because they require individuals to possess the ability to anticipate future conflicts (Koyama 2000). Indeed, only few experiments provide suggestive evidence that animals are capable of planning ahead, and here the focus is on apes (Mulcahy & Call 2006; Osvath & Osvath 2008; Osvath 2009) and on only one corvid species, the Western scrub jay (Raby et al. 2007; Raby & Clayton 2009). A situation in which animals can expect aggression is during feeding. When food is clumped and easy to monopolize, the likelihood of competition is stronger but animals can try to reduce the chance of conflicts by tension-reduction strategies (Koyama 2000).

1.7 Corvids

Corvids are an interesting family to study because of their exceptional socio-ecology, neurobiology, and life history (Emery 2006). They are feeding generalists and known to show a wide geographical distribution. They also have large brains in relation to body size (Emery 2006). Corvids are known to perform well in cognitive tests and are often found to have cognitive skills comparable to those of primates (Emery & Clayton 2004). A long developmental period allows corvids more opportunities to learn the essential skills for later life.

Ravens (*Corvus corax*) are the largest corvids, show one of the largest distribution ranges in the corvid family, and can live in difficult habitats (Heinrich & Smolker 1998). Ravens are scavengers, co-occur with large predators, and show flexibility to use human-made resources such as garbage dumps (Marzluff et al. 2007). The social system of ravens can be divided into two classes: on the one hand the vagrant non-breeders and on the other hand the territorial breeders (Goodwin 1976). The non-breeders are known to form relationship networks (Fraser & Bugnyar 2010a), at least in captivity. Selva et al. (2011) found that ravens which are in a stable pair bond show lower stress levels than non-territorial ravens. This indicates that ravens in bigger flocks might compete more with one another, live in a more unpredictable environment, and are subjected to a higher predation risk. Flocks of ravens show a high degree of fission-fusion dynamic and thus are relatively unstable in respect to group size and composition (Heinrich 1989, but see Braun et al. 2012). Nevertheless, non-breeders establish a dominance hierarchy which determines the access to food (Heinrich 1989). They may also recruit others to food, probably because the appearance in a group helps them to overpower dominant territory owners defending food (Heinrich & Marzluff 1991) or to deal with dangerous predators (Heinrich 1989).

Beside this cooperative behavior before feeding, little is known about the individual strategies during feeding, notably the sharing of food. This is surprising because ravens do not only form a network of social relations but display advanced socio-cognitive skills such as tactical deception (Bugnyar & Kotrschal 2002; Bugnyar & Heinrich 2006), perspective taking (Bugnyar et al.

2004), and attribution (Bugnyar & Heinrich 2005; Bugnyar 2011), raising the possibility that they could strategically decide with whom to feed and use their relationships accordingly.

The fact that ravens show different strategies with regards to foraging and food manipulation leads to the question of how they behave when only one food resource is available and when it is possible to monopolize this resource. In the experiment described in the present master thesis, I investigated food sharing in captive ravens (*Corvus corax*) under different ecological conditions (food that can or cannot be monopolized) and with different social options (with or without choice with whom to feed).

1.8 Questions and Hypotheses

The aim of my study was to investigate food sharing and conflict management skills of ravens in a competitive foraging situation. I first assessed how ravens respond to different levels of food accessibility, i.e. when meat (of a given quality and amount) was presented in one single piece, two pieces, or in as many pieces as birds in the group. The prediction was that conflicts would arise mainly in those conditions when food was clumped (1 or 2 pieces), and thus was easy to monopolize. Since males have a competitive advantage over females due to their body size and weight, males were expected to show more aggressive behavior than females and to have better access to clumped food. Of the situations in which food was clumped, the 1 piece condition offered less opportunity than the 2 piece condition in respect to where and with whom to (try to) feed. It was hypothesized that the 1 piece condition leads to more conflicts than in the 2 piece condition.

In the second step I assessed which effect(s) the food manipulation had on interactions other than conflicts, when these effects occurred, and how. The birds were expected to intersperse the conflicts with affiliative interactions such as preening or co-feeding. This behavior will hereafter be referred to as buffering. There are two possible strategies when the birds could buffer the conflicts. The first strategy would be to act before they are confronted with the competitive situation to prevent conflicts, i.e. show pre-conflict management. This would result in high rates of affiliative behavior before feeding in expectation of competition but lead to no difference between conditions (number of food pieces) because the ravens could not know in advance which condition they would be subjected to. The second strategy would be the buffering of the conflicts after the conflicts occurred, in an attempt to return to a stable and balanced emotional state and to repair the relationships. It was hypothesized that the birds would show higher rates of affiliative behavior after feeding and that this is most pronounced in the condition with the most tension and conflict potential. This could be the 1 piece condition in terms of absolute number of agonistic interactions but also the 2 piece condition, in terms of the decision making process regarding the feeding partners.

Moreover, I wanted to know if the birds would show different types of affiliative behavior or if they utilize one very specific behavior. They could share food, which leads to a direct benefit, but they also could preen, touch, or sit in contact and engage in non-food related behaviors such as trading for access to food and exchange services.

In the final step I assessed whether the social relationships between the individuals, as measured in daily life interactions, can explain the observed patterns during the experimental manipulations. I hypothesized that the qualities of the various relationships are taken into account when choosing with whom to feed and when showing affiliative behaviors and conflict management. Birds with valuable relations were expected to share food, i.e. feeding together from the same patch. Particularly in the 2 piece condition birds were expected to actively join or leave a patch depending on who else is there. I also hypothesized that birds with valuable relations would engage in affiliative behaviors post conflict, i.e. after feeding. Since siblings (kin) share highly valuable relationships they were expected to show more socio-positive behavior towards each other than towards non-siblings. Furthermore, female-female relations were expected to be less effective than male-female and male-male relations during the experiment because the relationships between females tend to be generally less compatible and less secure than those between males and between males and females (Fraser & Bugnyar 2010).

2 Material and Methods

2.1 Subjects and settings

Subjects were twelve parent-raised ravens (six males, six females, born in spring 2010. In mid-September the birds were brought to the new research station of the Department of Cognitive Biology from the University of Vienna at Haidlhof (Figure 1), which is located near Bad Vöslau in Lower Austria.

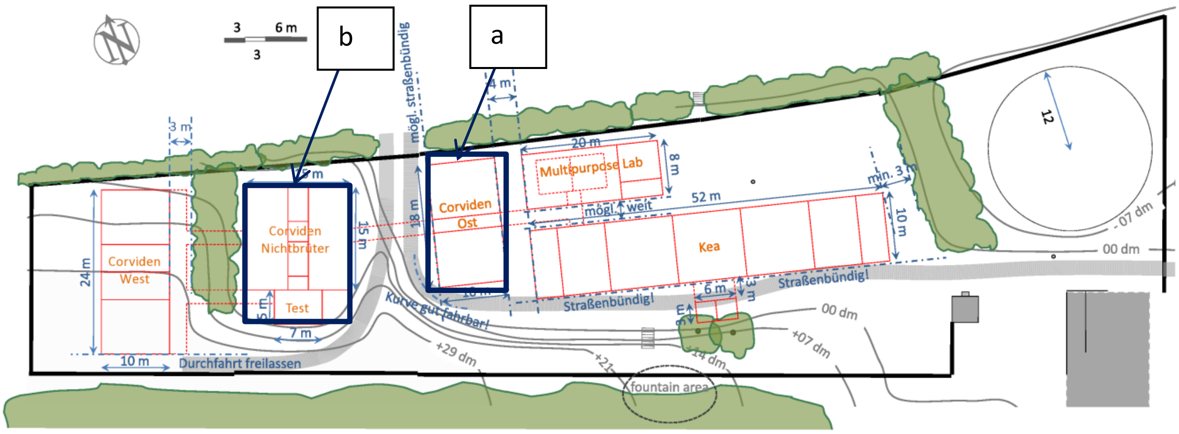

Figure 1 Plan of the Research Station Haidlhof (drawn by Dr. *Gyula Gajdon*): Ravens were first housed in the east aviary (a) and then in the middle (b) aviary

Table 1 Subjects: siblings are always listed in sequence and the different grey shades mark the borders between the sibling groups

ID	Origin	Age	Sex	Subgroup	Type of breeding location
Sven	WildparkWels	2010	male	A	Animal park
Jonas	Wildpark Wels	2010	male	A	Animal park
Lasse	Wildpark Wels	2010	male	A	Animal park
Anton	Alpenzoo Innsbruck	2010	male	A	Zoo
Heidi	Alpenzoo Innsbruck	2010	female	A	Zoo
Astrid[*]	Wildpark Wels (hand-raised)	2010	female	A	Animal park
Joey[*]	Allgäu (hand-raised)	2010	female	A	Private owner
Jakob	Wildpark Bayrischer Wald	2010	male	B	Animal park
Willi	Wildpark Bayrischer Wald	2010	male	B	Animal park
Elen	Wildpark Bayrischer Wald	2010	female	B	Animal park
Klara	Wildpark Bayrischer Wald	2010	female	B	Animal park

---

[*] The two hand-raised birds were kept in group A until all birds moved together then they were kept separately. They did not participate in the experiment and were not part of the analysis.

Carmen[†]	Wildpark Bayrischer Wald	2010	female	B	Animal park
Lena	Klosterneuburg	2010	female	B	Private Breeder
Sophie	Klosterneuburg	2010	female	B	Private Breeder

The colony of ravens at Haidlhof was established in 2010 and consisted of four sibling groups which were parent-raised and two hand-raised birds (see Table 1). Birds were marked with colored rings for individual identification. To simulate a natural situation, sibling groups were introduced to each other in a stepwise procedure. After arrival at the research station at the 10th and the 11th of September 2010, birds were divided into two groups (A and B see Table 1), in which they were kept for the next one and a half month. During this time, birds were housed in two adjacent but visually separated outdoor aviaries, both of which were composed of two sections: the big section (8x10x4.5 m) contained natural vegetation and diverse ground cover (wood chips, soil and gravel) and the small section (4x3x4m) contained only a sand-floor and a few perches (see Fig 1 area a). On 2nd November, all parent-raised birds were transferred to a new aviary complex (Fig. 1 area b) and fused into one social group. The hand-raised birds remained in the original aviary. This new aviary was approximately double the size of the previous ones (15x15x4.5m) and could be divided into two functional parts with two middle compartments in between (for detail see Figure 2). Additionally birds had access to a complex (called Petrarium) (5x7x4m) that consisted of small rooms and was visually isolated from the rest of the aviary (Figure 2). This complex was designed to provide opportunities for avoiding conspecifics and caching food out of sight of the other birds. All parts of the aviary were equipped with wooden perches and several kinds of natural substrate.

The ravens were fed twice a day, in the morning (between 8-9 am) and in the afternoon (between 12-3 pm). When experiments were scheduled, they got only a small snack in the morning and most of the food in the afternoon, after the experiments.

[†] Escaped on the 9th of December and could only be analyzed until this date.

