The quality of breeding-pair relationships in ravens and crows

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Content

1. Abstract

Long-term monogamous bird species form pairs and stay together for several breeding seasons, ideally for their lifetime. In these pairs, a high level of cooperation and coordination among the partners is important for fitness relating factors like defending a territory and raising chicks. Yet, individual differences in the pair partners' behavior can be large and may contribute to differences in pair bond quality. In this study, I examined the pair bond quality in two closely related corvid species, common ravens (*Corvus corax*) and carrion/hooded crows (*Corvus corone/cornix*), which were part of the captive colony of the Department of Cognitive Biology, University Vienna and kept under identical conditions at two research sites. Over one breeding season, I observed affiliative-, agonistic-, and self-directed behaviours, the tolerance at a food source and behaviours referring to parental care at the nest. In addition, I created an experimental situation of scramble competition for food. Because of the similar social systems of ravens and crows, I did not expect to find any differences between the species, but a significant variation between the pairs within a species. While I found unexpected variation in behaviours between the species, the prediction about inter-pair variation could be confirmed. As expected, partners differed in the (high) rate of affiliative behaviour and (low) rate of agonistic behaviour; interestingly, these categories were not directly correlated across individuals and pairs. I found a connection between breeding success and tolerance at a food source, indicating that differences in pair bond quality might have a fitness function. In conclusion, the studied pairs generally followed the definition of pair bond quality but with individual and species specific differences. To analyze these differences and the influencing factors in detail, further studies are necessary.

2. Zusammenfassung

Langzeitmonogame Vogelarten formen Brutpaare und bleiben über mehrere Brutsaisonen oder sogar ein Leben lang zusammen. In diesen Paaren sind fitnesssteigernde Faktoren wie Kooperation, Koordination und Interaktion bedeutend, damit das Territorium verteidigt werden kann und die Jungen erfolgreich aufgezogen werden können. Die individuellen Verhaltensunterschiede können stark sein und zu Unterschieden in der Paarbindungsqualität führen. In dieser Arbeit wurde die Paarbindungsqualität bei zwei nahe verwandten Corvidenarten, Kolkraben (*Corvus corax*) und Raben- und Nebelkrähen (*Corvus corone/cornix*) untersucht, die Teil einer in Gefangenschaft lebenden Kolonie der Abteilung für kognitive Biologie an der Universität Wien waren und unter identischen Bedingungen in zwei Forschungsstationen gehalten wurden. Analysiert wurden dabei agonistische- und affiliative Verhaltensweisen, Komfortverhalten, Toleranz und Brutpflege am Nest über eine Brutsaison. Zusätzlich wurde für die Experimente eine futterbezogene Konkurrenzsituation geschaffen. Aufgrund der sehr ähnlichen sozialen Systeme von Raben und Krähen, habe ich keine Unterschiede zwischen den beiden Arten erwartet, jedoch eine starke Variation innerhalb einer Art. Während letzteres bestätigt werden konnte, habe ich unerwartete Unterschiede zwischen den Arten gefunden. Wie erwartet, unterschieden sich die Paare anhand der (hohen) Raten an affiliativem Verhalten und der (niedrigen) Raten an agonistischem Verhalten. Interessanterweise gab es aber keine direkte Korrelation der Kategorien. Anhand der Experimente konnte eine Verbindung zwischen Toleranz und Bruterfolg festgestellt werden, was vermuten lässt, dass Unterschiede in der Paarbindungsqualität möglicherweise eine Fitnessfunktion haben. Zusammenfassend kann man sagen, dass die untersuchten Paare der Definition der Paarbindungsqualität folgen. Um jedoch genaues über den Einfluss der einzelnen Faktoren und deren Zusammenhang sagen zu können, sind weitere Studien notwendig.

3. Introduction

3.1. Social relationships

Hinde (1976) defined relationships as a succession of interactions in a social context. It can be described via three interacting stages, interactions, relationships and social structure. An interaction implies a minimum of two individuals and one type of behaviour which can be referred to an incident. To value an interaction it is necessary to know either, what the individuals do (content) or how they do it (quality). Specific interactions can differ according to relationships, for example dependent on dominance status. Otherwise, repeated interactions can lead to a relationship. Therefore the individuals have to know each other. The behaviour within a relationship is influenced by individual history and expectations arose from former experiences with the other individual. A relationship is unlikely to be stable, as it implies a changing pattern of interactions over time caused for example by learning. In a relationship, interaction differs dependent on the context, as the same type of behaviour can be actively given, passively received or mutually performed, like grooming. Social structure is based on a more abstract level that refers to a patterning of relationships, excluding the individuals concern. The social structure of a group is not stable either. Individuals enter or leave a group or dominance hierarchies change over time.

The social intelligence hypothesis predicts that life in an individualized group, which is structured by different types of social relationships, is a driving force for brain evolution (Whiten & Byrne 1987). This hypothesis is sustained by studies on primates. Dunbar (1992) tested the social brain hypothesis and found a correlation between neocortex size and group size. He suggests that the increasing neocortex size is a limiting factor for group size, as the number of relationships one individual can monitor is correlated to the number of neocortical neurons. Living in groups may have been a diving force for increasing cognitive abilities and thus increasing brain size in relation to body size in the evolution of primates (Byrne 2000). In most mammals and bird species, neither group size nor –structure seems to be the decisive factor of increasing brain size, but the mating system, as species, which form long-time bonds, have larger brains. This indicates that living in a long time pair bond requires cognitive abilities (Emery et. al. 2007; Dunbar & Shultz 2007).

3.2. Why forming a pair bond? → Monogamy

Monogamy is defined by Kleiman as a long time exclusive relationship between one male and one female (Kleiman 1977). There are different kinds of monogamy. Serial monogamy means for a pair to stay together for one breeding season only. The next season, they search for other partners. In contrast, in long-time monogamy, the partners stay together for several breeding seasons, ideally for the entire lifetime. In either form of monogamy, one or even both partners may take part in extra pair copulations (Kappeler 2009), indicating that pair partners do not necessarily have exclusive sexual access.

Monogamy is the most common mating system among birds, as 9/10 of all known passerine bird species are monogamous. The reason why monogamy occurs can be explained in different ways, as different species and the different sexes have various motives (Lack 1968; Kappeler 2009). Males and Females diverge in their genetic interests, what results in sexual conflicts. To evolve an assertive monogamous mating system, these conflicts have to be reduced and a pair bond has to be advantageous for both mates (Rice 2000). Whereas, a desertion should be disadvantageous (Wittenberger & Tilson 1980). One immediate benefit for both partners would be that they may gain in rank and/or increase their dominance status (Emery et. al. 2007). Another benefit of having only one mate could be, that more offspring can be produced and raised, if both, male and female, care for the brood (Lack 1968). Röell (1978) showed in an experiment with jackdaws, that the loss of either parent leads to total nest failure. Provisioning of nestlings is also positively correlated with nestling growth rate. The trade-off between provisioning few chicks well vs provisioning many chicks poorly may prevent male birds from succeeding in bigamous or polygynous relationships (Henderson & Hart 1993). Monogamy should rather evolve in territorial species, to compensate the costs of polygyny (Wittenberger & Tilson, 1980). The basis of monogamy is the pair bond. When male prairie voles have a choice of different mating systems, they choose bonding with only one female. (Blocker & Ophir, 2016).

Considering the physiological background for bonding, a connection between pair bonding and oxytocin receptors in neural structures was found in different mammal- and bird species. In human, oxytocin may play an important role in parent-infant bonding (Gordon et. al. 2010). A relation between oxytocin level and relationships was also found in chimpanzees. After grooming with bond partners, non-kin or kin, the urinary oxytocin level gets higher than after grooming with non-bond partners (Crockford et. al. 2013). Also foodsharing affects the urinary oxytocin level in chimpanzees, but independent of the social bond or kinship (Wittig et. al. 2014). Monogamous Prairie Voles have a high density of oxytocin receptors in the nucleus accumbens, also known

as the reward center of the brain (Ophir et. al. 2012). RNA interference showed an influence of Vasopressin 1a receptor expression in the ventral pallidum on pair bond formation in males (Barrett et. al. 2013). Partner loss in prairie voles effects males in an emotional and physiological way. It leads to anxiety-like and depressive-like behaviours and influences the cell density of oxytocin-immunoreactivity, vasopressin-immunoreactivity and corticotrophin-releasing hormone-immunoreactivity cells in the paraventricular nucleus (Sun et. al. 2014). As in mammals, the loss of oxytocin production in the magnocellular and parvocellular neurons of the hypothalamus, leads to behavioral changes in gregariousness and pair bonding in zebra finches (*Taenioypygia guttata*) (Pedersen & Tomaszycki, 2012; Klatt & Goodson 2013; Kelly & Goodson 2014). Studies show, that a vasopressin knockdown decreases the social contact within a large group and has sex-specific effects on aggression towards the opposite sex. After oxytocin knockdown, it comes to a reduction of pair bonding and social contacts in females as well as the contact sit events in both sexes (Kelly & Goodson 2014). Also injections of an oxytocin-antagonist lead to a decrease of the likelihood to form stable pairs (Pedersen & Tomaszycki, 2012; Klatt & Goodson 2013)

Pair bonding over a long time can have consequences for the breeding success in birds. So, for example in blue-footed-boobies, the timing of breeding is affected by pair bonding duration. The longer a relationship lasts, the earlier they begin to lay eggs and the more offspring survives (Sánchez-Macouzet 2014).

3.3. Pair bond quality

To form and maintain a pair bond, a good cooperation between the partners is necessary, which in turn may lead to a strong affiliative relationship. Good relationship quality or a valuable relationship was defined by Van Schaik & Aureli (2000) as partners showing high rates of friendly behaviour and comparably low rates of agonistic conflicts, providing agonistic support against a third party and spending more time in proximity.