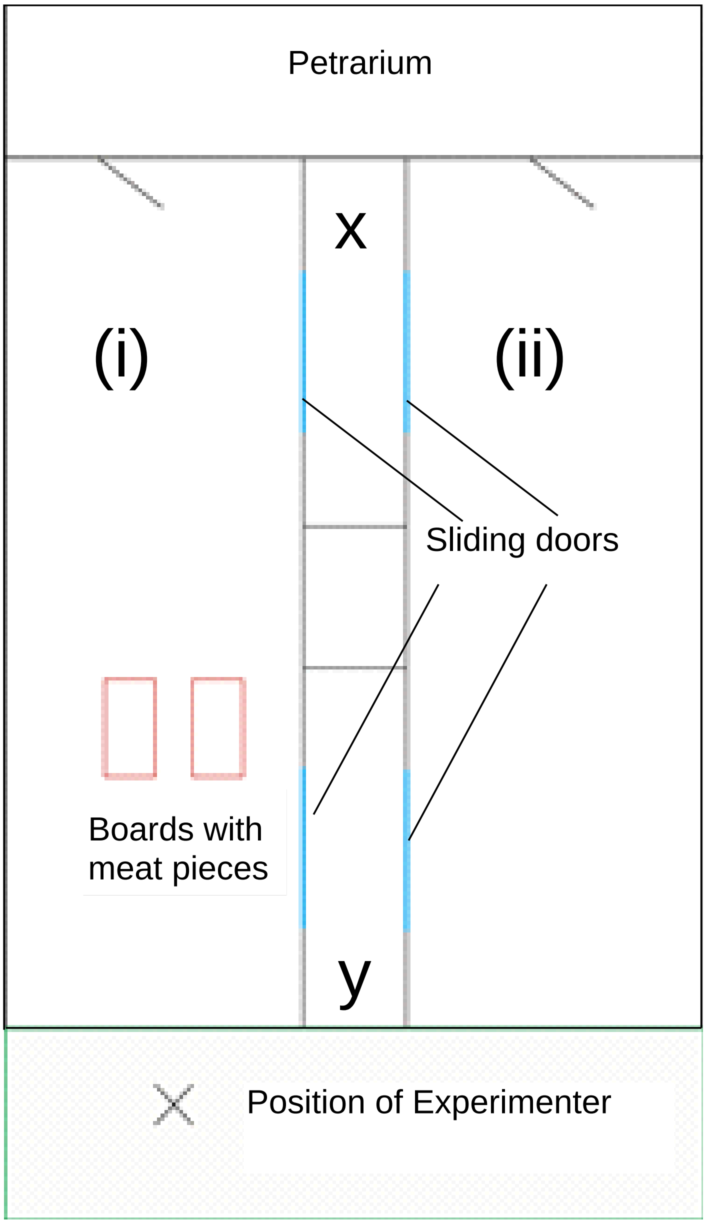

Figure 2 Aviary b, which has been housing the group of parent-raised ravens after its fusion: X marks the position of the experimenter during the focal protocols and the experiment. (i) marks the left part of the aviary, (ii) marks the right part of the aviary, The place of the boards with the meat pieces alternated between (i) and (ii). (X) and (y) mark the small compartments between the two big parts which could be closed with the sliding doors

During focal observations one of the middle compartments (x in Fig. 2) between the two aviary parts (i) and (ii) was locked to prevent birds from going out of sight. However, during the experiment the doors remained open to allow the birds to use the whole aviary (e.g. to escape when they got chased by another individual). At the onset of the study, all subjects were experimentally naïve.

2.2 Procedures

Focal sampling

After a habituation phase of four days, I started to observe the birds four times per week using the focal sampling method. Each individual was observed five minutes per day. All individuals in the same condition were observed on the same day in a randomized order. There were four different observation conditions: morning before feeding, morning after feeding, afternoon before feeding, and afternoon after feeding. Morning observations took place between 8-11 am and afternoon observations between 1-4 pm. The after-feeding condition always started approximately 45 minutes after the animals had been fed. I videotaped (Canon Legria HF S10) all observation sessions and additionally used a microphone (Sennheiser) to record the calls of the birds. Later I analyzed the social protocols with a behavior coding program (Solomon Coder by András Péter) focusing on all self-directed, affiliative, and agonistic behaviors (see Table 2).

Table 2 Ethogram of behavior collected and analyzed during experiment and focal protocols

Affiliative (without food/object)
➢ **Touch/hold**: One bird touches another one's body
o Touch beak
o Touch foot
➢ **Touch-touch**: two birds touch each other simultaneously
o Touch-touch bill
o Touch-touch foot
➢ **Contact sit**: Two birds sit next to each other in a reaching distance
o Who initiates contact
o Sitting together in contact
o Who terminates contact sit
➢ **Preening**: One bird touches feathers with bill
o Autopreening: oneself → self-directed behavior
o Allopreening: Of another bird
Agonistic (without food/object)
➢ **Displacement**: One bird approaches and the other retreats within two seconds
this occurs without vocalizations from the receiver → lower intensity
o Submissive bird retreats without being threatened
o Submissive bird retreats after being only visually threatened
➢ **Challenged displacement** (**forced retreat**): One bird approaches and the other retreats with defensive vocalizations
o Submissive bird retreats without physical contact
o Submissive bird retreats after a physical contact
➢ **Threat/peck**: one bird threatens another one without the other one retreating
o Threat visually: One bird pecks in the direction of another bird without making physical contact

o Peck: One bird pecks the other bird (with physical contact)
➢ **Fight**: Two birds hitting each other
o One/Both jumping in the air, hitting with feet and beaks
o One is down on the ground, one is sitting on top, both hitting with beaks
➢ **Chase**: one bird pursues another one in flight (e.g. after a fight)
➢ **Intervention**: One bird interferes in a social interaction (agonistic/affiliative)between two or more birds
o Passive: The third party approaches and watches the others
o Active: The third party actively gets involved in the interaction (includes taking turns in a chase flight)
▪ At the same time
▪ Shortly (<1min) afterwards.
Affiliative (with food/object)
➢ **Co-Action**: two or more birds feed/manipulate next to each other in a reaching distance
o Co-feeding: two or more birds feed next to each other but not on the same food piece
o Co-manipulation: two or more birds manipulate on the same fixed object or the ground
➢ **Sharing**: two or more birds share one item
o Share food: Two birds feed on the same food piece
o Share object: Two birds manipulate one portable object together
➢ **Transfer**: One bird gives an item to another bird or lets the other one take it
o Passive(tolerated theft): The bird with the item allows it to be taken by another individual
o Active giving: The owner gives the item to another bird
➢ **Begging/Asking**: One individual touches another's beak and/or vocalizes with/without wing flapping for item
➢ **Offering**: One individual visually presents an item to another individual
Agonistic (with food/object)
➢ **Scrounging**: making use of a resource in somebody else's possession
o Stealing: One bird approaches another bird with an object/food, takes it and stays
o Snatching: One bird approaches another bird with an object/food, takes it and leaves
o Pilfering: One bird takes an object/food another bird has hidden
➢ **Scrounging attempts**: failure of making a use of a resource in somebody else's possession
o Stealing Attempt: One bird tries to take it but other bird leaves with item/food
o Snatching Attempt: One bird tries to snatch but gets threatened away
o Pilfering Attempt: One bird tries to pilfer cached food/item but gets threatened away and/or does not find it
Legend: Item = food or object

Monopolizable Food Experiment

I started running experiments at the beginning of November 2010 after the fusion of the two subgroups. I ran the experiments three times a week always at 10:30 am. To lower the hunger level I fed the birds two hours before with bread, fruit, and cheese. I chose this specific schedule, because it gave us enough time to conduct focal samples before.

The experiment consisted of three different phases: before-feeding (20 min), feeding (30min), and after-feeding (20 min). In the 20 minutes before feeding the birds could not see the food and did not know which condition they would be confronted with. At the beginning of the feeding phase, the food was offered to the ravens by a second experimenter; in the monopolizable conditions, it was fixed on a board to prevent birds from moving it. Before the after-feeding phase started, the remaining food was removed by the experimenter. The whole experiment was videotaped for later analysis. I used behavioral sampling to score all agonistic and affiliative interactions between the animals (see Table 2). Additionally I took scan samples every 30 seconds to determine where the birds were located within the aviary, the mean distance between the individuals, and, specifically, who was next to whom.

Three pseudo-randomly alternating conditions were presented, which differed in the degree to which the food was monopolizable: (i) one piece of meat (0.8 kg) on one board, (ii) two pieces of meat (total of 0.8 kg in total) on two boards, (iii) twelve pieces (0.8 kg in total) scattered around the aviary. The latter (iii) featured the control condition, in which food was not clumped and every individual should be able to get a piece. When two pieces were presented I placed the two boards at a distance of about two meters from each other so that the birds could see both boards at the same time and could choose which of the food resources to go to. The amount of food and the quality of meat was kept constant throughout the three conditions presented each week.

In approximately half of the sessions a second person was present especially in the before-feeding phase. After running a Generalized Linear Mixed Model (=GLMM) in which all factors were included, there was a significant effect of the second person in the before-feeding phase and therefore this phase was excluded from comparison in the discussion but mentioned for completeness in the results. As it appeared that the ravens might be affected by the onlookers, three different categories (zero risk, low risk and high risk) were created depending on the frequency of the person’s presence and birds’ experience with that person, negative (handling or treatments) and positive (got fed by the person) and included as a factor in the analysis.

2.3 Statistical analyses

I divided the social behaviors into agonistic and affiliative and summed up all behaviors (Tab. 2) independent of whether they were food related or not. To test for differences between conditions I used a Friedman Test. To further examine any significant results I used a Wilcoxon signed ranks test for post-hoc analysis and a Bonferroni Correction for repeated testing to determine which conditions differed. This set of analyses I used for each experimental phase and for the affiliative and the agonistic behaviors separately.

To analyze if there is a difference in social behavior in the different conditions in the respective phases, a GLMM was used implemented in the glmmADMB module (H. Skaug, D. Fournier and A. Nielsen) of the software R 2.13.0 (R development Core Team 2008). The GLMM allows analyzing individual data. This package is advantageous because it allows for the simultaneous modeling of random effects and excess zeros for count data. The data was split up in all possible individual dyads and since not all individuals interacted with each other, I used a zero inflated model. After choosing the best model I tested for the effects of kinship, condition, phase, dyad, and presence of onlooker. I ran three different models one on agonistic behavior, one on affiliative behavior, and one on preening. Since the preening model and the affiliative behavior showed consistent results in the before-feeding phase and the feeding phase I described only the after-feeding phase of the preening behavior in the result section. However all results are plotted in the appendix. The selection of the model was accomplished by limiting interactions which were not at least slightly significant. When an interaction was significant I split up the data into one component of the interaction. I repeated this procedure until there were no interactions left.

To analyze if there was a correlation between agonistic behavior in the feeding phase and preening behavior in the after-feeding phase I ran a one tailed Mantel test with “zt” which is a software tool for simple and partial Mantel tests, created by Eric Bonnet and Yves Van de Peer. I also correlated the nearest-neighbor data at the feeding board or in the two meter surrounding area with the preening data from the focal protocols to determine which effect the daily social life relationships have on tolerance levels at the feeding site. Here I split the nearest neighbor data into the different conditions (1 piece or 2 pieces) and the preening data into three different time phases (first two month, second two month, third two month) and run the test in “R” with the “ncf-package: spatial nonparametric covariance functions” implemented by Ottar N. Bjornstad (2009).

3 Results

3.1 Effect of the accessibility of food on conflict behavior

To answer the question if the level of accessibility has an effect on the conflict behavior the three different conditions (1 piece, 2 pieces, 12 pieces) were compared in every phase under consideration of the agonistic behavior. The agonistic interactions were expected to increase during feeding when food can be monopolized. Unexpectedly, the Friedman rank sum test showed a significant difference between the different conditions in the before-feeding phase (chi-squared=6.84, df=2, p<0.05). A Wilcoxon signed ranks test revealed a significant difference between the 1 piece and control conditions, and between the 1 piece and 2 piece conditions, but these significance levels did not remain after a Bonferroni correction (1 piece and 2 piece: p=0.11, 1 piece and control: p=0.17 and 2 piece and control: p=0.55, Figure 3). During the feeding phase, the difference between the conditions was highly significant (Friedman test: chi-squared=13.82, df=2, p<0.001, Figure 3). A Wilcoxon signed ranks test and a Bonferroni correction revealed no significant difference between the two monopolizable conditions (p=0.97) but between the monopolizable conditions and the control (1 piece and control: p<0.01, 2 piece and control: p<0.01). In the after-feeding phase, there was no difference between the three conditions (Friedman test: chi-squared=0.19, df=2, p=0.91) in the frequency of agonistic interactions (Figure 3). These results support the prediction that the conflict potential is higher when food is clumped.

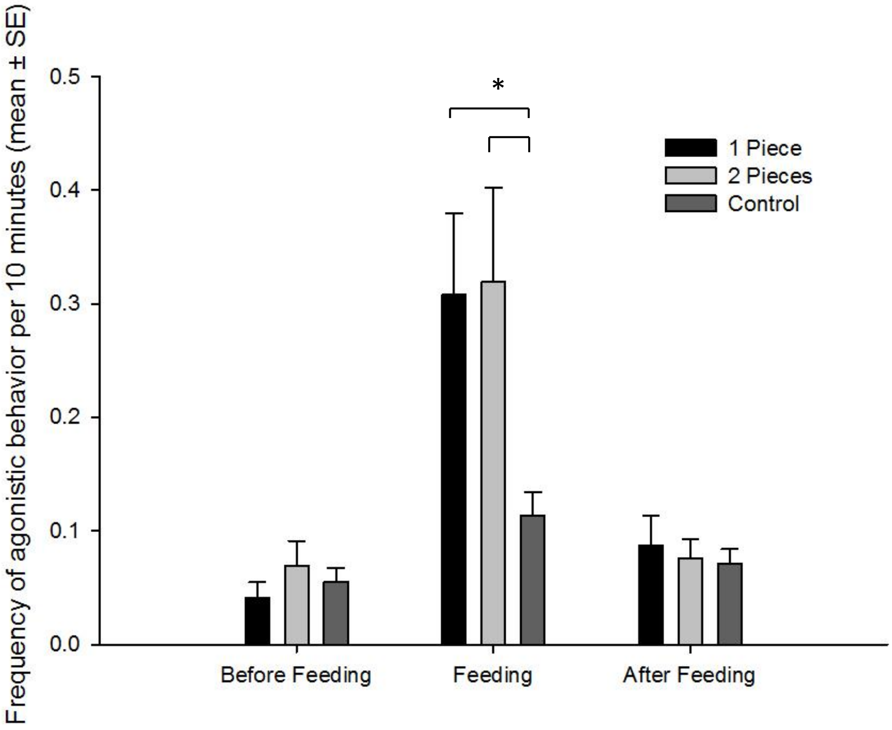

Figure 3 Frequency of the agonistic behavior in the three phases for all three conditions

3.2 Effects of sex-combination and kin on agonistic behavior

To investigate which factors affect conflict behavior a GLMM was run for zero inflated data in which the presence of a second human observer, the kinship, the condition, the phases, and the dyads (= sex combinations) were included. Additionally the interactions between these factors were included. In the before-feeding phase an interaction was found between kinship and dyad. Therefore I split the data into kin and non kin. In the before-feeding phase no significant difference was found between related individuals independent of the condition (1 piece to 2 pieces z=0.46, p=0.65, 1 piece to control z=0.95, p=0.34 and between 2 pieces and control z=0.62, p=0.54) in the agonistic behavior. In the unrelated individuals a significant difference was found between the 1 piece and the other two conditions (1 piece to 2 pieces z=2.08, p<0.05 and 1 piece to control z=2.15, p<0.05) but no such difference was revealed between the 2 piece and the control (z=0.16, p=0.87) condition.

Table 3 Effects of sex combinations on agonistic behavior in the phases for all conditions

Dyad	Before Feeding	Feeding	Feeding Kin	After Feeding
♀ -♀	n.s	* (1>C)[‡]	** (kin<non kin)	Did not work
♀-♂	n.s	(1>2*,C***)	n.s	n.s.
♂-♀	* (1<2,C)	*** (1,2>C)	*** (kin< non kin)	n.s
♂-♂	n.s	*** (1,2>C)	n.s	n.s

After splitting up the data into dyads, every dyad was examined separately. In the before-feeding phase the dyads showed no difference in the agonistic behavior between the conditions except that males showed more agonistic behavior towards females in the 1 piece condition than in the others (Table 3). The difference was unexpected because the birds did not know with which condition they would be confronted with. A possible explanation is the presence of a second person during some of the trials, which was shown to be a significant factor in the before-feeding phase, especially between related individuals. There was a significant difference in the agonistic behavior depending how “risky” the other person was. The birds showed significantly more agonistic behavior towards each other when no second person was present than low risk (z=2.97, p<0.01) and high risk (z=3.07, p<0.01) persons were present but there was no significant difference between low or high risk (z=0.49, p=0.63) persons.

In the feeding condition there were significant interactions between condition and dyad, and between kinship and dyad. Thus, the data were split by dyad and by kinship. After the splitting up the data in kinship the interaction between condition and dyad remained. Overall the birds showed the most aggression in the 1-piece condition during feeding, independent of the sex combination (Table

---

[‡] n.s= not significant, *:p=0.05; **:p=0.01; ***:p=0.001

3) but in particular the frequency of agonistic behavior from females against males was significantly higher during the 1 piece condition as compared to the other two. In all the other sex combinations the birds showed more aggression in the two monopolizable conditions than in the control condition (Table 3).

The dyads did not show a difference in the agonistic behavior between the conditions in the after-feeding phase, but there is a trend that females were more aggressive against males in the control than in the 2 piece condition (Table 3). A reason for this could be snatching attempts when the food was spread in the aviary.

In the after-feeding phase related birds did not behave differently independent of the conditions (1 piece to 2 pieces z=0.14, p=0.89 and 1 piece to control z=1.47, p=0.14 and between 2 pieces and control z=1.3, p=0.2). However, the unrelated individuals showed less agonistic behavior following the 2 piece than following the 1 piece (z=1.97, $p<0.05$) or the control (z=2.72, $p<0.01$) condition. Similar results were found in the before-feeding phase but this time the response was reversed. The effects of non-kin were unexpected. The dyads showed no significant difference in the agonistic behavior between the different conditions.

3.3 Buffering of conflicts with affiliative behavior?

To examine whether the birds were able to buffer the conflicts their affiliative behavior in general, and their preening behavior in specific, were analyzed. The Friedman rank sum test showed no significant difference between the different conditions in the before-feeding phase (chi-squared=2.48, df=2, p=0.29). Also during the feeding phase, there was no difference between the conditions (Friedman test: chi-squared=0.21, df=2, p=0.9, Figure 4). In the after-feeding phase, there was a significant difference between the three conditions (chi-squared=17.72, df=2, $p<0.001$) in the frequency of affiliative interactions (Figure 4). A Wilcoxon signed ranks test revealed a significant difference between the 1 piece and control conditions, and between the 2 piece and control conditions, which also remained after a Bonferroni correction (1 piece and 2 piece: p=0.06, 1 piece and control: $p<0.05$ and 2 piece and control: $p<0.01$, Figure 4).

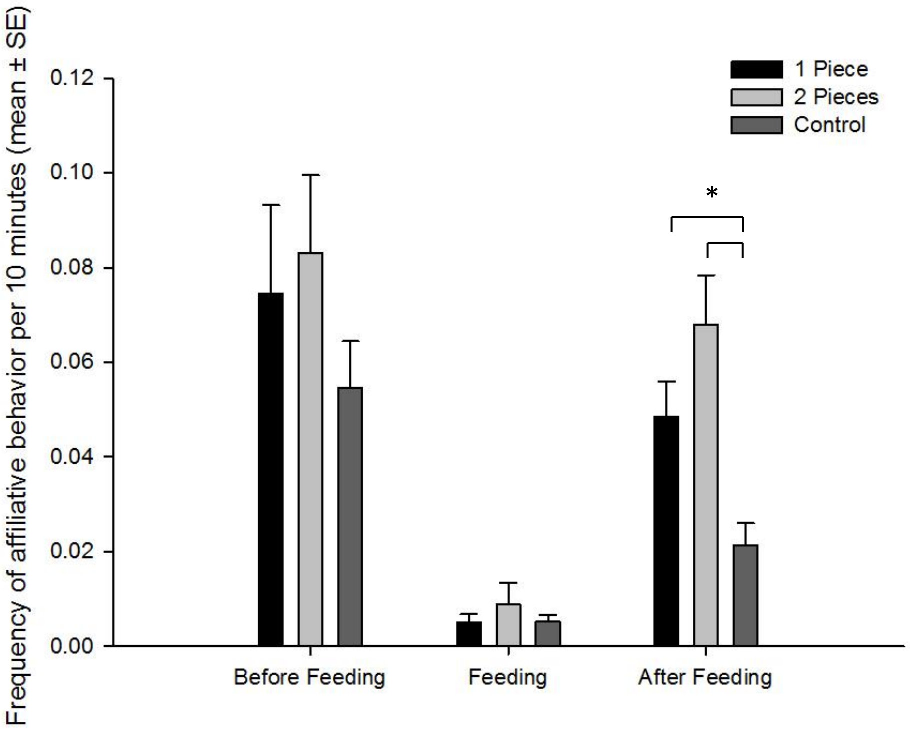

Figure 4 Frequency of the affiliative behavior in the three phases for all three conditions

A GLMM for zero inflated data was run in which the same factors as in the model of the agonistic behavior were included. The birds showed no difference in the affiliative behavior between conditions in the before-feeding phase (difference between 1 and 2 pieces z=0.14, p=0.89, between 1 piece and control z=-0.44, p=0.66 and between 2 piece and control z=-0.59, p=0.56). This is in accordance with the hypothesis and speaks against pre-conflict management.

In the before-feeding phase a significantly larger number of socio-positive behaviors was observed between siblings than between unrelated birds (z=-12.73, p<0.001). Female-female dyads showed significant less affiliative behavior than any other sex combinations in the before-feeding phase (Table 4). The other sex combinations did not differ in the before-feeding phase (p>0.05).

Table 4 Effects of sex combinations on affiliative behavior in the phases for all conditions

Dyad	Before Feeding	Feeding	After Feeding non kin	After Feeding
♀ -♀	***(< ♀-♂)	n.s	***(< ♂-♂)	.(C> 1)
♀-♂	n.s	n.s		n.s
♂-♀	***(> ♀ -♀)	. (> ♀ -♀)	**(<♂-♂)	.(2 >C)
♂-♂	**(> ♀ -♀)	. (>♂-♀)	*(>♀-♂)	.(1,2 >C)

In the feeding phase birds showed significantly more affiliative behaviors towards related than unrelated individuals (z=-8.17, p<0.001) and a trend indicated that females showed less socio-positive behaviors towards each other than males towards females. The remaining sex combinations did not show any significant differences except another trend that males behaved more nicely towards females than towards males (Table 4).

In the after-feeding phase an interaction between dyad and kin was found wherefore the data were split. In the after-feeding phase related birds showed significantly more socio-positive behavior in the 2 piece condition than in the control (z=-1.72, p=0.09). However there was no difference between the 2 piece and 1 piece condition (z=-0.18, p=0.86) and the 1 piece condition did not differ from the control condition (z=-1.55, p=0.12). The unrelated individuals did not differ in the affiliative behavior between conditions (difference between 1 and 2 pieces z=0.61, p=0.54, between 1 piece and control z=-1.4, p=0.16 and between 2 pieces and control z=-1.64, p=0.1). Within the group of kin individuals there was almost no difference between the combinations of sex in respect to affiliative behaviors except a trend indicating that males showed more socio-positive behavior towards females than towards males (z=-1.74, p=0.08). In the after-feeding phase unrelated males showed significantly more socio-positive behavior to each other than the other sex combinations (Table 4). Males seemed to show more socio-positive behavior in the after-feeding phases of the monopolizable conditions while females showed more affiliative behavior towards females in the control than in the monopolizable conditions (Table 4). The results of the males, in contrast to those of the females, are in accordance with the hypothesis.

Because of the unexpected results of the after-feeding phase, I had a detailed look at the preening behavior of the birds during this phase. Allopreening is a non-food related behavior which occurs mainly between individuals who have a good relationship. For the preening behavior a GLMM was calculated for zero-inflated data, but in the analysis the presence of another observer was excluded, because the model did not work with too many factors. Since the before-feeding and the feeding phase did not differ between affiliative behavior and preening behavior, only the after-feeding phase is described.