It is species specific, how the mates show, with whom they have a valuable relationship. For example graylag geese form breeding pairs which stay associated throughout the year, even in foraging flocks. Even though, there is no evidence for affiliative behaviours like allopreening or food sharing, they show affiliation by supporting their partners and offspring in social conflicts (Schreiber et. al. 2005). On the contrary, rook pairs show lots of physical contact like food sharing or allopreening and support each other in case of disputes with a third party. In rooks, affiliative behaviour rises along the different stages of pair formation. Food sharing, as one of the most important factors of a pair bond, already occurs in the early stages, maybe because of

the similarity to parental feeding (Emery et.al. 2007). In common guillemot (*Uria aalge*), the rate of allopreening influences the long-term fitness. It also reduces stress and fights within the pair. All in all there is a high behavioral variability between the pair's interactions (Lewis et. al. 2007).

Cords and Aureli (2000) pointed out three components of relationship quality associated with reconciliation. Value was defined as direct benefits one can gain out of a relationship. As in a dyad, both partners cannot have the same value, this tends to be asymmetrical. Security means that a relationship is stable and unlikely to change, so the partner's behaviour is predictable. Compatibility is defined as the general tenor of social interactions in a relationship. Fraser and Bugnyar (2010a) tested these components in a group of young ravens. In this non-breeder group, value was shown mainly between siblings. The other two components, compatibility and security, were more likely to occur in male-male- or mixed-sex dyads than in female-female dyads.

3.4. The social life of corvids

Corvids include 120 species, including common ravens (*Corvus corax*) and carrion – and hooded crows (*Corvus corone/cornix*). As large-brained birds, they are renowned for their social cognition abilities and their high adaptability in their behaviour (Güntürkün & Bugnyar 2016). Several species of corvids are long time monogamous and many of them defend territories for breeding (Heinrich 1999). Corvids are long living birds and have a long period of development (Clayton & Emery 2007). The social behaviour of ravens, and also crows, shows age-specific differences, as young individuals spend their first years in nonbreeding flocks (Goodwin 1976) with high degrees of fission-fusion dynamics (Braun & Bugnyar 2012). In ravens, it takes a longer time, or rather 3 to 4 years, to achieve sexual maturity, than it takes in crows, which sexually mature in 2 to 3 years (Miller et. al. 2016).

Affiliative relationships form early on, typically already in non-breeder state (ravens: Loretto et. al. 2012; jackdaws: von Bayern et. al. 2007; rooks: Scheid et. al. 2008). Even after a long time of separation, ravens are able to recognize former group members and to remember relationship qualities (Boeckle & Bugnyar, 2012). They can also deduce the relationship between other group members (third party understanding; Massen et. al. 2014a) and apply this knowledge in third party interventions (Massen et. al. 2014b). Fraser and Bugnyar (2011) also found reconciliation in a captive raven group. After an aggressive conflict, they reconcile with proximity and affiliative behaviour. This pattern has been proposed to repair the relationship and strengthens it. Another post-conflict behaviour found in raven groups is consolation. That means that an individual, a so

called bystander, directs affiliative behaviour to a victim of a former conflict to console it. Often, this bystander affiliation is solicited, as the victim affiliates with the bystander. These bystander-victim relationships are very likely to be highly valuable (Fraser & Bugnyar, 2010b).

The non-breeder phase of corvids end, when they get breeders. Some species, like ravens, therefore defend a territory, which is occupied for lifetime. In carrion crows, breeding behaviour differs dependent on the habitat. In some habitats they breed cooperatively, while the young help their parents to raise the offspring. But in years, when adult mortality is high, they occupy their own territory (Baglione & Canestrari 2016; Clayton & Emery 2007). One theory, why crows sometimes form family groups says that there must be benefits of a delayed dispersal in addition the indirect fitness gained by helping raising siblings, like better excess to resources (Chiaraty et. al. 2011). The life histories of carrion- and hooded crows are very similar. They form mixed flocks and there are some hybrid zones, where they form mixed breeding pairs. Although hybrid females are known to sometimes have disadvantageous in their reproductive performance, all in all, hybrids do not have lower reproductive success (Saino & Villa 1992).

3.4.1. The meaning of vocal communication

In songbirds, vocal communication is an important part of corvid's social life (Fraser & Bugnyar 2010a). In breeding pairs, both mates defend the territory or nest, mostly against conspecifics, by vocal behaviour (Bossema & Benus 1985). In ravens, paired males and females adapt their long distance calls and thus produce pair specific vocal displays (Enggist-Dueblin & Pfister 2002). Displays in ravens can have different meanings, dependent on the situation. The self-aggrandizing display or self-assertive display (SAD) is shown by males and females. It comes with different vocalizations, fluffed feathers, bowing and crouching. This behaviour can lead to a fight, but is also an important part of pair bonding and courtship. In the breeding season, females often perform "begging" behaviour by lifting the wings frequently while making grunt-noises like juveniles do before getting fed. This occurs because females get fed by males during the breeding phases. Begging often comes with crouching and bowing to show submission or "respect" (Lorenz 1939; Gwinner 1964; Heinrich 1989)

3.4.2. Food directed behaviour

Corvids are omnivorous. Despite of their broad diet, ravens and carrion/hooded crows have a preference for meat, which they typically need to compete for with conspecifics and/or heterospecifics such as predators or other scavengers. (Heinrich 1989).

According to social relationships, an important part of food directed behaviour concerns cofeeding and food sharing or –offering. Cofeeding is feeding from a food source, without monopolizing it. Food sharing means to directly feed another individual. It is common in monogamous birds to feed the partner (Scheid et. al. 2008). In corvids, food sharing occurs more frequently than in many primates (Duque & Stevens 2016). Food sharing is a factor that helps to form a pair bond and to stabilize it (Ligon & Ligon 1978). In rooks, a positive correlation of cofeeding and contact sitting could be found, what strengthens the assumption of a connection to pair bonding (Scheid et. al. 2008). Food directed affiliative behaviours often occur reciprocally. This means that an altruistic behaviour gets rewarded later. Fraser and Bugnyar (2012) found that ravens support those individuals more often, they got preened from in the past. They thus show long-term reciprocity with individuals they have a good relationship with. Ravens also cooperate in experimental tasks like for example a loose string apparatus. Massen et.al. (2015) showed that in an experiment, where ravens were paired to dyads and had to pull a string together (each on one side) to get food. Every dyad was tested twice, to see if they would cooperate again. The ravens did not cooperate with everyone, but with those they had a good relationship with. Although it was a matter of tolerance, with whom they wanted to work and thus share food, the ravens were paying attention to the outcome. If one individual cheated once by first cooperatively pulling the string and then monopolizing the whole food, the partner was not willing to cooperate again in the second trial (Massen et. al. 2015). In another loose-string test, where ravens had an open choice with whom they want to cooperate (experiments in a triad and with the whole group of 11 individuals) Asakawa-Haas et. al. (2016) showed that these corvids are more likely to cooperate with friends than with non-friends. This is probably a matter of tolerance, as they prefer to have their friends in proximity and this is not necessarily dependent on relationship quality.

3.5. Hypotheses and Predictions

The aim of this study was to examine relationship qualities of breeding pairs of common ravens and carrion/hooded crows. I followed the hypothesis that relationship quality is a key factor in long-term monogamous species and predicted to find high rates of affiliative behaviour and close proximity, but low rates of aggression within breeding pairs. Because of similar social systems, I did not expect to find a significant difference in the behavioral patterns indicative of social relations between the species. However given the fitness effects of pair bonds, I did expect variation between the pairs within a species. I tested possible effects explaining this variation. Focusing on the duration of pair bonding, I reasoned that when two individuals are in a relationship for a long time, they should be skilled in several forms of cooperation, as they already have experiences with the other one and in raising their young together. Finally, I tested if high pair bond quality results in high breeding success.

4. Methods

4.1. Study sites

The Study started in March 2016 in two different studying sites. One in Haidlhof, Bad Vöslau in lower Austria and one at the Konrad Lorenz Forschungsstelle (KLF) in the Cumberland Wildpark in Grünau, upper Austria. Both sites are in a quiet surrounding with adjacent fields and woods.

Haidlhof is a science research station, belonging to the University of Vienna and the Veterinary Medicine University of Vienna since 2010. In the area, where the research took place, there are mainly kept ravens, crows and keas, but also chickens, kune-kune pigs and cows. At least once a month, there are groups of visitors walking through the research station.

The Konrad Lorenz Forschungstelle, which is part of the University of Vienna, is a field station near Grünau im Almtal in cooperation with Cumberland Wildpark. In Grünau, there are kept many different Eurasian wild animals and visitors can walk through the park every day.

4.2. Studying Subjects

The studying subjects are breeding pairs of common ravens (*Corvus corax*), 3 pairs in Grünau and 4 pairs in Bad Vöslau, and carrion and hooded crows and their hybrids (*Corvus corone/cornix*), 3 pairs in Grünau and 2 pairs in Bad Vöslau. All animals involved are held in captivity. The studying subjects are all marked with colored leg-rings for individual identification.

The Aviaries in Grünau are 80m^2 for the ravens and 15m^2 for the crows. In Haidlhof, they are 80m^2 for the ravens and 16m^2 for the crows. All aviaries are equipped with stones or pebble stones for caching and playing, as well as branches. Every pair has a pot filled with water and one or more feeding stones or a table. All ravens and crows have roofed compartments, where they can hide from the rain, snow or sun. There is also a nest box in every aviary. At the ravens, it is in the height of 5m, at the crows in the height of 3m. The animals get fed three times a day, in the morning, at noon and in later the afternoon, with all kinds of food, considering the balanced diet. Once a month all corvids get tested on parasites. When they are infected, they get a special diet and medication for the next weeks.

Table 1 shows all individuals and information about sex, age, pair duration, means how long they were together at this time, former experience, defined as if they had at least 1 successfully breeding season, and forced housing, here seen as whether they chose each other freely as partners or were put together. To former experience it is to say, that Astrid and Heidi had other

partners before and also had breeding success. Tom and Horst had offspring for the first time. Rumo & Gerti and Paul & Luise laid eggs but they didn't hatch. Bärchen & Petra, Walter & Bärbel and Juno & Caruso tried to build a nest or at least carried some branches around more frequently.