In the after-feeding phase the birds showed significantly less preening in the 1 piece than in the 2 piece (z=3.14, p<0.01) and the control (z=1.99, p<0.01) conditions. In the 2 piece condition the birds preened each other more often than in the control condition (z=-0.84, p=0.4). Related individuals preened each other significantly more often than unrelated ones in the after-feeding phase (z=-6.22, p<0.001). These results are in line with the expectations and also with the results of the affiliative behavior of the males. The birds showed different affiliative behaviors during the time after feeding depending on the condition which suggests that the birds might buffer the conflicts after they occurred.

Table 5 Proportion of preening behavior in respect to the total amount of affiliative behavior [%]

	1P	2P	control
BF	44.71	45.37	15.54
F	16	45.24	0
AF	10.77	34.2	82.46

3.4 Correlation between agonistic behavior during the feeding phase and preening behavior during the after-feeding phase

To see if there is a link between the agonistic behavior during the feeding phase and the preening behavior in the after-feeding phase a Mantel test was calculated performing a one-tailed test. The receiver data of the agonistic behavior during the feeding phase correlate significantly with the sender data of the preening during the after-feeding phase (Mantel test r=-0.18, p<0.05). Additionally there is a trend indicating that receivers of agonistic behavior correlate with receivers of preening (r=0.18, p=0.07).

I also correlated the preening data of the focal protocols with the preening data in the after-feeding phase and there was a significant correlation between individuals which preened each other on a daily basis and the individuals which preened each other in the after-feeding phase (Mantel test: r=0.46, p<0.01).

3.5 Nearest Neighbor

To find out if the birds who are affiliated with each other on a daily basis also prefer to feed in close proximity, a Mantel test was run in R. The grooming values of each individual were compared with the nearest neighbor scans during the experimental feeding phase. A matrix with each individual in the header and in the first row was created, comparing the matrices of preening with the matrices of nearest neighbor. Different categories of the location of the birds within the aviary were defined. The most important categories here are the “board” category, describing individuals within reach of the food, and the “2 meter” category, including birds within a 2 meter radius of the board.

Additionally the preening data were split into three time periods: the two months before the birds were consolidated (period 1), the first two months after they were consolidated (period 2), and the third and fourth month afterwards (period 3), to see if the relationships between the individuals changed over time.

1 Piece

During the 1 piece condition there was a significant correlation between nearest neighbors at the board and preening frequencies outside of the experiment (Mantel-test: r=0.46, p<0.001). The same applies for the two meter surrounding (Mantel test: r=0.36, p<0.001).

Comparing the preening frequency in period 1 and the nearest neighbors at the board shows that there is no correlation (Mantel test: r=0.14, p=0.14). The nearest neighbors at the board correlate significantly with the preening frequencies in time period 2 (Mantel test: r=0.41, p<0.01) and time period 3 (Mantel test: r=0.49, p<0.01).

2 Pieces

In the condition in which the birds could choose with whom to feed there was a high correlation between the nearest neighbor at the board and the total preening frequency received from that bird outside the experiment (Mantel test: r=0.5, p<0.001). When the data are split by “board” they both correlate significantly with the preening frequency (board 1 Mantel test: r=0.49, p<0.001; board 2 Mantel test: r=0.36, p<0.01). Also the nearest neighbors in two meter radius around the boards correlate significantly with the preening rate (Mantel test: r=0.4, p<0.01).

Comparison of the preening frequency in period 1 with the nearest neighbors at the boards shows no correlation (Mantel test: r=0.17, p=0.12). The nearest neighbors at the board correlate significantly with the preening frequencies in time period 2 (Mantel test: r=0.45, p<0.01) and time period 3 (Mantel test: r=0.52, p<0.01). When two pieces were presented, the birds were more able to choose with whom to feed than when one piece was presented that all the birds had to feed from.

4 Discussion

4.1 Effects of Condition and Kinship

To examine the effect of the experimental set up on the social interactions of the birds the experiment was split into three phases, comparing the behavior beforehand with the social interactions during a competitive situation and analyzing how the birds deal with the conflicts afterwards. I examined if conflict management varies, depending on the situation the birds are confronted with. When only one food resource was present, they had to compete with all other birds, but if two food resources were present they could strategically feed with birds they had a better relationship with. At the beginning of each experimental session the frequency of conflicts was low and the frequency of affiliative behavior was high. During the competitive situation conflicts arose and the frequency of affiliative behavior dropped. In the after-feeding phase the frequency of conflicts decreased and the frequency of affiliative behavior increased again in all conditions, but more so in specific conditions.

In the before-feeding phase the birds did not show any difference in the affiliative behavior, which is expected because they did not know which condition they would be confronted with. The same applies for the related individuals regarding the agonistic behavior. Among the unrelated individuals the birds showed the most aggression in the 1 piece condition. In the before-feeding phase another human who also observed the birds was sometimes present. Both, the identity of the person and how well the birds knew the person differed. Depending on this difference and whether the birds had negative (handling or treatment) or positive (often got fed from the person) experiences with the person, I calculated a risk factor that had an effect on the results. It thus seems likely that the birds had higher stress levels when a person representing a high risk factor was present and they consequently showed less agonistic behavior and instead a higher allo-grooming rate which is believed to be a tension reduction strategy (Keverne et al. 1989; Aureli 1992; Schino 2001). However, a difference in the agonistic behavior was only found in the 1 piece condition, not in the 2 piece and control conditions, which is not in line with this explanation. Even more unexpected is the fact, that this effect only occurs in the unrelated individuals. When analyzed with the Friedman Test the difference between the conditions in the before-feeding phase disappeared completely. The results of the before-feeding phase in general support the hypothesis that the birds did not show pre-conflict management since they did not know with which condition they would be confronted with.

During the feeding phase the ravens behaved similarly in all three conditions with respect to the affiliative behavior, which is explained by their focus on getting access to the food and dealing with the competitive situation. In respect to the agonistic behavior, the birds differed between monopolizable (1 and 2 piece condition) and distributed food. When food was clumped, conflicts increased. This is in line with the expectations that the level of conflict should depend on the level of the accessibility of the food. Interestingly, the level of agonistic behavior did not differ between the conditions in which one or two food sources were available.

In the before-feeding and feeding phases related individuals showed more affiliative behavior towards each other than unrelated individuals. These results are in accordance with my expectations and corroborate results from other studies (Russell & Hatchwell 2001; Fraser & Bugnyar 2010a).

Most interestingly, in the after-feeding phase kin individuals showed more affiliative behavior when they were able to choose with whom to feed than when food pieces were distributed in the aviary. One explanation could be that the birds showed conflict management after the monopolizable food situation. The aggression frequency was higher if food was patched and the birds had to compete for the food resource. Consequently, when more conflicts arose in the first place there was more need for dealing with the consequences afterwards. (Fraser & Bugnyar 2010b, 2011) found that ravens were not only capable of reconciliation after conflicts but also showed bystander affiliation. Their studies and the present study have in common that these behaviors occurred after intense conflicts which is the same in the monopolizable food situation. The results of the Friedman Test showed a significant difference between all conditions in the after-feeding phase. In contrast, the GLMM showed no difference between the 1 piece and the control condition which also applies to the difference between the 1 piece and 2 piece conditions. Between 2 piece and control conditions there was a significant difference, which shows that most affiliative behavior occurred in the 2 piece condition and fewest in the control condition. The differences only appeared between related individuals, while unrelated individuals did not show any difference between the different conditions in the after-feeding phase. In contrast, in respect to the agonistic behavior there was no difference between related individuals in any of the conditions, while between unrelated individuals there was more agonistic behavior recorded in the 1 piece and control conditions than in the 2 piece condition. The results of the after-feeding phase demonstrate that the birds behaved in a more socio-positive way in the 2 piece condition (less aggression, more affiliative behavior) than in the other two conditions. The results indicate that the birds repaired valuable relationships after conflict, which is similar to results of other studies of ravens (Fraser & Bugnyar 2011) and also to studies in primates (Fraser et al. 2008).

Some authors claim that preening is an indicator for the quality of relationships (Dunbar 1991; Silk et al. 1996; Silk 2002). This and the fact that preening is not a food-related behavior (as would be sharing or co-feeding) is the reason why we looked specifically at the allo-preening data from the experiments. Grooming is one of the most common altruistic behaviors amongst primates and, possibly, amongst other mammals and birds (Dunbar 1991; Mooring et al. 2004; Radford & Plessis 2006). Allo-grooming or in this case allo-preening is known to strengthen bonds between individuals and to reduce stress (Dunbar 1991; Aureli et al. 1999). In primates, for example, allo-grooming occurs at a higher rate after intragroup conflicts of great intensity and conflicts involving same-sex individuals (Schino et al. 1998).

When the birds were in a monopolizable food situation, I removed the food before the start of the after-feeding phase. We could not remove the food in the control condition because it was not fixed to start with and the birds could move around with the food. Although there was not a lot of agonistic behavior during the control situation it still occurred. In the after-feeding phase some of the birds still had some food left and conflicts concerning the last food pieces happened regularly. Hence it is possible that the birds showed less socio-positive behavior in the after-feeding phase of the control condition because they were still occupied with the last pieces of food.

4.2 Sex differences

In the before-feeding phase socio-positive behavior between female-female dyads occurred less often than between the other dyads. This result is in line with the findings of Fraser & Bugnyar (2010a) which indicate that females do not develop a strong bond with each other.

In the before-feeding phase none of the dyads showed any difference in the agonistic behavior in any of the conditions except the male-female dyads which showed more agonistic behavior in the 1 piece than in the other two conditions. Again, the presence of a second human observer is a possible explanation for the differences as it had an effect on the male-female dyads in the before-feeding phase.

In the feeding phase female-female dyads showed less socio-positive behavior than male-female dyads which also showed more affiliative behavior than male-male dyads. Again, these results are in accordance with the findings from Fraser and Bugnyar (2010a), which also did not differ in a competitive situation. Males spent more time at the food and as a consequence less time with affiliative behavior.

In the after-feeding phase related female dyads behaved the same way as the other dyads, however unrelated females showed less socio-positive behavior than unrelated male-male dyads. Relationships between unrelated individuals seem to be more valuable between males than between females. A reason for this might be that non breeder males form alliances with each other to overpower other males (Fraser & Bugnyar 2010a).

4.3 Use of social relations

The nearest neighbor at the food correlated with the allo-preening frequency outside the experimental situation which shows that affiliated birds feed in close proximity to each other. This is in line with the expectation that birds which share a valuable relationship also show affiliative behavior during a competitive situation.

An interesting result was that the preening frequencies in the period before birds were moved together did not correlate with the nearest neighbors at the food. A possible explanation for this might be that the birds had to develop their relationships after they arrived at the research station and it took some time to establish them. Another explanation could be that after the fusion of the different groups it was more necessary to strengthen existing relationships to overpower the "strangers".

The preening rate of the focal protocols correlated with the preening rate in the after-feeding phase, which can be explained by post-conflict management. Also the preening frequency during the after-feeding phase supports the hypothesis that male-male relationships are more important than female-female ones. (Cords & Thurnheer 1993) tested the effect of the quality of a relationship on the frequency of reconciliation. After manipulating a situation where longtail macaques (*Macaca fascicularis*) had to work together to gain access to food, they found that reconciliation after a conflict was more likely when the partner's value was enhanced during the experimental phase. According to the valuable relationship hypothesis, individuals in a valuable relationship are more likely to reconcile (de Waal & Aureli 1997; Watts 2006). Social relationships are important because of different reasons. In various species, alliance-formation occurs and is an important factor in the acquisition and maintenance of dominance ranks (Chapais 1992). Furthermore alliances can also help in obtaining access to females or food. The hypothesis that male-male relationships have a higher long-term importance in ravens originates from the idea that coalitions are used to overpower other males which is a phenomenon also observed in wild chimpanzees (Watts 2002, 2002). Another explanation could be that males are stronger and more often the aggressors of a conflict than females. Therefore, they might make the first step towards reconciliation more often after a conflict occurred. This hypothesis is also supported by the findings from the 2 piece and control conditions indicating that females preened each other less often than males preen other males or females.