Table1: green=Grünau, violet=Haidlhof, n=no, y=yes, a=attempt, ne= nesting

Ravens						
Name	Sex	Age	Pair duration	Former Experience	Forced Housing	Breeding success
Matte	m	5	3	y	n	y
Lellan	f	5	3	y	n	y
Orm	m	5	3	y	n	y
Sophie	f	6	3	y	n	y
Rumo	m	8	4	n	n	a
Gerti	f	7	4	n	n	a
Horst	m	4	1	n	n	y
Astrid	f	6	1	y	n	y
Paul	m	4	1	n	n	a
Luise	f	4	1	n	n	a
Rocky	m	4	1	n	n	y
Joey	f	6	1	n	n	y
Tom	m	4	1	n	n	y
Heidi	f	6	1	y	n	y
Crows						
Name	Sex	Age	Pair duration	Former Experience	Forced Housing	Breeding Success
Bärchen	m	8	5	0	n	ne
Petra	f	9	5	0	n	ne
Walter	m	5	3	0	y	ne
Bärbel	f	3	3	0	y	ne
Willi	m	4	1	0	y	n
Momo	f	2	1	0	y	n
Corbi	m	4	2	0	n	n
Reiner	f	4	2	0	n	n
Caruso	m	3	1	0	y	ne
Juno	f	4	1	0	y	ne

4.3. Observations and Experiments

The research took place in both studying sites over one breeding season (from the beginning of March 2016 till the end of August 2016), defined here as 4 phases of reproduction. Phase 1, the breeding phase, (March/beginning of April) was defined as the time, when the female was incubating. The nestling phase, or phase 2, (April, except Paul & Luise: Mai), when the young were still in the nest. Phase 3, the fledgling phase (Mai/June), when the offspring was out of the nest, but still with the parents. And at least phase 4, the after-young-phase (July/August), started when the offspring left and the parents were alone again.

When the chicks hatched, all animal keepers and students took care of having as little contact as possible. Before the chicks came out of the nest, they were all marked with colored leg rings. After the fledgling phase, the young ravens from Haidlhof and KLF were put together, first in an extra aviary at Haidlhof and later they were brought to Grünau im Almtal and were released.

I collected the data in Bad Vöslau and got the data from Grünau from Friederike Böhm (University of Greifswald, Germany). During the breeding phase, 32 observations per pair were videotaped, each for 20 minutes. For the other phases, every session was split in 20 minutes of observation and 20 minutes of feeding experiment and was videotaped for later analyses. Per Phase per pair we did 16 observations and 16 experiments. Experiments did not start until the second phase to not interrupt the female while incubating. The data was collected by scan sampling and behaviour sampling.

4.3.1. Behaviour sampling

One pair was observed for 40 minutes per session. Selected behaviour patterns (see table 2 and table3) were noted and categorized. Some behaviours were counted as durations and some as frequencies. Some pairs were observed in the morning and some in the afternoon. To avoid biases, order was changed randomly. The behavioral analyses were evaluated by an ethogram.

Table2: Ethogram for the behaviours measured in frequencies

Frequencies	
displacement	one bird comes near the other one and the other one leaves immediately
stealing	one individual takes food directly from the other ones beak
retrieving	pilfering the cache of another individual
stealing_try	trying to take food directly from the other ones beak
retrieving_try	trying to pilfer a cache
foodsharing	one individual puts food directly into the other ones beak
shake	shaking the whole body
beak_wipe	wiping the beak at an object - left and right
initiates_fight	starting a fight
wins_ fight	is the winner of the fight
loud_call	long distance calls
soft_call	quiet calls directed to the partner
initiates_contactsit	starting the contact sit
terminates_contactsit	ending the contact sit
feeding_young	putting food directly into the beak of a chick
peck_threat	pecking with the beak on another ones body, or at least clearly in the other ones direction, aggressively
scratch	scratching itself
touch_bill	one individual touches the beak of the other one with its beak
touch_foot	one individual touches the foot of the other one with its foot
caches	hiding food under a stone or in a hole and covering it
recaches	one individual takes its own cache and caches the food elsewhere
nest_material	carrying nest material like branches

Table3: Ethogram for the behaviours measured in durations

Durations	
fight	both individuals attack each other aggressively. One is sitting on the other one
chase	one individual chases the other one. One is obviously flying away from the other one - often with loud calls
contact_sit	sitting in proximity - under 1/2 meters away, in reaching distance, so they could touch each other without moving
allopreening	one individual preening the feathers of the other one, stroking feathers with the beak
SAD	self aggrandizing display- feathers fluffed up, various, short calls.
autopreening	one individual preening its own feathers, stroking feathers with the beak
cofeeding_OS	both individuals feeding at the same feeding site, - same feeding stone
beakholding	one individual holding the other ones beak – > 3 seconds
partner_SAD	self aggrandizing displays from both partners at the same time- feathers fluffed up, personalized short calls.
cofeeding_TS	both individuals feeding simultaneously but either at one feeding stone
feeding_alone	one individual feeding at one feeding site. The other one doesn't.

4.3.2. Scan sampling

Additionally, during every session, the pairs were scanned every 5 minutes to measure proximity. Therefor categories were defined:

Table4: distance categories for scan sampling

Distance				
0-1m	1-2m	2-3m	3-4m	>4m

4.3.3. Experiments

The experiments were performed directly after the 20 min of observation. Therefor one feeding plate was placed on each side of the aviary a few weeks before the study started, because of the neophobia, so the birds could get used to them. When the experiments started, it was differed between 2 conditions. In condition one, 8 pieces of Frolic or Greaves were offered on one plate all on one side of the aviary. In condition two, 4 pieces of Frolic or Greaves were offered on each plate on both sides of the aviary. The size of the food offered was adapted to the two species, so the pieces for the crows were half the size as the ones for the ravens.

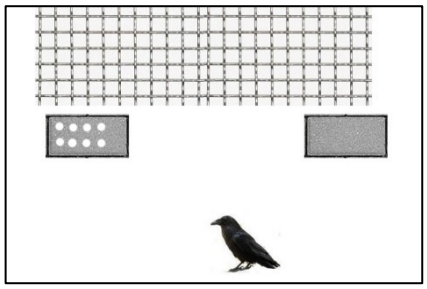


Figure1: Condition 1: eight pieces of frolic or greaves on one plate

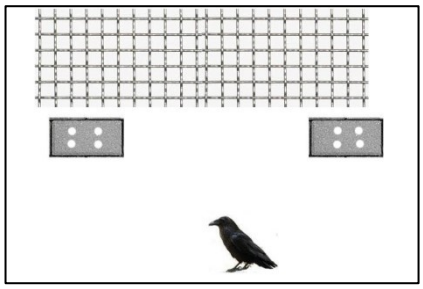


Figure2: Condition 2: eight pieces of frolic or greaves on two plates

4.3.4. Additional sampling

Additionally, I collected data for Friederike Böhm's study. Therefor we used turkey or chicken necks, again dependent on the species. Turkey for the ravens and chicken for the crows. The food was fixed with a chain, so that the birds were not able to monopolize the food source. Here the experiments were also split into two conditions. In condition one, one piece of a turkey or chicken neck was offered on a plate on one side of the aviary. In condition two, one chicken or turkey neck was cut into two equal pieces, one placed on each side of the aviary.

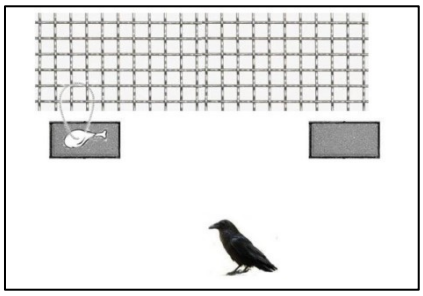


Figure3: one piece of meat offered on one plate

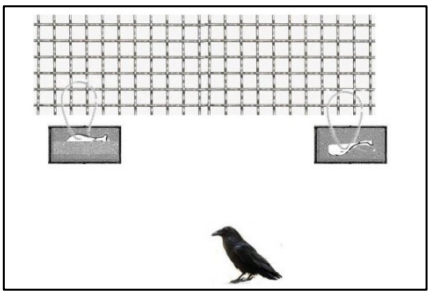


Figure4: one piece of meat offered of two plates

4.3.5. Nest camera

To be able to watch the parent-offspring interaction over the breeding season, nest cameras were placed above the nest boxes. The videos could be watched over a live stream on YouTube (ravenbreedcam.andraspeter.com). Unfortunately, this was only possible in the Haidlhof research station and not in Grünau. I watched the videos two times every day for half an hour over the breeding phase and noted who was breeding and how long.