Another explanation for the preening in the after-feeding phase could be the "biological market theory" (Noë & Hammerstein 1994). This theory describes how social commodities or services can be exchanged between conspecifics or between different species. Various studies followed this approach and found that grooming among conspecifics is often traded for grooming in return which would result in direct reciprocity (Hemelrijk & Ek 1991; Tiddi et al. 2011). Grooming can also be traded for other social benefits, including tolerance (Barrett et al. 1999) and agonistic support (Schino 2007). In a meta-analysis of 36 independent tests on 14 different species Tiddi et al. (2011) found a significant correlation between grooming and agonistic behavior in primates. The reason why the birds preened in the after-feeding phase during the present experiment might be that they were tolerated at the food source or that they wanted to be tolerated in the future. What speaks against this is the significant correlation between the individuals which received aggression and the birds which preened afterwards. This means that birds who received a lot of aggression preened more frequently afterwards. This would be in line with the expectation that the birds buffer conflicts after they occurred and show post-conflict management.

Another possible explanation, supported by the findings of (De Waal 1997), would be that the birds wanted to trade preening for access to food. He found that grooming in chimpanzees increased the probability that the recipient of the service will share with its donors. It could be that the birds tried to improve their relationships after experiencing a competitive situation to gain better access to food in future situations. It would make sense that the birds only show this strategic behavior after a 2 piece situation, because here they were able to choose with whom to feed. They experienced a situation in which it is important to have good relationships with individuals who are of a higher rank and as a consequence have better access to food. From the view of the victim it would make sense to focus on repairing the highly valuable relationships after conflict. Similar results have recently been found in Barbary macaques (McFarland & Majolo 2011a).

To find out, which of these possible explanations is correct more experiments are needed, to observe how the birds behave when they know beforehand with which condition they will be confronted with. If they were able to change their behavior according to future benefits they would increase their preening behavior in the 2 piece condition, which is the only condition where they can benefit from improving their relationships beforehand. Di Sorrentino et al. (2010) recently showed that capuchin monkeys are able to show such types of conflict prevention. The monkeys increased their grooming behavior before an expected feeding situation, but not selectively to specific partners. This conflict prevention requires the animal to hold expectations about future events based on past experience (di Sorrentino et al. 2010) which could also be the case in ravens.

Conclusion

In this study I confronted sub-adult ravens with different types of competitive foraging situations. As predicted, when food was clumped, conflicts increased. The accessibility of the food affected the conflict frequency. Depending on the intensity of the conflicts and on the conflict opponent, receivers of aggression showed preening behavior afterwards which could be interpreted as post-conflict management. Birds that shared good relationships outside of the experiment were able to feed in close proximity during the test. Social relationships seem to help ravens in a competitive situation. Additional experiments are necessary, to find out which mechanism explains the results that the birds preened more frequently after conflicts when they were allowed to choose with whom to feed and compete over the food resource.

Acknowledgments

First of all I want to thank Prof. Thomas Bugynar for supervising my master thesis and for his scientific advices. Furthermore, a big thanks to Mag. Julia Müller for proofreading and Mag. Markus Böckle for the support with statistics. Special thanks to Gernot and my family for their social support.

References

Alexander, R. D. 1974. The Evolution of Social Behavior. *Annual Review of Ecology and Systematics*, **5**, 325–383.

Amici, F., Aureli, F. & Call, J. 2008. Fission-Fusion Dynamics, Behavioral Flexibility, and Inhibitory Control in Primates. *Current Biology*, **18**, 1415–1419.

Armitage, G. C. 1999. Development of a Classification System for Periodontal Diseases and Conditions. *Annals of Periodontology*, **4**, 1–6.

Aureli, F. 1992. Post-conflict behaviour among wild long-tailed macaques (Macaca fascicularis). *Behavioral Ecology and Sociobiology*, **31**,

Aureli, F. & Schaik, C. P. van. 1991a. Post-conflict Behaviour in Long-tailed Macaques (Macaca fascicularis). *Ethology*, **89**, 89–100.

Aureli, F. & Schaik, C. P. van. 1991b. Post-conflict Behaviour in Long-tailed Macaques (Macaca fascicularis). *Ethology*, **89**, 101–114.

Aureli, F. & Waal, F. B. M. D. 2000. *Natural Conflict Resolution.* University of California Press.

Aureli, F., Preston, S. D. & de Waal, F. B. M. 1999. Heart Rate Responses to Social Interactions in Free-Moving Rhesus Macaques (Macaca mulatta): A Pilot Study. *Journal of Comparative Psychology*, **113**, 59–65.

Aureli, F., Cords, M. & van Schaik, C. P. 2002. Conflict resolution following aggression in gregarious animals: a predictive framework. *Animal Behaviour*, **64**, 325–343.

Barrett, L., Henzi, S. P., Weingrill, T., Lycett, J. E. & Hill, R. A. 1999. Market forces predict grooming reciprocity in female baboons. *Proceedings of the Royal Society of London. Series B: Biological Sciences*, **266**, 665 –670.

Braun, A., Walsdorff, T., Fraser, O. N. & Bugnyar, T. 2012. Socialized sub-groups in a temporary stable Raven flock? *Journal of Ornithology*,

Brown, G. R., Almond, R. E. A. & Bergen, Y. v. 2004. Begging, Stealing, and Offering: Food Transfer in Nonhuman Primates. *Advances in the study of behaviour*, **34**, 265–295.

Bugnyar, T. 2011. Knower–guesser differentiation in ravens: others' viewpoints matter. *Proceedings of the Royal Society B: Biological Sciences*, **278**, 634 –640.

Bugnyar, T. & Heinrich, B. 2005. Ravens, Corvus corax, differentiate between knowledgeable and ignorant competitors. *Proceedings of the Royal Society B: Biological Sciences*, **272**, 1641 –1646.

Bugnyar, T. & Heinrich, B. 2006. Pilfering ravens, Corvus corax, adjust their behaviour to social context and identity of competitors. *Animal Cognition*, **9**, 369–376.

Bugnyar, T. & Kotrschal, K. 2002. Observational learning and the raiding of food caches in ravens, Corvus corax: is it 'tactical' deception? *Animal Behaviour*, **64**, 185–195.

Bugnyar, T., Stöwe, M. & Heinrich, B. 2004. Ravens, Corvus corax, follow gaze direction of humans around obstacles. *Proceedings of the Royal Society of London. Series B: Biological Sciences*, **271**, 1331 –1336.

Byrne, R. & Whiten, A. 1989. *Machiavellian Intelligence : Social Expertise and the Evolution of Intellect in Monkeys, Apes, and Humans (Oxford Science Publications).* {Oxford University Press, USA}.

Chapais, B. 1992. The role of alliances in social inheritance of rank among female primates. In: *Coalitions and alliances in humans and other animals*, Oxford University Press.

Clutton-Brock, T. H. 1989. Review Lecture: Mammalian Mating Systems. *Proceedings of the Royal Society of London. B. Biological Sciences*, **236**, 339 –372.

Cordoni, G. & Palagi, E. 2008. Reconciliation in Wolves (Canis lupus): New Evidence for a Comparative Perspective. *Ethology*, **114**, 298–308.

Cords, M. 1997. Friendship, alliances,reciprocity and repair. In: *Machiavellian intelligence II: extensions and evaluations*, pp. 177–198. Cambridge University Press.

Cords, M. & Aureli, F. 2000. Reconciliation and Relationship Qualities. In: *Natural Conflict Resolution*, pp. 177–199. Univ of California Pr.

Cords, M. & Thurnheer, S. 1993. Reconciling with Valuable Partners by Long-tailed Macaques. *Ethology*, **93**, 315–325.

de Waal, F. B. M. 1986. *Deception in the natural communication of chimpanzees. In: Deception: Perspectives on Human and Nonhuman Deceit.* (R.W. Mitchell & N. S Thompson, eds.), pp.221-244. State University of New York Press.

de Waal, F. B. M. & Aureli, F. 1997. Conflict Resolution and Distress Alleviation in Monkeys and Apes. *Annals of the New York Academy of Sciences*, **807**, 317–328.

de Waal, F. B. M. 1997. The Chimpanzee's service economy: Food for grooming. *Evolution and Human Behavior*, **18**, 375–386.

di Sorrentino, E. P., Schino, G., Visalberghi, E. & Aureli, F. 2010. What time is it? Coping with expected feeding time in capuchin monkeys. *Animal Behaviour*, **80**, 117–123.

Dunbar, R. I. M. 1991. Functional Significance of Social Grooming in Primates. *Folia Primatologica*, **57**, 121–131.

Dunbar, R. I. M. 1998. The social brain hypothesis. *Evolutionary Anthropology*, **6**, 178–90.

Emery, N. J. 2006. Cognitive ornithology: the evolution of avian intelligence. *Philosophical Transactions of the Royal Society B: Biological Sciences*, **361**, 23 –43.

Emery, N. J. & Clayton, N. S. 2004. The Mentality of Crows: Convergent Evolution of Intelligence in Corvids and Apes. *Science*, **306**, 1903 –1907.

Emlen, S. T. 1982. The Evolution of Helping. I. An Ecological Constraints Model. *The American Naturalist*, **119**, 29–39.

Engh, A. L., Siebert, E. R., Greenberg, D. A. & Holekamp, K. E. 2005. Patterns of alliance formation and postconflict aggression indicate spotted hyaenas recognize third-party relationships. *Animal Behaviour*, **69**, 209–217.

Fraser, O. N. & Bugnyar, T. 2010a. The quality of social relationships in ravens. *Animal Behaviour*, **79**, 927–933.

Fraser, O. N. & Bugnyar, T. 2010b. Do Ravens Show Consolation? Responses to Distressed Others. *PLoS ONE*, **5**, e10605.

Fraser, O. N. & Bugnyar, T. 2011. Ravens Reconcile after Aggressive Conflicts with Valuable Partners. *PLoS ONE*, **6**, e18118.

Fraser, O. N., Schino, G. & Aureli, F. 2008. Components of Relationship Quality in Chimpanzees. *Ethology*, **114**, 834–843.

Fraser, O. N., Koski, S. E., Wittig, R. M. & Aureli, F. 2009. Why are bystanders friendly to recipients of aggression? **2**, 285–291.

Goodwin, D. 1976. *Crows of the world.* Published in cooperation with the British Museum (Natural History) by Comstock Pub. Associates.

Hamilton, W. D. 1964. The genetical evolution of social behaviour. I. *Journal of Theoretical Biology*, **7**, 1–16.

Hart, B. L. & Hart, L. A. 1992. Reciprocal allogrooming in impala, Aepyceros melampus. *Animal Behaviour*, **44**, 1073–1083.

Hart, B. L., Hart, L. A., Mooring, M. S. & Olubayo, R. 1992. Biological basis of grooming behaviour in antelope: the body-size, vigilance and habitat principles. *Animal Behaviour*, **44**, 615–631.

Heinrich, B. 1989. *Ravens in winter.* Summit Books.

Heinrich, B. & Marzluff, J. M. 1991. Do common ravens yell because they want to attract others? *Behavioral Ecology and Sociobiology*, **28**,

Heinrich, B. & Smolker, R. 1998. Play in common ravens (Corvus corax). In: *Animal Play*, (Ed. by M. Bekoff), Cambridge University Press.

Hemelrijk, C. K. & Ek, A. 1991. Reciprocity and interchange of grooming and 'support' in captive chimpanzees. *Animal Behaviour*, **41**, 923–935.

Hinde, R. A. 1979. *Towards understanding relationships.* London: Academic Press.

Humphrey, N. 1976. The social function of intellect. In: *Growing points in ethology*, pp. 303–317. Cambridge University Press.

Isaac, G. 1978. The food-sharing behavior of protohuman hominids. *Scientific American*, **238**,

Jolly, A. 1966. Lemur Social Behavior and Primate Intelligence. *Science*, **153**, 501–506.

Keverne, E. B., Martensz, N. D. & Tuite, B. 1989. Beta-endorphin concentrations in cerebrospinal fluid of monkeys are influenced by grooming relationships. *Psychoneuroendocrinology*, **14**, 155–161.

Koyama, N. F. 2000. Conflict Prevention before Feeding. In: *Natural Conflict Resolution*, pp. 130–132. Univ of California Pr.

Koyama, N. F. 2001. The Long-Term Effects of Reconciliation in Japanese Macaques Macaca fuscata. *Ethology*, **107**, 975–987.

Krause, D. J. & Ruxton, G. D. 2002. *Living in groups.* Oxford University Press.

Kummer, H. 1978. On the value of social relationships to nonhuman primates: A heuristic scheme. *Social Science Information*, **17**, 687–705.

Kutsukake, N. & Clutton-Brock, T. H. 2010. Grooming and the value of social relationships in cooperatively breeding meerkats. *Animal Behaviour*, **79**, 271–279.

Lazaro-Perea, C., Arruda, M. de F. & Snowdon, C. T. 2004. Grooming as a reward? Social function of grooming between females in cooperatively breeding marmosets. *Animal Behaviour*, **67**, 627–636.

Majolo, B., de Bortoli Vizioli, A. & Schino, G. 2008. Costs and benefits of group living in primates: group size effects on behaviour and demography. *Animal Behaviour*, **76**, 1235–1247.

Marzluff, J. M., Angell, T. & Ehrlich, P. R. 2007. *In the Company of Crows and Ravens.* Yale University Press.

McFarland, R. & Majolo, B. 2011a. Grooming Coercion and the Post-Conflict Trading of Social Services in Wild Barbary Macaques. *PLoS ONE*, **6**, e26893.

McFarland, R. & Majolo, B. 2011b. Exploring the Components, Asymmetry and Distribution of Relationship Quality in Wild Barbary Macaques (Macaca sylvanus). *PLoS ONE*, **6**, e28826.

Miller, R. C. 1922. The Significance of the Gregarious Habit. *Ecology*, **3**, 122–126.

Mooring, M. S. & Hart, B. L. 1995. Costs of allogrooming in impala: distraction from vigilance. *Animal Behaviour*, **49**, 1414–1416.

Mooring, M. S., Blumstein, D. T. & Stoner, C. J. 2004. The evolution of parasite-defence grooming in ungulates. *Biological Journal of the Linnean Society*, **81**, 17–37.

Mulcahy, N. J. & Call, J. 2006. Apes Save Tools for Future Use. *Science*, **312**, 1038 –1040.

Noë, R. & Hammerstein, P. 1994. Biological markets: supply and demand determine the effect of partner choice in cooperation, mutualism and mating. *Behavioral Ecology and Sociobiology*, **35**, 1–11.

Noë, R., Schaik, C. P. & Hooff, J. A. R. A. M. 1991. The Market Effect: an Explanation for Pay-off Asymmetries among Collaborating Animals. *Ethology*, **87**, 97–118.

Osvath, M. 2009. Spontaneous planning for future stone throwing by a male chimpanzee. *Current Biology*, **19**, R190–R191.

Osvath, M. & Osvath, H. 2008. Chimpanzee (Pan troglodytes) and orangutan (Pongo abelii) forethought: self-control and pre-experience in the face of future tool use. *Animal Cognition*, **11**, 661–674.

Packer, C. & Ruttan, L. 1988. The Evolution of Cooperative Hunting. *The American Naturalist*, **132**, 159–198.

Parker, C. 1979. Sexual selection and sexual conflict. In: *Sexual Selection and Reproductive Competition in Insects*, pp. 123–166. Academic Press Inc.

Pitcher, T. J., Green, D. A. & Magurran, A. E. 1986. Dicing with death: predator inspection behaviour in minnow shoals. *Journal of Fish Biology*, **28**, 439–448.

Preuschoft, S. & Van Schaik, C. P. 2000. Dominance and Communication. In: *Natural Conflict Resolution*, pp. 77–105. Univ of California Pr.

Pulliam, R. 1973. On the advantages of flocking. *J. Theor. Biol.*, **38**,

Raby, C. R. & Clayton, N. S. 2009. Prospective cognition in animals. *Behavioural Processes*, **80**, 314–324.

Raby, C. R., Alexis, D. M., Dickinson, A. & Clayton, N. S. 2007. Planning for the future by western scrub-jays. *Nature*, **445**, 919–921.

Radford, A. N. & Plessis, M. A. 2006. Dual function of allopreening in the cooperatively breeding green woodhoopoe, Phoeniculus purpureus. *Behavioral Ecology and Sociobiology*, **61**, 221–230.

Richard C., C. 1995. Altruism among non-relatives: alternatives to the ‘Prisoner’s Dilemma’. *Trends in Ecology & Evolution*, **10**, 84–86.

Russell, A. F. & Hatchwell, B. J. 2001. Experimental evidence for kin-biased helping in a cooperatively breeding vertebrate. *Proceedings of the Royal Society of London. Series B: Biological Sciences*, **268**, 2169 –2174.

Schino, G. 1998. Reconciliation in Domestic Goats. *Behaviour*, **135**, 343–356.

Schino, G. 2001. Grooming, competition and social rank among female primates: a meta-analysis. *Animal Behaviour*, **62**, 265–271.

Schino, G. 2007. Grooming and agonistic support: a meta-analysis of primate reciprocal altruism. *Behavioral Ecology*, **18**, 115 –120.

Schino, G. & Aureli, F. 2009. Chapter 2 Reciprocal Altruism in Primates: Partner Choice, Cognition, and Emotions. *Advances in the study of behaviour*, **39**, 45–69.

Schino, G., Ventura, R. & Troisi, A. 2003. Grooming among female Japanese macaques: distinguishing between reciprocation and interchange. *Behavioral Ecology*, **14**, 887 –891.

Scott, C. 2001. Social dominance and stress hormones. *Trends in Ecology & Evolution*, **16**, 491–497.

Selva, N., Cortés-Avizanda, A., Lemus, J. A., Blanco, G., Mueller, T., Heinrich, B. & Donázar, J. A. 2011. Stress associated with group living in a long-lived bird. *Biology Letters*, **7**, 608 –610.

Silk, J. B. 2002. Using the 'F'-Word in Primatology. *Behaviour*, **139**, 421–446.

Silk, J. B., Cheney, D. L. & Seyfarth, R. M. 1996. The form and function of post-conflict interactions between female baboons. *Animal Behaviour*, **52**, 259–268.

Silk, J. B., Alberts, S. C. & Altmann, J. 2006. Social relationships among adult female baboons (Papio cynocephalus) II. Variation in the quality and stability of social bonds. *Behavioral Ecology and Sociobiology*, **61**, 197–204.

Smith, J. E., Kolowski, J. M., Graham, K. E., Dawes, S. E. & Holekamp, K. E. 2008. Social and ecological determinants of fission–fusion dynamics in the spotted hyaena. *Animal Behaviour*, **76**, 619–636.

Stanford, C. B. 1999. *The hunting apes: meat eating and the origins of human behavior.* Princeton University Press.

Stevens, J. R. & Gilby, I. C. 2004. A conceptual framework for nonkin food sharing: timing and currency of benefits. *Animal Behaviour*, **67**, 603–614.

Stopka, P. & Macdonald, D. W. 1999. The Market Effect in the Wood Mouse, Apodemus sylvaticus:Selling Information on Reproductive Status. *Ethology*, **105**, 969–982.

Stöwe, M., Bugnyar, T., Schloegl, C., Heinrich, B., Kotrschal, K. & Möstl, E. 2008. Corticosterone excretion patterns and affiliative behavior over development in ravens (Corvus corax). *Hormones and Behavior*, **53**, 208–216.

Tiddi, B., Aureli, F., Polizzi di Sorrentino, E., Janson, C. H. & Schino, G. 2011. Grooming for tolerance? Two mechanisms of exchange in wild tufted capuchin monkeys. *Behavioral Ecology*, **22**, 663 –669.

Trivers, R. L. 1972. Parental investment and sexual selection. In: *Sexual selection and the descent of man: the Darwinian pivot*, (Ed. by B. G. Campbell), pp. 136–179. Transaction Publishers.

Trivers, R. L. 1974. Parent-Offspring Conflict. *American Zoologist*, **14**, 249 –264.

Vahl, W. K. & Kingma, S. A. 2007. Food divisibility and interference competition among captive ruddy turnstones, Arenaria interpres. *Animal Behaviour*, **74**, 1391–1401.

Van Schaik, C. P. 1989. The ecology of social relationships amongst female primates. In: pp. 195–218.

Ward, P. & Zahavi, A. 1973. The Importance of Certain Assemblages of Birds as 'information-centres' for Food-finding. *Ibis*, **115**, 517–534.

Watts, D. P. 2002. Reciprocity and interchange in the social relationships of wild male chimpanzees. *Behaviour*, **139**, 343–370.

Watts, D. P. 2006. Conflict Resolution in Chimpanzees and the Valuable-relationships Hypothesis. *International Journal of Primatology*, **27**, 1337–1364.

Weaver, A. 2003. Conflict and Reconciliation in Captive Bottlenose Dolphins, Tursiops Truncatus. *Marine Mammal Science*, **19**, 836–846.

Appendix

Zusammenfassung

Strukturierte Gruppen zeichnen sich durch das Bilden von sozialen Beziehungen aus, deren Qualität verschiedenste Bereiche des täglichen Lebens beeinflusst. Agonistische Verhaltensweisen wie z.B. Konflikte können wichtige soziale Bindungen schädigen, weshalb es wichtig ist, Mechanismen zu entwickeln, die Konflikte verhindern bzw. mögliche Schäden reparieren.

Das Ziel meiner Studie war, die sozialen Strategien von subadulten Raben *(Corvus corax)* während kompetitivem Nahrungserwerb zu erforschen, wobei ich mich besonders auf das Konfliktverhalten während dem Nahrungserwerb und dem soziopositivem Verhalten danach konzentrierte. Um eine kompetitive Situation zu schaffen, präsentierte ich den zwölf Raben verschiedene Futtersituationen, wobei ich variierte, wie leicht das Futter zu monopolisieren ist (1 Futterstück, 2 Futterstücke oder 12 Futterstücke).

Wie erwartet, nahmen Konflikte bei monopolisierbaren Futter (1 oder 2 Futterstücke), im Vergleich zu der Situation mit 12 Futterstücken zu. Wenn die Tiere die Möglichkeit hatten (2 Futterstücke), fraßen sie neben Individuen, mit denen sie affiliiert waren. Zusätzlich zeigen die Resultate, dass Individuen, die „Opfer“ sehr vieler Konflikte während dem Nahrungserwerb waren, häufiger in der Nachfutterphase andere kraulten (=preening). Außerdem zeigten die Vögel signifkant mehr Kraulverhalten gegenüber anderen in der Nachphase, wenn sie die Möglichkeit hatten, zu wählen, mit wem sie an der Futterstelle fressen (=2 Futterstücke). Diese Resultate sind der erste experimentelle Nachweis dafür, dass Raben Konflikte abzupuffern versuchen und dass sie je nach Wert einer sozialen Beziehung diese im Nachhinein reparieren.

Abstract

Social relationships are the building blocks of many societies of group-living animals. They can built on affiliative behaviors (e.g. food sharing) or agonistic behaviors (e.g. conflicts), both defining the quality of a particular relationship. Agonistic behaviors can damage important social bonds and, therefore, it should be advantageous for individuals to develop mechanisms to buffer conflicts and to repair any damage caused.