Picture1: Luise in the nest

Picture2: Young ravens

4.4. Analyses

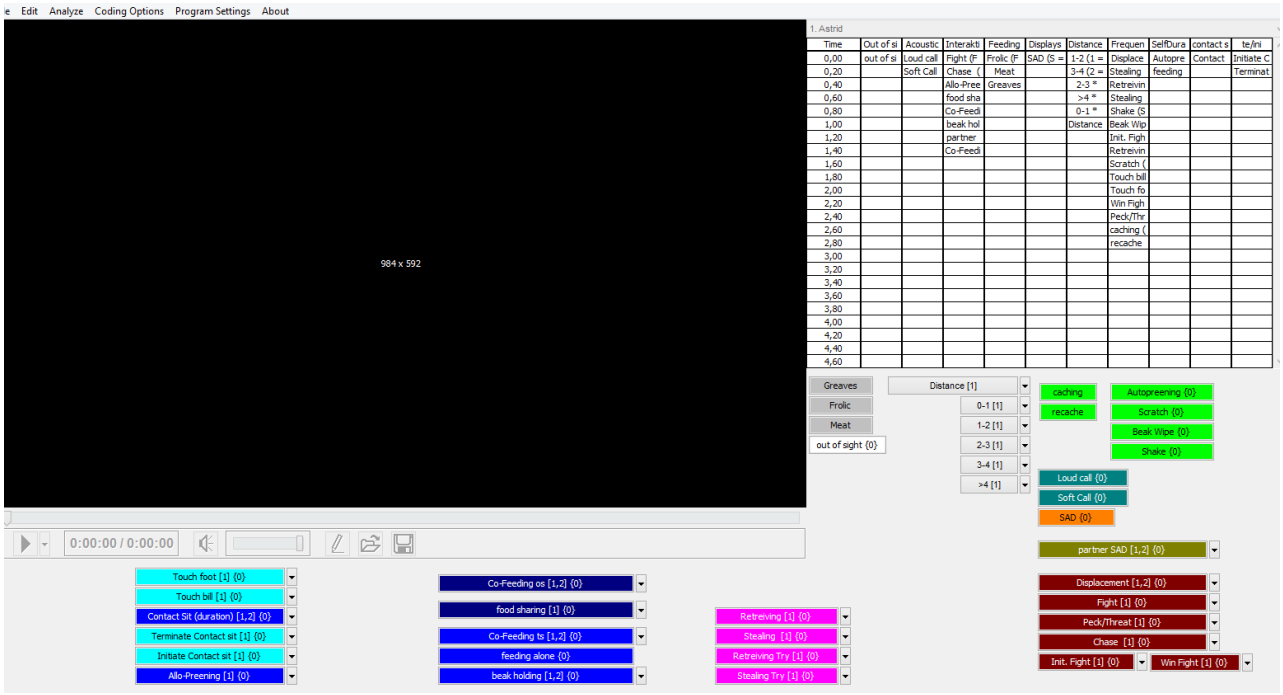
4.4.1. Observer Reliability

To be sure, that the data sampled by two different people, Friederike Böhm and me, is combinable and can be analyzed together, we performed an observer reliability test, where we both watched a video of the same breeding pair independently for 10 minutes and coded the different behavioral patterns with Solomon coder. Then we exported the data into an excel sheet and compared the two data sets and analyzed, how much they resemble. Therefore a cohen's kappa test was conducted. We considered a result <0.6 as unacceptable, results >0.7 as a good match and >0.8 as a very good match.

The observer reliability test showed a very good match of the two observers, Friederike Böhm and Daniela Schwarz. The cohen's kappa test showed a very good match of 84%. The results of this test show, that it is possible to combine the two datasets.

4.4.2. Coding

All Videos recorded from phase 2 and phase 4, were coded with the program "Solomon Coder". All necessary behaviours, related to pair bond quality were included. I did not analyze the data of phase 1 and 3 because in phase 1, no experiments took place and as the female was at the nest most of the time, only the male could have been observed in those pairs with breeding success. In phase 3, the chicks were out of the nest and influencing the parents' behaviour. In these phases, the data of the successful breeding pairs was not combinable with the data of the other pairs. So, for this study, only the phases 2 and 4 were coded and used for further analyses.



Picture3: Screenshot of Solomon Coder

4.4.3. Statistical Analyses

The Data of Solomon Coder was exported to an Excel Sheet. Further Analyses were done with the Statistic-program "R" version 3.3.1 (R Core Team 2016) including the packages psych (Revelle 2017), REdaS (Maier 2015) and GPArotation (Bernaards & Jennrich 2005) for the PCA and lme4 (Bates et.al. 2015) for the glmm.

Measuring differences in pair bond quality:

To find out more about the pair bond quality and the differences within the pairs and between the species, I created categories for the behaviours, inspired by literature:

Affiliative Behaviours	
frequencies	**durations**
touch_bill	contact_sit
touch_foot	allopreening
o_foodsharing	beakholding

Agonistic Behaviours	
frequencies	**durations**
fight	displacement
chase	peck_threat

Proximity
distance

Agonistic Support
Partner_SAD

Tolerance
Cofeeding OS
Cofeeding TS

Parental Investment
Breeding
Feeding Chicks

As frequencies and durations cannot be shown in one graph, the percentage of affiliative behaviours measured in frequencies per pair were calculated in relation to all affiliative

behaviours measured in frequencies. The same was done with affiliative behaviours measured in durations and with agonistic behaviours. As the food during the experiments was available only for a few seconds, the data was taken from both, observations and experiments. Except of cofeeding, this was only coded during the experiments. As the time, food was on the feeding stone, differed from experiment to experiment, a ratio was calculated cofeeding_ratio= cofeeding(duration)/food_available(in sec). Breeding could have only been measured at phase1 at those Haidlhof-pairs, which laid eggs. The feeding_young data was only taken from phase 2, from those pairs, which had offspring.

For all analyzed parameters, a shapiro-test was conducted to see, if the data is normally distributed. For the normal distributed data, with two independent variables, a t-test was performed. Otherwise, a Mann-Whitney-U test, or a Kruskal-Wallis-test in case of more independent variables, was conducted.

Correlations with PCA:

3 PCAs (Principle Component Analysis) were conducted, one for observational data only, one for experimental data only and one for all data, to see if they can be combined. To find out, if a PCA with this data is permissible and useful, a KMO (Kaiser-Mayer-Olsen criteria) was conducted. A result >0.5 was considered as positive. The PCA should show, which behaviours are correlating and cluster together. With a scree plot, the optimal number of components was determined. Behaviours, which hardly occurred over the tests or with a small eigenvalue were omitted. The other categories were rotated. To be able to pool the data (observation and experiment), all behaviours with a food context were excluded.

4.4.4. Factors influencing pair bond quality

The factors influencing pair bond quality were detected with a GLMM (generalized linear mixed model). As respond variables, I chose cofeeding and foodsharing. For that, these variables, first measured in durations, were changed into binomial variables (Yes/No). “Pair” was used as a random factor. Fixed factors included the PCA clusters (affiliative, agonistic, proximity and self_directed), as well as experience, species and breeding success.

5. Results

5.1. Pair bond quality

5.1.1. Affiliative behaviour

The shapiro-test was done separately for ravens and crows. For the affiliative behaviours measured in frequencies, the shapiro-test showed no normal distribution of the data, neither in in ravens ($p<0,001$, $W=0.393$), nor in crows ($p<0.001$, $W=0.178$).
With the Mann-Whitney-U test, I found a significant difference between the two species ($p<0.001$, $W=46421$) with a significant higher rate in ravens, and a significant difference within the ravens with a Kruskal-Wallis-Test ($p<0.005$, $chi^2=15.069$) but not within the crows ($p=0.05$, $chi^2=9.303$).

For those behaviours, measured in durations, the shapiro-test showed no normal distribution, not in ravens ($p<0,001$, $W=0.670$) and not in crows ($p<0.001$, $W=0.577$).
The Mann-Whitney-U test showed a significant difference between the two species ($p<0.001$, $W=48631$). The Kruskal-Wallis tests showed a significant difference within the ravens ($p<0.001$, $chi^2=51.673$) and within the crows ($p<0.001$, $chi^2=62.352$)
With the spearman correlation test a significant positive correlation ($p<0.001$, $t=5.081$) between the frequency and duration data was found, as visible in figure5. Often, when the frequency-bars are higher, the duration bars are higher too and vice versa.

It is also noticeable, that the percentage of affiliative behaviour in the pairs which did not form themselves but were put together and thus were defined as “forced pair housed” is very low. Also Rocky and Joey showed a low rate of affiliative behaviour.

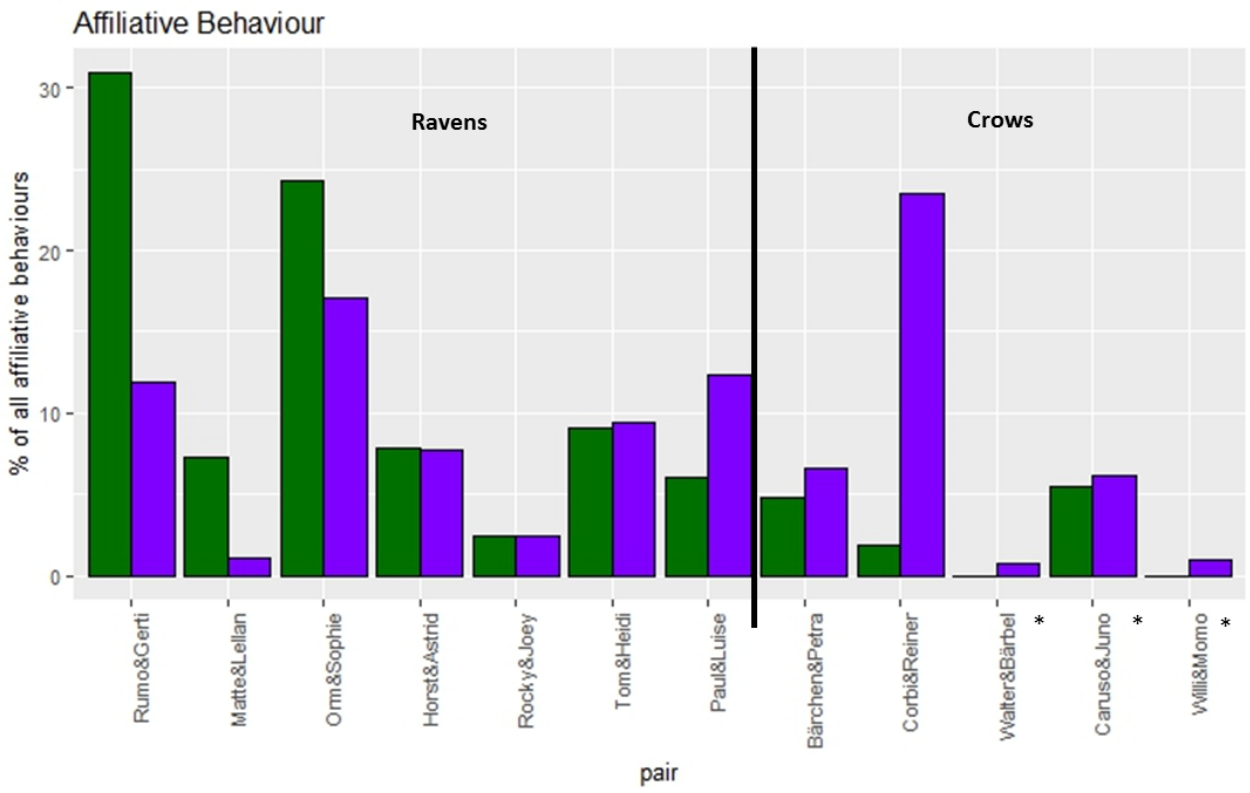


Figure5: Percent of affiliative behaviours shown per pair in relation to all affiliative behaviours shown by all pairs. *=forced housing =durations, = frequencies

5.1.2. Agonistic behaviour

For the agonistic behaviours measured in frequencies, the shapiro-test showed no normal distribution of the data, neither in ravens ($p<0{,}001$, $W=0.167$), nor in crows ($p<0.001$, $W=0.335$).
The Mann-Whitney-U test showed highly significant differences ($p<0.001$, $W=35996$) in agonistic behaviours measured in frequencies, between ravens and crows with a higher rate of agonistic behaviours in crows.
The Kruskal-Wallis test showed a significant difference within the crows ($p<0.001$, $chi^2=25.255$).

For the agonistic behaviours measured in durations, the shapiro-test showed no normal distribution of the data in crows ($p<0.001$, $W=0.080$).
The Mann-Whitney-U test showed significant differences ($p<0.001$, $W=38976$) in agonistic behaviours measured in durations between the two species.
The Kruskal-Wallis test showed a significant differences within the crows ($p<0.05$, $chi^2=10.817$).

Due to the few agonistic events shown in ravens, the difference within this species and the correlation test could not be performed.

As visible in figure6, most raven pairs, except Rumo&Gerti and Matte&Lellan, showed no agonistic behaviour at all over all observations and experiments.

Considering both, figure5 and figure6, it seems that pairs, who have a higher rate of affiliative behaviour, show a lower rate of agonistic behaviour.

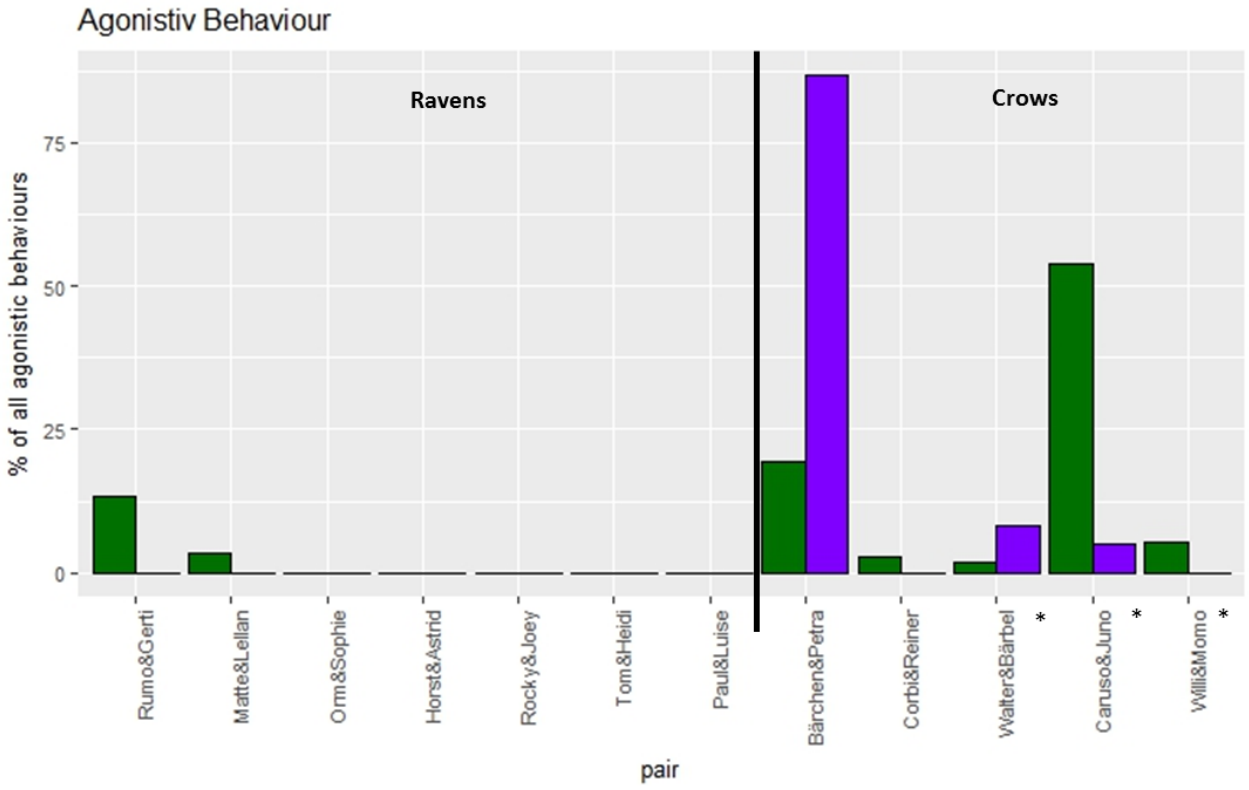


Figure6: Percent of agonistic behaviours shown per pair in relation to all agonistic behaviours shown by all pairs. *=forced housing =durations, = frequencies

5.1.3. Show off/ agonistic support

In show off, what was measured as a proxy for agonistic support (towards outsiders), the average of the partner-SAD duration per pair was measured. No normal distribution of the data was found (ravens: $p<0.001$, $W=0.433$, crows: $p<0.001$, $W=0.272$).

With the Mann-Whitney-U test a significant difference ($p<0.001$, $W=47408$) between the species was found, with a higher mean rate of agonistic support in ravens.

The agonistic support in figure7 showed strong differences between the pairs of both species (Kruskal-Wallis: ravens $p<0.001$, $chi^2=70.953$, crows $p<0.001$, $chi^2=23.059$). It is to say, that agonistic support hardly occurred in crows.

Those pairs with "forced pair housing", showed nearly no partner-SAD. Orm&Sophie and Astrid&Horst showed the highest rate of agonistic support.

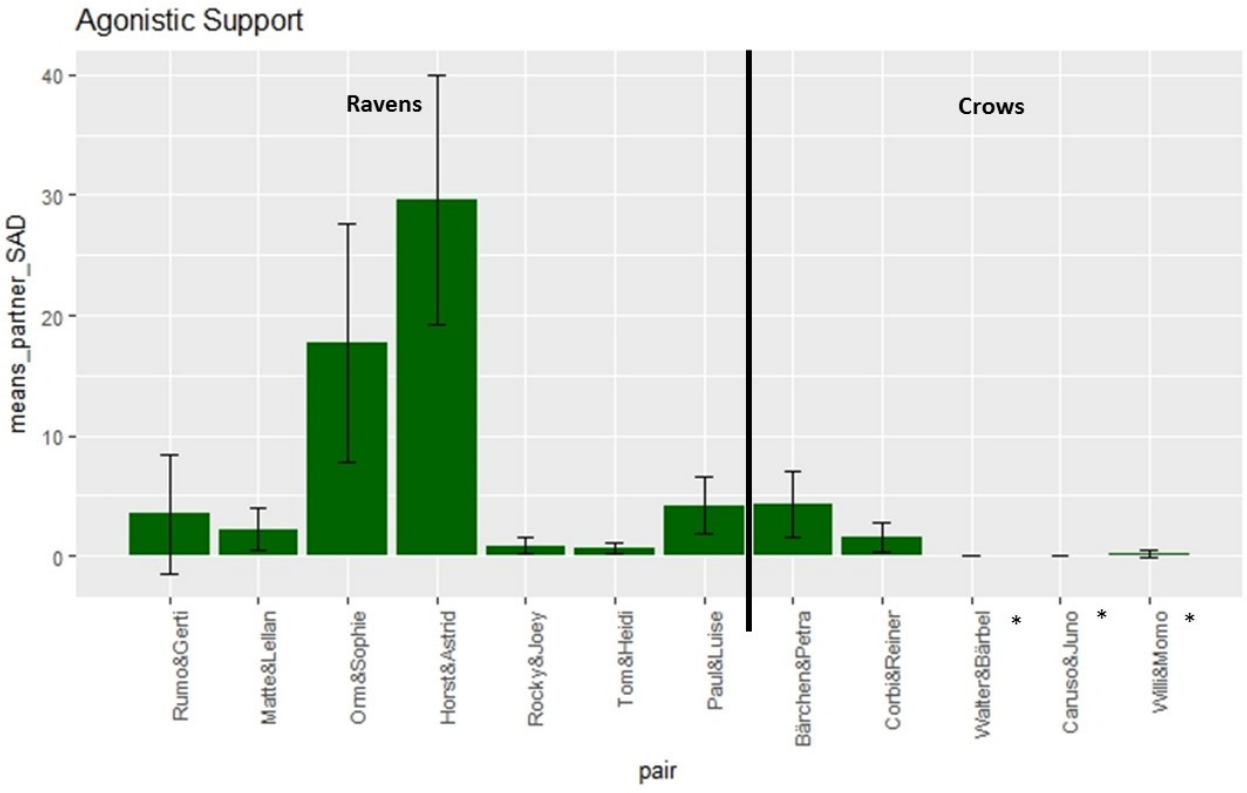


Figure7: Means of the partner_SAD duration for each pair with errorbars. *=forced housing

5.1.4. Proximity

The shapiro-test showed no normal distribution over the data of the mean distance from male to female (ravens: $p<0.001$, $W=0.975$, crows: $p<0.005$, $W=0.979$).