The aim of the present study was to investigate the social strategies of ravens in a competitive foraging situation with a focus on conflict and post conflict management. I confronted 12 parent-raised ravens (*Corvus corax*) with different feeding situations in which I varied the level to which the food could be monopolized (1 Piece, 2 Pieces or 12 Pieces). In the 1 and 2 Piece conditions

food was fixed and could not be carried off to a position in which it would be easier to defend. As expected, when the food was clumped and, therefore, constituted a limited resource conflicts increased. Furthermore, the results supported the prediction that, when given the choice, birds prefer to eat with their affiliates ('friends'). Interestingly, ravens engaged in high rates of after-feeding allo-preening after the 2 Piece condition. Individuals, which received a lot of aggression in the feeding phase, preened more often afterwards. These results are the first experimental evidence to the hypothesis that ravens are capable of using post-conflict management and that the extent to which they actively repair a damaged relationship correlates with the value and closeness of that particular relationship.

Miriam Sima

Curriculum Vitae

PERSONAL DATA

Name: Sima Miriam

Sex: Female

Nationality: Austria

Date and Place of Birth: December 14th, 1987 in Klagenfurt (Austria)

Personal Status: Unmarried

Degree: Bakk. rer. nat.

Private Address: Reznicekgasse 10 3/4, 1090 Wien, Austria

Phone: +43 65805019905

E-Mail: miriam_jenifer@yahoo.de

EDUCATION

- 2006-2009: Bachelor Behaviour at the University of Graz
  “Bachelor of science (Bakk. rer. nat.)”
- 2009- present: Master Behaviour, Neurobiology and Cognition at the University of Vienna

RESEARCH EXPERIENCE

- Project investigating conflict behaviour in crows (*Corvus corone*)
  April 2010-present
  Conflict management in the Carrion and the Hooded Crows
  Department of Cognitive Biology, University of Vienna
  Supervisors: Prof. Thomas Bugnyar and Dr. Orlaith Fraser
- Project investigating the ontogeny of calls in the common raven (*Corvus corax*)
  July 2010-September 2010
  Department of Cognitive Biology, University of Vienna
  Supervisors: Prof. Thomas Bugnyar and Mag. Markus Böckle
- Master thesis: Food monopolization in the common raven (*Corvus corax*)
  September 2010-February 2011
  Department of Cognitive Biology, University of Vienna
  Supervisor: Prof Thomas Bugnyar
- Follow up experiment: Effect of group composition on accessibility of food in the common raven (*Corvus Corax*)
  March 2011-July 2011
  Department of Cognitive Biology, University of Vienna
  Supervisor: Prof Thomas Bugnyar
- Project design and preliminary data collection: Investigating future planning abilities in the common raven (*Corvus Corax*)
  July 2011-October 2011
  Department of Cognitive Biology, University of Vienna

Supervisor: Prof Thomas Bugnyar

- Internship: Investigating future planning abilities in the common raven (*Corvus Corax*)
  and planning experiment in great apes
  Play experiments in the common raven; Introduction to eye-tracking
  January 2012-March 2012
  Lund University Cognitive Science, Sweden
  Supervisor: Dr Mathias Osvath

AWARDS, HONORS AND GRANTS

January 2011: Grant for good marks (Leistungsstipendium) University of Vienna

December 2011: Funding: KWA (Kurzes wissenschaftliches Arbeiten im Ausland) University of Vienna

WORK EXPERIENCE AND ADDITIONAL QUALIFICATIONS

2007-2010:	3 summer periods guide at the Monkey Mountain Landskron (Japanese Macaques)
1991-present:	Member of the Austrian Water Rescue Team; since 2004 life-guard
2009:	Diving licence
2010:	helped building up aviaries at the new Research Station Haidlhof of the University of Vienna
English:	fluent, written and spoken, Toefl Test taken December 2011
Italian:	basic knowledge, written and spoken

Statistical programming language R: basic knowledge

Driving license

PUBLICATIONS AND TALKS

Böckle M., Sima M. & Bugnyar T.: Ontogeny in the calls of the common raven (*Corvus corax*). (in prep)

Blum C., Sima M., Weigerstorfer K. & Bugnyar T.: Inter- and intraspecific conflict behavior in crows (*Corvus corone*) (in prep)

Poster: Sima M. & Bugnyar T.: Whom to dine with? Food monopolization experiments with young, parent-raised ravens (*Corvus corax*)
Department of Cognitive Biology, University of Vienna and Haidlhof Research Station, University of Veterinary Medicine Vienna presented at the CompCog Conference: Current challenges and applications of comparative cognition Prague, 25-27 May 2011

Invited talk at the Lund University: Whom to dine with? Strategies of ravens in food monopolization experiments on the 8th of February 2012 in the Cognition Seminar

List of Figures and Tables

GLMMs

Table 4 Agonistic behavior in the before-feeding phase split up in kinship

BF Kin		Estimate	Std. Error	z value	Pr(>|z|)	
	(Intercept)	-1.995	0.72075	-2.77	5.64E-03	**
	Minutes together	0.001	0.00596	0.17	8.67E-01	
Condition 1 P	Condition 2P	0.17326	0.37869	0.46	0.64729	
	Condition control	0.34535	0.36239	0.95	0.3406	
Condition 2 P	Condition control	0.17209	0.27769	0.62	0.53544	
Risk factor low	Risk factor zero	1.8284	0.61571	2.97	0.00298	**
	Risk factor high	0.21315	0.43892	0.49	0.62723	
Risk factor high	Risk factor zero	1.6152	0.52648	3.07	0.00216	**
Dyad f_m	Dyad m_f	3.291	1.0473	3.14	0.00168	**
	Dyad m_m	3.7381	1.0489	3.56	0.00037	***
Dyad f_f	Dyad f_m	-2.29	1.081	-2.12	0.03414	*
	Dyad m_f	1.001	0.40671	2.46	0.01385	*
	Dyad m_m	1.4481	0.41549	3.49	0.00049	***
Dyad m_f	Dyad m_m	0.44713	0.28046	1.59	0.1109	
BF Non kin		**Estimate**	**Std. Error**	**z value**	**Pr(>|z|)**	
	(Intercept)	-2.3896	0.41723	-5.73	1.00E-08	***
	Minutes together	0.01137	0.00485	2.35	0.019	*
Condition 1 P	Condition 2P	0.47059	0.22657	2.08	0.038	*
	Condition control	0.50202	0.23378	2.15	0.032	*
Condition 2 P	Condition control	0.03144	0.19658	0.16	0.873	
Risk factor low	Risk factor zero	0.55368	0.47178	1.17	0.241	
	Risk factor high	0.16767	0.24299	0.69	0.49	
Risk factor high	Risk factor zero	0.38602	0.37863	1.02	0.308	
Dyad f_m	Dyad m_f	3.286	0.56024	5.87	4.50E-09	***
	Dyad m_m	3.3095	0.56226	5.89	4.00E-09	***
Dyad f_f	Dyad f_m	-3.1139	0.45706	-6.81	9.60E-12	***
	Dyad m_f	0.17212	0.39282	0.44	0.661	
	Dyad m_m	0.19561	0.39947	0.49	0.624	
Dyad m_f	Dyad m_m	0.02349	0.20336	0.12	0.908	

Table 5 Agonistic behavior in the after-feeding phase split up in kinship

AF Kin		Estimate	Std. Error	z value	Pr(>|z|)	
	(Intercept)	-3.3395	6.87E-01	-4.86	1.20E-06	***
	Minutes together	0.00562	3.18E-03	1.77	0.07713	.
Condition 1 P	Condition 2P	0.04588	0.31996	0.14	0.886	
	Condition control	0.51628	3.51E-01	1.47	0.1413	
Condition 2 P	Condition control	0.4704	0.36312	1.3	0.19517	
Dyad f_m	Dyad m_f	0.03652	0.46902	0.08	0.9379	
	Dyad m_m	0.87448	0.47963	1.82	0.0683	.
Dyad f_f	Dyad f_m	0.65065	0.45997	1.41	0.1572	
	Dyad m_f	0.68717	0.45444	1.51	0.1305	

	Dyad m_m	1.5251	0.45844	3.33	0.00088	***
Dyad m_f	Dyad m_m	0.83795	0.37491	2.24	0.025	*
AF Non kin		**Estimate**	**Std. Error**	**z value**	**Pr(>|z|)**	
	(Intercept)	-2.1165	0.3422	-6.18	6.20E-10	***
	Minutes together	0.0141	0.0029	4.85	1.20E-06	***
Condition 1 P	Condition 2P	-0.3944	0.2002	-1.97	0.0488	*
	Condition control	0.2931	0.1984	1.48	0.1396	
Condition 2 P	Condition control	0.6875	0.2528	2.72	0.0065	**
Dyad f_m	Dyad m_f	2.4817	0.4176	5.94	2.80E-09	***
	Dyad m_m	2.348	0.4211	5.58	2.50E-08	***
Dyad f_f	Dyad f_m	-2.1411	0.304	-7.04	1.90E-12	***
	Dyad m_f	0.3406	0.3611	0.94	0.3456	
	Dyad m_m	0.207	0.368	0.56	0.5738	
Dyad m_f	Dyad m_m	-0.1336	0.1844	-0.72	0.4687	

Table 6 Agonistic behavior in the 3 phases in the female-female dyads

F_F		Estimate	Std. Error	z value	Pr(>|z|)	
BF	(Intercept)	-6.6812	2.8046	-2.38	0.017	*
	Minutes together	0.01435	0.00717	2	0.045	*
Condition 1 P	Condition 2 P	0.24534	0.41649	0.59	0.556	
	Condition control	0.50712	0.43234	1.17	0.241	
Condition 2 P	Condition control	0.26178	0.38326	0.68	0.495	
Kin	Non kin	0.74952	0.47275	1.59	0.113	
F	(Intercept)	-5.5839	1.67E+00	-3.35	8.10E-04	***
	Minutes together	0.0161	2.60E-03	6.19	6.10E-10	***
Condition 1 P	Condition 2 P	-0.3245	0.2563	-1.27	0.2055	
	Condition control	-0.6129	0.2617	-2.34	0.01918	*
Condition 2 P	Condition control	-0.2885	0.2741	-1.05	0.2926	
Kin	Non kin	0.8067	0.281	2.87	0.0041	**

Table 7 Agonistic behavior in the 3 phases in the male-female dyads

M_F		Estimate	Std. Error	z value	Pr(>|z|)	
BF	(Intercept)	-2.9946	2.13E+00	-1.41	0.159	
	Minutes together	0.00906	5.56E-03	1.63	0.103	
Condition 1 P	Condition 2 P	0.68004	0.30619	2.22	2.60E-02	*
	Condition control	0.78998	0.30906	2.56	1.10E-02	*
Condition 2 P	Condition control	0.10994	0.25392	0.43	0.665	
Kin	Non kin	0.11313	0.31672	0.36	0.721	
F	(Intercept)	-4.5725	0.99064	-4.62	3.90E-06	***
	Minutes together	0.01722	0.00207	8.32	< 2e-16	***
Condition 1 P	Condition 2 P	0.06178	0.12536	0.49	0.6221	
	Condition control	-0.8554	0.14315	-5.98	2.30E-09	***
Condition 2 P	Condition control	-0.91718	0.14748	-6.22	5.00E-10	***

Kin	Non kin	0.66573	0.16516	4.03	5.60E-05	***
AF	(Intercept)	-5.7559	1.785	-3.22	0.00126	**
	Minutes together	0.01155	0.00315	3.67	0.00024	***
Condition 1 P	Condition 2 P	-0.3947	0.25917	-1.52	0.12777	
	Condition control	0.04479	0.24861	0.18	0.85701	
Condition 2 P	Condition control	0.4395	0.31102	1.41	0.15763	
Kin	non kin	0.73652	0.2975	2.48	0.0133	*