There was no significant difference found between ravens and crows, as tested with Mann-Whitney-U ($p>0.05$, $W=38814$). I found a significant difference between the mean distance of the pairs within a species (ravens $p<0.001$, $chi^2=75.006$, crows $p<0.001$, $chi^2=27.086$)

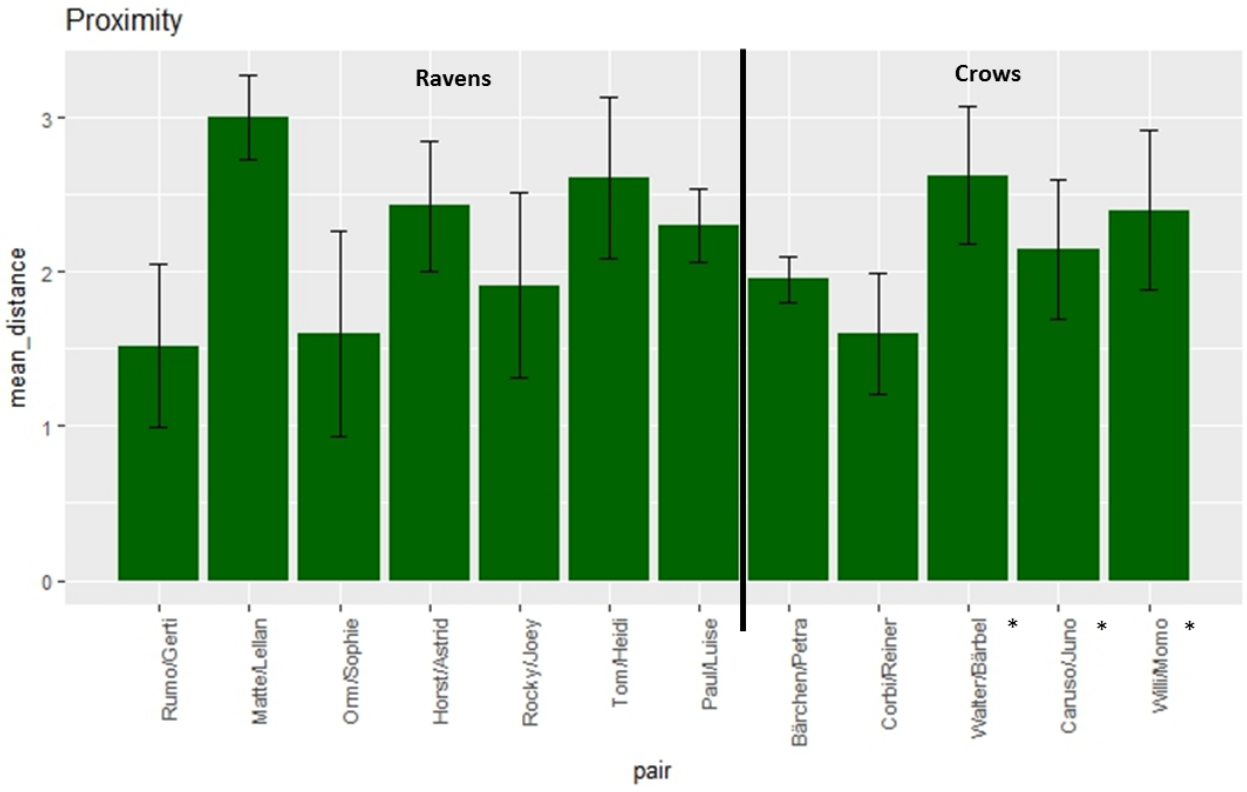


Figure8: Meandistances between male and female within a pair with errorbars. *=forced housing

5.1.5. Tolerance at a food source

The shapiro-test showed no normal distribution in ravens ($p<0.001$, $W=0.477$) or crows ($p<0.001$, $W=0.364$).

There are no significant differences between the species ($p>0.05$, $W=42462$), but the kruskal-wallis-test showed a significant difference within the species (ravens $p<0.001$, $chi^2=26.151$, crows $p<0.001$, $chi^2=19.870$)

In figure9 we can see that Walter&Bärbel and Rumo&Gerti showed no cofeeding at all.

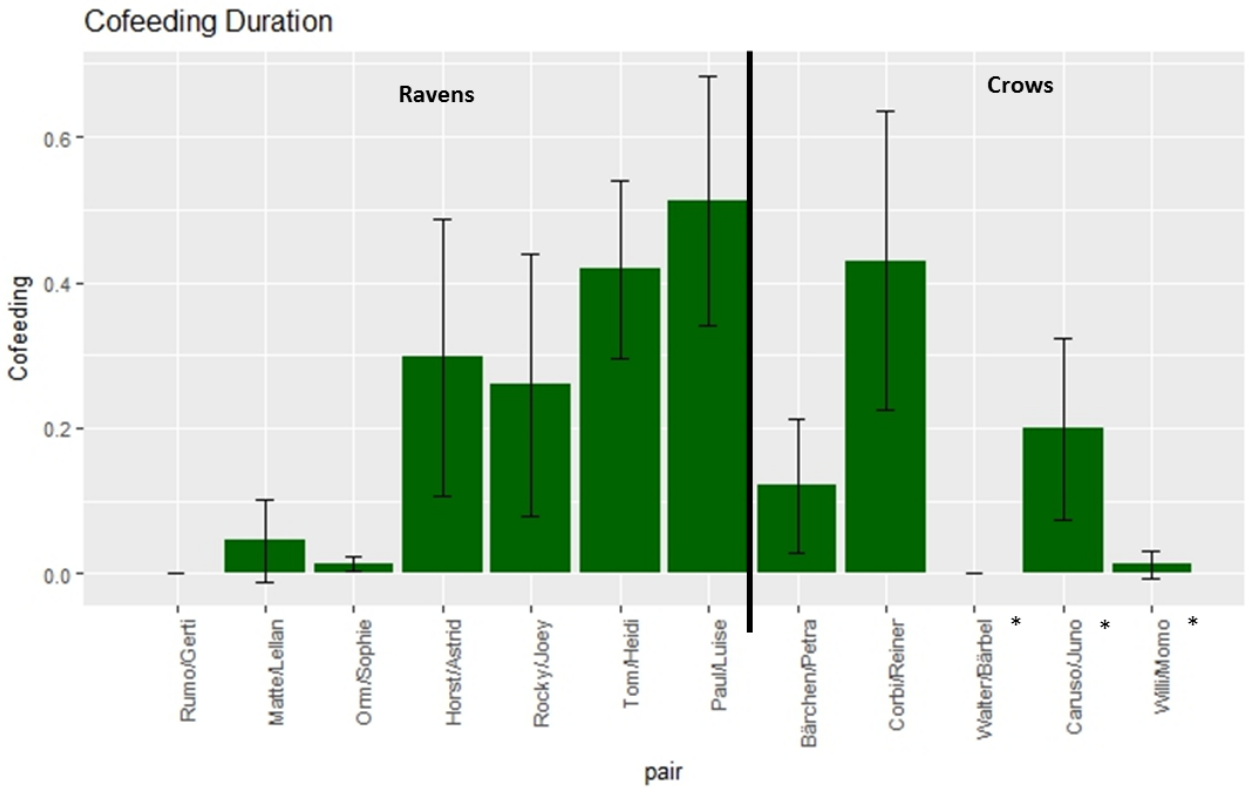


Figure9: ratio of cofeeding duration in relation to the time, the food was available, with errorbars. *=forced housing

To see if feeding alone can be seen as a tolerance factor, two correlation tests were conducted.

As shown in figure10, there was a weak but significant negative correlation between the ratio of cofeeding and the ratio of feeding_alone. Spearman correlation test shwed a p value < 0.05, rho= -0.224. However, a correlation between feeding_alone and foodsharing could be found (figure11) ($p<0.05$, $rho=0.154$)

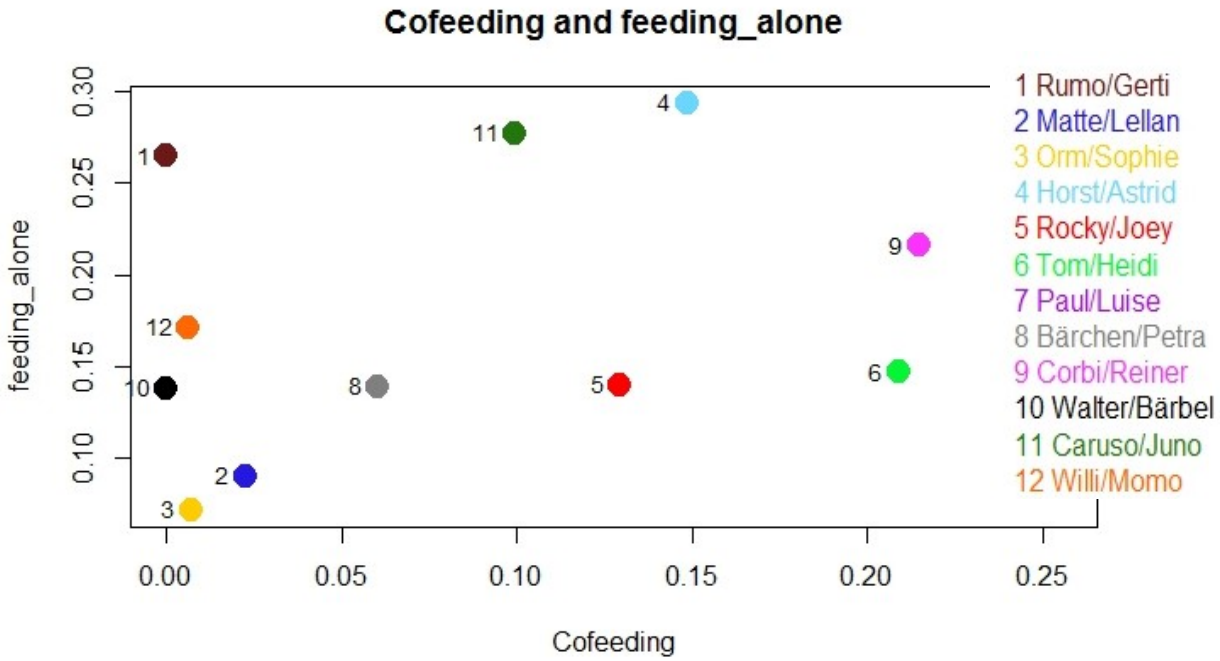


Figure10: Correlation of the ratio of cofeeding and the ratio of feeding_alone

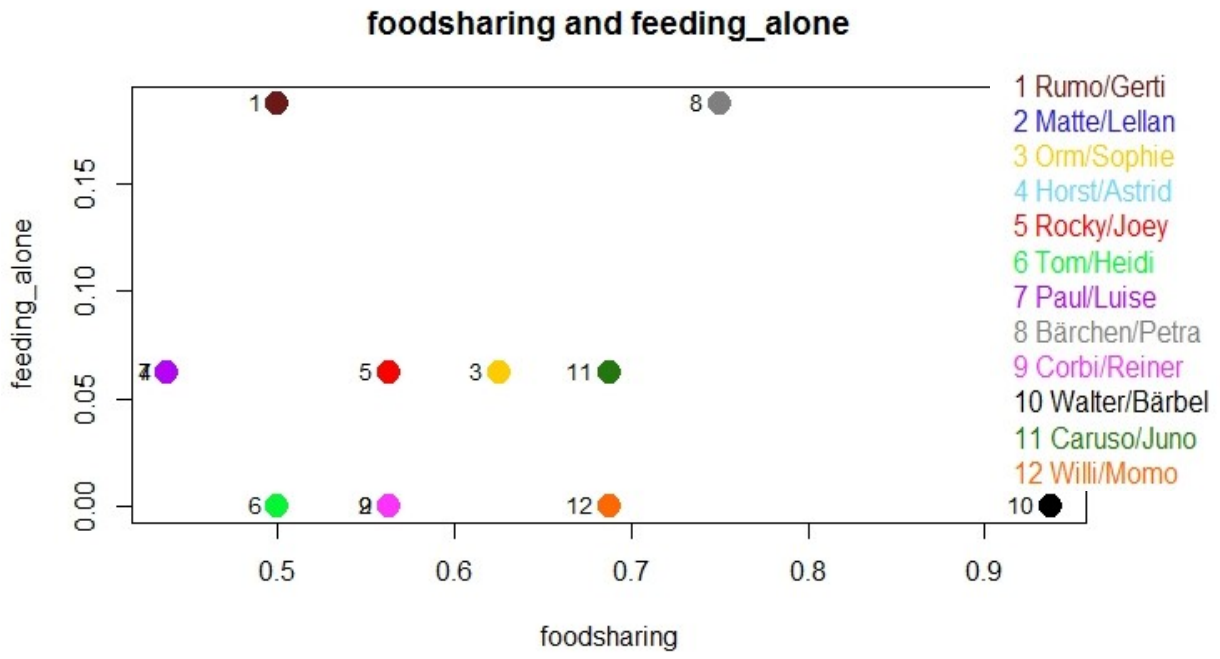


Figure11: Correlation of feeding_alone (yes/no) and foodsharing (yes/no)

5.1.6. Parental investment

The shapiro-test showed no normal distribution ($p<0.001$, $W=0.7863$).
With the KW-test, no significant difference between the mean breeding duration could be detected ($p>0.05$, $chi^2=6.723$)
Breeding data was only available from the Haidlhof raven pairs. Tom was the only male that was watched breeding 2 times.

The mean "feeding-young" data from the pairs who successfully hatched was also not normally distributed ($p<0.001$, $W=0.618$).

There was no significant difference found between the pairs (KW: $p=0.627$, $chi^2=2.597$) and not between the sexes (Wilcoxon: $p=0.637$, $W=1726$). It can be assumed that males and females are feeding the chicks equally frequent.

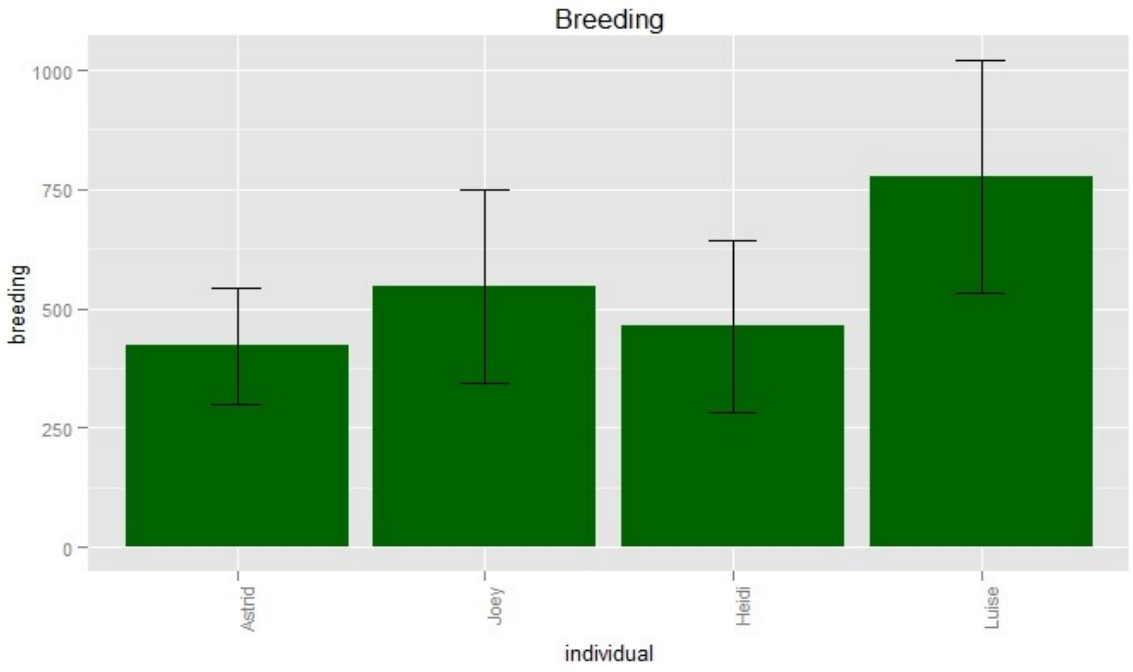


Figure12: Mean breeding duration of the Haidlhof females and Tom with errorbars.

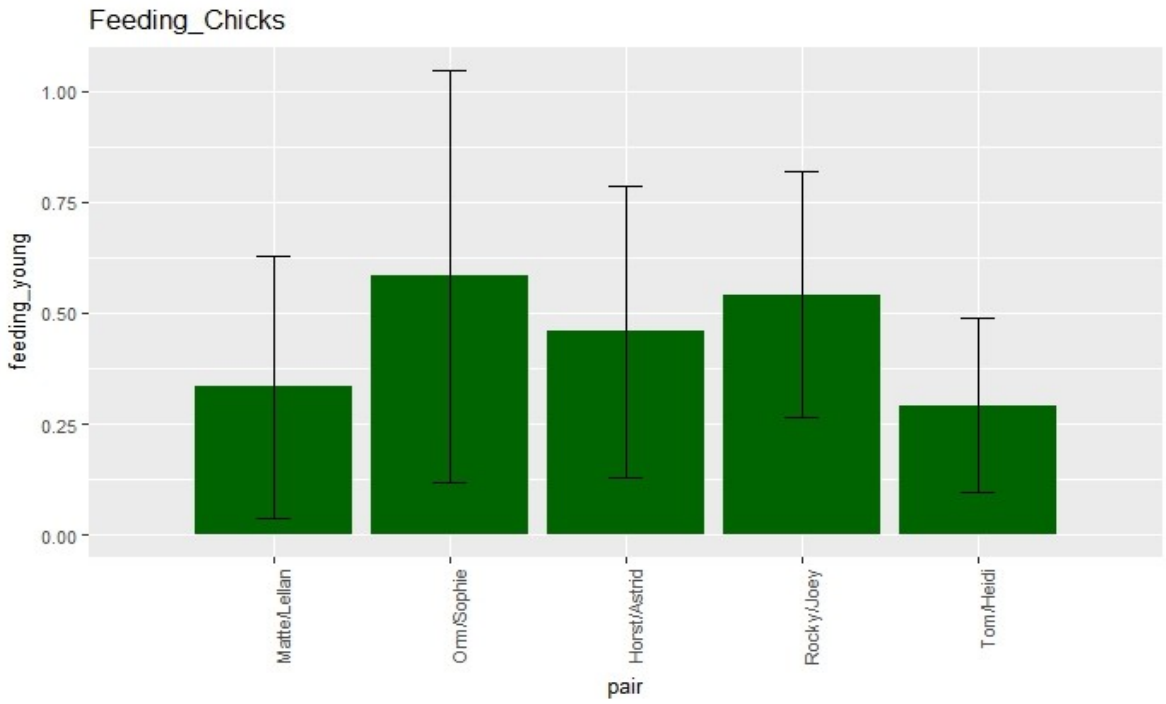


Figure13: Mean feeding events from the parents to the chicks with errorbars.

5.1.7. Correlations with PCA

The analyses of the behaviours with the principle component analyses showed correlations between some behavioral patterns. As seen in table5, the correlations showed hardly any differences considering observations only and experiments only. So I decided to work with a complete PCA including all experiments and observations.

Table5: results PCA with observational data only

Observation							
	TC1	TC2	TC3	TC4	TC5	TC6	TC7
terminates_contactsit	0.82						
initiates_contactsit	0.77						
contact_sit	0.64						
distance	-0.75						
autopreening		0.8					
shake		0.84					
scratch		0.69					
beakholding						0.72	
touch_foot						0.54	
SAD				0.75			
loud_call			0.75				
chase							0.75
displacement							0.51
beak_wipe					-0.62		
peck_threat			0.66				

Table6: results PCA with experimental data only

Experiment							
	TC1	TC2	TC3	TC4	TC5	TC6	TC7
terminates_contactsit	0.8						
initiates_contactsit	0.79						
contact_sit	0.66						
distance	-0.76						
autopreening		0.79					
shake		0.84					
scratch		0.7					
beakholding					0.49		
touch_foot					0.45	-0.52	
SAD				0.77			
loud_call			0.76				
chase						0.72	
displacement						0.51	
beak_wipe					-0.74		
peck_threat			0.66				0.8

To get a table of highly correlating behaviours in categories, I first did a PCA with all coded behavioral patterns without a food context and omitted fight, wins_fight and initiates_fight because they hardly occurred over the study. Peck_threat, soft_call and allopreening were also excluded because of their low commonality (h2) or because they showed no correlation value over 0.5 (table7).