Table 8 Agonistic behavior in the 3 phases in the female-male dyads

F_M		**Estimate**	**Std. Error**	**z value**	**Pr(>|z|)**	
	(Intercept)	-7.05	6.5662	-1.07	0.28	
BF	Minutes together	1.98E-02	0.0247	0.8	0.42	
Condition 1 P	Condition 2 P	1.152	1.4617	0.79	0.43	
	Condition control	1.6427	1.219	1.35	0.18	
Condition 2 P	Condition control	0.4909	0.9368	0.52	0.6	
Kin	Non kin	0.0216	1.086	0.02	0.98	
	(Intercept)	0.04649	2.2871	0.02	0.98378	
F	Minutes together	0.00901	0.00371	2.43	0.01516	*
Condition 1 P	Condition 2 P	-0.76884	0.34175	-2.25	0.02447	*
	Condition control	-1.2196	0.31988	-3.81	0.00014	***
Condition 2 P	Condition control	-0.45072	0.34666	-1.3	0.19354	
Kin	Non kin	-0.07878	0.38777	-0.2	0.839	
	(Intercept)	7.3422	2.8716	2.56	0.0106	*
AF	Minutes together	0.00137	0.00458	0.3	0.7646	
Condition 1 P	Condition 2 P	-0.5653	0.6023	-0.94	0.348	
	Condition control	0.46726	0.5439	0.86	0.3903	
Condition 2 P	Condition control	1.0326	0.58693	1.76	0.0785	.
Kin	Non kin	-2.007	0.4905	-4.09	4.30E-05	***

Table 9 Agonistic behavior in the 3 phases in the male-male dyads

M_M		**Estimate**	**Std. Error**	**z value**	**Pr(>|z|)**	
	(Intercept)	0.9352	1.9177	0.49	0.6258	
BF	Minutes together	-0.0229	0.0133	-1.72	0.0859	.
Condition 1 P	Condition 2 P	-0.3306	0.4123	-0.8	0.4226	
	Condition control	-0.1553	0.3762	-0.41	0.6798	
Condition 2 P	Condition control	0.1754	0.3075	0.57	0.5685	
Kin	Non kin	-0.2573	0.2952	-0.87	0.3833	
	(Intercept)	-1.6624	1.1983	-1.39	0.16535	
F	Minutes together	0.0186	0.0049	3.8	0.00015	***
Condition 1 P	Condition 2 P	0.042	0.2053	0.2	0.83768	
	Condition control	-0.8453	0.2037	-4.15	3.30E-05	***

Condition 2 P	Condition control	-0.8874	0.243	-3.65	0.00026	***
Kin	Non kin	0.1265	0.1839	0.69	0.49155	
	(Intercept)	2.3562	1.6937	1.39	0.1642	
AF	Minutes together	-0.0196	0.0197	-0.99	0.32	
Condition 1 P	Condition 2 P	0.264	0.4791	0.55	0.5816	
	Condition control	-1.0134	0.7715	-1.31	0.189	
Condition 2 P	Condition control	-1.2774	1.1499	-1.11	0.2666	
Kin	non kin	-0.683	0.2635	-2.59	0.0095	**

Table 10 Socio-positive behavior in the before-feeding and the feeding phase

		Estimate	**Std. Error**	**z value**	**Pr(>|z|)**	
BF	(Intercept)	-1.7127	0.49376	-3.47	0.00052	***
	Minutes together	0.02556	0.00532	4.8	1.60E-06	***
Condition 1 P	Condition 2P	0.03224	0.22651	0.14	0.88682	
	Condition control	-0.10188	0.23361	-0.44	0.66276	
Condition 2 P	Condition control	-0.13411	0.22705	-0.59	0.5547	
Risk factor high	Risk factor low	-0.6941	0.26212	-2.65	0.0081	**
	Risk factor zero	-1.6528	0.41823	-3.95	7.80E-05	***
Risk factor low	Risk factor zero	-0.95872	0.5217	-1.84	0.0661	.
Kin	Non kin	-2.8705	0.22557	-12.73	< 2e-16	***
Dyad f_f	Dyad f_m	1.3439	0.32961	4.08	4.60E-05	***
	Dyad m_f	1.809	0.53368	3.39	0.0007	***
	Dyad m_m	1.5913	0.52883	3.01	0.00262	**
Dyad f_m	Dyad m_f	0.46513	0.48153	0.97	0.3341	
	Dyad m_m	0.24745	0.48172	0.51	0.6075	
Dyad m_f	Dyad m_m	-0.21768	0.26305	-0.83	0.4079	
F	(Intercept)	-3.3693	0.64057	-5.26	1.40E-07	***
	Minutes together	0.00299	0.00204	1.46	0.14296	
Condition 1 P	Condition 2P	0.03799	0.28918	0.13	0.89547	
	Condition control	-0.16614	0.30418	-0.55	0.58494	
Condition 2 P	Condition control	-0.20413	0.30151	-0.68	0.49839	
Kin	Non kin	-2.689	0.32914	-8.17	3.10E-16	***
Dyad f_f	Dyad f_m	0.5648	0.43639	1.29	0.19558	
	Dyad m_f	0.99023	0.53491	1.85	0.06414	.
	Dyad m_m	0.34722	0.54581	0.64	0.52468	

Dyad f_m	Dyad m_f	0.42542	0.50701	0.84	0.40143	
	Dyad m_m	-0.21758	0.52701	-0.41	0.67971	
Dyad m_f	Dyad m_m	-0.64301	0.38152	-1.69	0.09191	.

Table 11 Socio-positve behavior in the after-feeding phase split up in the kinship

		Estimate	Std. Error	z value	Pr(>|z|)	
AF Kin	(Intercept)	-1.6278	0.54662	-2.98	0.0029	**
	Minutes together	0.01384	0.00388	3.57	0.00036	***
Condition 1 P	Condition 2P	0.06158	0.34509	0.18	0.85836	
	Condition control	-0.58534	0.37714	-1.55	0.12065	
Condition 2 P	Condition control	-0.64692	0.37564	-1.72	0.08504	.
Dyad f_f	Dyad f_m	0.13481	0.56363	0.24	0.81096	
	Dyad m_f	0.56272	0.49368	1.14	0.25435	
	Dyad m_m	-0.14626	0.49245	-0.3	0.76646	
Dyad f_m	Dyad m_f	0.42791	0.50162	0.85	0.39363	
	Dyad m_m	-0.28107	0.49474	-0.57	0.56996	
Dyad m_f	Dyad m_m	-0.70898	0.40818	-1.74	0.0824	.
AF Non kin	(Intercept)	-2.7923	0.87535	-3.19	0.00142	**
	Minutes together	0.00797	0.00736	1.08	0.2787	
Condition 1 P	Condition control	-0.93275	0.5672	-1.64	0.1	
	Conditionz1P	-0.24908	0.40575	-0.61	0.539	
Condition 2 P	Condition 2P	0.24908	0.40575	0.61	0.5393	
Dyad f_f	Dyad f_m	0.89609	0.57621	1.56	0.11991	
	Dyad m_f	0.78006	0.6738	1.16	0.24699	
	Dyad m_m	2.242	0.67346	3.33	0.00087	***
Dyad f_m	Dyad m_f	-0.11602	0.54587	-0.21	0.832	
	Dyad m_m	1.3459	0.55363	2.43	0.015	*
Dyad m_f	Dyad m_m	1.4619	0.47968	3.05	0.0023	**

Table 12 Socio-positive behavior in the after-feeding phase split up in the different dyads

After feeding		Estimate	Std. Error	z value	Pr(>|z|)	
F_F	(Intercept)	-3.647	1826.4	0	0.998	
	Minutes together	0.014	0.007	2	0.046	*
Condition 1 P	Condition 2P	0.458	0.369	1.24	0.214	

	Condition control	1.308	0.739	1.77	0.077	.
Condition 2 P	Condition control	0.85	0.678	1.25	0.21	
Kin	Non kin	-2.957	0.546	-5.41	6.20E-08	***
M_F	(Intercept)	8.2536	2.9563	2.79	0.0052	**
	Minutes together	0.01256	0.00554	2.26	0.0235	*
Condition 1 P	Condition 2P	0.39914	0.49634	0.8	0.4213	
	Condition control	-0.62021	0.60933	-1.02	0.3087	
Condition 2 P	Condition control	-1.0193	0.59909	-1.7	0.0889	.
Kin	Non kin	-1.9994	0.50778	-3.94	8.20E-05	***
F_M	(Intercept)	14.949	5.263	2.84	0.00451	**
	Minutes together	0.00678	0.01176	0.58	0.56408	
Condition 1 P	Condition 2P	0.29986	0.51926	0.58	0.56362	
	Condition control	-0.75254	0.68135	-1.1	0.26938	
Condition 2 P	Condition control	-1.0524	0.77418	-1.36	0.17403	
Kin	Non kin	-3.0725	0.90895	-3.38	0.00072	***
M_M	(Intercept)	4.5152	2.9096	1.55	0.121	
	Minutes together	-0.0284	0.0244	-1.16	0.244	
Condition 1 P	Condition 2P	0.5238	0.6477	0.81	0.419	
	Condition control	-1.7496	0.9518	-1.84	0.066	.
Condition 2 P	Condition control	-2.2734	1.3131	-1.73	0.083	.
Kin	Non kin	-0.8936	0.4876	-1.83	0.067	.

Table 13 Preening behavior during the 3 different phases

		Estimate	**Std. Error**	**z value**	**Pr(>|z|)**	
BF	(Intercept)	-5.9732	1.5963	-3.74	0.00018	***
	Minutes together	0.02256	0.00652	3.46	0.00054	***
Condition 1P	Condition 2P	0.51232	0.45986	1.11	0.26525	
	Condition control	-1.2831	0.55755	-2.3	0.02137	*
Condition 2 P	Condition control	-1.7954	0.55003	-3.26	0.0011	**
Kin	Non kin	-3.4703	0.55256	-6.28	3.40E-10	***

Dyad f_f	Dyad f_m	0.78523	0.90792	0.86	0.38711	
	Dyad m_f	3.0235	1.0825	2.79	0.00522	**
	Dyad m_m	2.8832	1.0621	2.71	0.00664	**
Dyad f_m	Dyad m_f	2.2383	0.93935	2.38	0.01718	*
	Dyad m_m	2.0979	0.91476	2.29	0.02183	*
Dyad m_f	Dyad m_m	-0.14039	0.62957	-0.22	0.82354	
F	(Intercept)	-23.123	125.48	-0.18	0.8538	
	Minutes together	0.0362	0.1639	0.22	0.82518	
Condition 1P	Condition 2P	0.8719	5.1753	0.17	0.86621	
	Condition control	-9.7189	59.247	-0.16	0.8697	
Condition 2 P	Condition control	-10.591	59.368	-0.18	0.85841	
Kin	Non kin	-3.9756	1.0377	-3.83	0.00013	***
Dyad f_f	Dyad f_m	11.818	113.69	0.1	0.91721	
	Dyad m_f	9.1684	113.69	0.08	0.93573	
	Dyad m_m	11.637	113.69	0.1	0.91847	
Dyad f_m	Dyad m_f	-2.6495	1.1988	-2.21	0.0271	*
	Dyad m_m	-0.1808	0.9462	-0.19	0.84845	
Dyad m_f	Dyad m_m	2.4687	0.8042	3.07	0.00214	**
AF	(Intercept)	-6.1508	1.6202	-3.8	0.00015	***
	Minutes together	0.0214	0.0068	3.14	0.00167	**
Condition 1P	Condition 2P	1.4401	0.5436	2.65	0.00807	**
	Condition control	1.0599	0.5321	1.99	0.04638	*
Condition 2 P	Condition control	-0.3802	0.4531	-0.84	0.4013	
Kin	Non kin	-3.2358	0.52	-6.22	4.90E-10	***
Dyad f_f	Dyad f_m	-0.2892	0.7297	-0.4	0.69187	
	Dyad m_f	1.1172	0.8785	1.27	0.2035	
	Dyad m_m	1.8085	0.8846	2.04	0.04092	*
Dyad f_m	Dyad m_f	1.1172	0.8785	1.27	0.2035	
	Dyad m_m	1.8085	0.8846	2.04	0.0409	*
Dyad m_f	Dyad m_m	0.6914	0.5535	1.25	0.2116	