Table7: results PCA with all data. Marked low correlations and low commonality

	TC1	TC2	TC3	TC5	TC4	TC6	h2	u2
autopreening	-0.05	0.84	-0.03	0.05	-0.02	-0.12	0.72	0.28
distance	-0.64	-0.13	0.03	0.12	-0.07	0.11	0.47	0.53
contact_sit	0.70	0.07	0.04	-0.07	0.02	-0.11	0.54	0.46
SAD	-0.02	0.06	-0.04	0.82	-0.09	-0.03	0.68	0.32
beakholding	0.06	0.02	0.83	-0.04	0.03	-0.02	0.71	0.29
allopreening	0.43	0.02	0.06	-0.46	-0.12	-0.08	0.46	0.54
chase	-0.02	0.01	0.03	-0.02	0.59	0.28	0.43	0.57
soft_call	-0.14	-0.16	-0.01	-0.07	-0.16	-0.49	0.29	0.71
touch_bill	0.41	0.16	0.08	0.16	0.09	-0.10	0.25	0.75
peck_threat	0.12	0.05	-0.04	-0.06	0.52	-0.18	0.32	0.68
touch_foot	-0.07	-0.02	0.83	0.04	-0.05	0.02	0.69	0.31
beak_wipe	-0.04	-0.02	-0.02	-0.04	-0.02	0.83	0.70	0.30
displacement	-0.10	-0.08	-0.03	0.04	0.73	-0.05	0.57	0.43
shake	0.03	0.77	0.00	0.02	-0.04	0.22	0.64	0.36
scratch	-0.01	0.69	0.05	-0.10	0.04	-0.06	0.50	0.50
loud_call	0.03	-0.06	0.07	0.74	0.14	0.00	0.59	0.41
initiates_contactsit	0.82	-0.08	-0.01	0.08	-0.04	0.06	0.69	0.31
terminates_contactsit	0.81	-0.07	0.00	0.00	-0.06	0.06	0.66	0.34

With the scree plot (figure12), the eigenvalue was analyzed and showed 6 principle components with an eigenvalue >1. So I decided to do the PCA with 6 clusters.

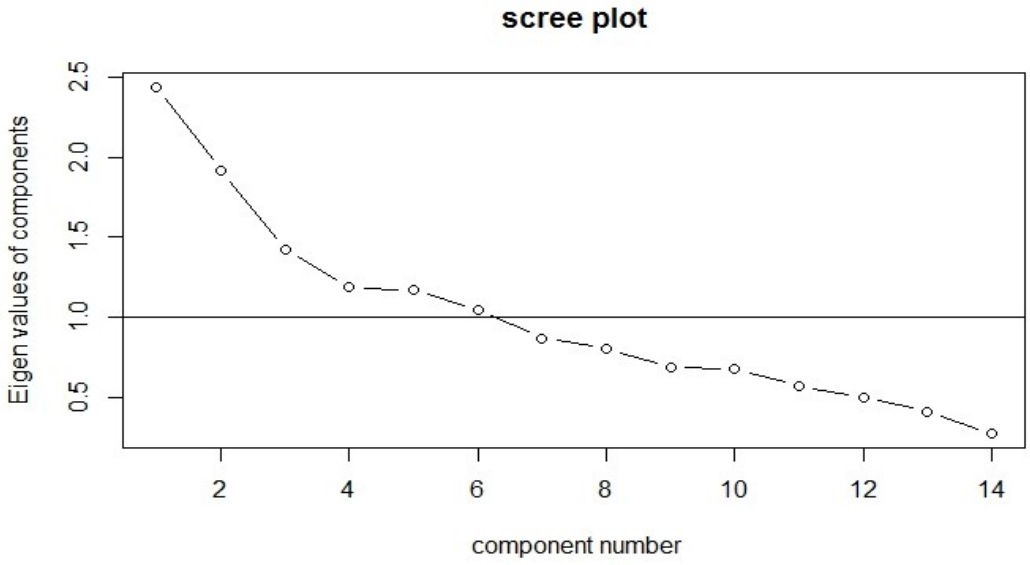


Figure14: sree plot of all eigenvalues

The Kaiser-Mayer-Olkin-Kriterium showed a value of 0.63.

In table8, the results of the combined observational and experimental data are shown. The 14 behaviours were reduced to 6 different components. The categories where named as followed: TC1= Proximity, TC2=self directed behaviour, TC3= affiliative, TC4= vocal behaviour TC5= agonistic, TC6= arousal. These components were taken as predictors in the following model, except TC6 and TC4, as the correlations with TC6 are too small to be considered. In TC4 the variables “SAD” and “loud call” did not correlate in the PCAs for observations or experiments only.

The four extracted components showed a reflection of 73% of the total variance. Component 1 explained 25%, component 2 20%, component 3 15% and component 5 13% of the total variance.

Table8: results PCA with combined observational and experimental data , cut 0.5

Observation and Experiment						
	TC1	TC2	TC3	TC4	TC5	TC6
terminates_contactsit	0.85					
initiates_contactsit	0.85					
contact_sit	0.69					
distance	-0.61					
autopreening		0.84				
shake		0.79				
scratch		0.69				
beakholding			0.83			
touch_foot			0.83			
SAD				0.80		
loud_call				0.77		
chase					0.79	
displacement					0.73	
beak_wipe						0.89

Table9: results PCA with combined observational and experimental data, all correlations.

	TC1	TC2	TC3	TC4	TC5	TC6	h2	u2
autopreening	-0.05	0.84	-0.03	0.05	-0.03	-0.13	0.73	0.27
distance	-0.61	-0.10	0.03	0.14	-0.01	0.25	0.48	0.52
contact_sit	0.69	0.06	0.04	-0.08	0.00	-0.21	0.55	0.45
SAD	-0.04	0.05	-0.04	0.80	-0.13	-0.03	0.65	0.35
beakholding	0.05	0.01	0.83	-0.05	0.02	-0.03	0.70	0.30
chase	0.04	0.06	0.02	-0.02	0.73	0.24	0.60	0.40
touch_foot	-0.06	-0.01	0.83	0.06	-0.03	0.02	0.70	0.30
beak_wipe	-0.02	0.00	-0.02	-0.04	0.00	0.89	0.80	0.20
displacement	-0.07	-0.06	-0.04	0.03	0.79	-0.18	0.67	0.33
shake	0.04	0.79	0.00	0.01	0.01	0.26	0.69	0.31
scratch	-0.01	0.69	0.05	-0.08	0.02	-0.14	0.51	0.49
loud_call	0.08	-0.03	0.07	0.77	0.16	-0.02	0.65	0.35
initiates_contactsit	0.85	-0.05	-0.01	0.09	-0.01	0.08	0.73	0.27
terminates_contactsit	0.85	-0.03	0.00	0.02	-0.02	0.08	0.72	0.28

5.2. Factors influencing pair bond quality

The glmer with cofeeding as a binomial response variable showed (table10) a significant effect of proximity and experience on whether the pairs fed at the same time or not:

Table10: R output of the glmer with cofeeding as response variable

Fixed effects:				
	Estimate	Std. Error	z value	Pr(>|z|)
(Intercept)	-2.739133	0.683450	-4.008	6.13e-05 ***
dyad_small$breeding_success1	1.421076	0.883012	1.609	0.10754
dyad_small$species2	-0.050547	0.769766	-0.066	0.94764
dyad_small$ago	-0.005631	0.222431	-0.025	0.97980
dyad_small$aff	-0.016633	0.122047	-0.136	0.89160
dyad_small$prox	0.449340	0.154240	2.913	0.00358 **
dyad_small$self	-0.116956	0.219887	-0.532	0.59480
dyad_small$experience1	-2.253902	0.747144	-3.017	0.00256 **

For the simplified test, the fixed factors, species, agonistic and affiliative were omitted. It showed an additional significant effect of breeding_success.

Table11: simplified glmer model

Fixed effects:				
	Estimate	Std. Error	z value	Pr(>|z|)
(Intercept)	-2.7774	0.3806	-7.298	2.93e-13 ***
dyad_small$breeding_success1	1.4576	0.6609	2.206	0.02741 *
dyad_small$prox	0.4480	0.1539	2.911	0.00360 **
dyad_small$self	-0.1162	0.2189	-0.531	0.59548
dyad_small$experience1	-2.2545	0.7468	-3.019	0.00254 **

The glmer with foodsharing as a binomial response variable showed no significant effect of any fixed variables in table12.

Table12: R output of the glmer with foodsharing as response variable

Fixed effects:					
	Estimate	Std. Error	z value	Pr(>|z|)	
(Intercept)	-3.16809	0.69898	-4.532	5.83e-06	***
dyad_small$breeding_success1	-1.13938	1.08382	-1.051	0.293	
dyad_small$species2	-0.67878	0.85985	-0.789	0.430	
dyad_small$ago	-0.36115	0.45305	-0.797	0.425	
dyad_small$aff	0.05605	0.14717	0.381	0.703	
dyad_small$prox	0.35809	0.25128	1.425	0.154	
dyad_small$self	0.28138	0.26415	1.065	0.287	
dyad_small$experience1	0.56822	0.99683	0.570	0.569	

6. Discussion

This study aims to examine and explain pair bond quality in long term monogamous species. It shows that there are differences in pair bond quality between the two studied corvid species and between the pairs within those. According to the very similar social systems of common ravens and carrion/hooded crows, I did not expect such high differences in nearly every factor considered as representative for pair bond quality.

6.1. Pair bond quality

Affiliative behaviours in this study are sociopositive intra-pair interactions. In a high quality relationship, these interactions should occur frequently (Van Schaik & Aureli, 2000). I found pair-specific differences in affiliative behaviour in ravens. Interestingly, according to the results, the rate of affiliative behaviours also differed between the species, as it was higher in ravens than in crows. The positive correlation between the frequencies and durations of affiliative behaviours shows that these factors stand in relation. Those pairs who show sociopositive interactions often also spend more time with these.

In contrast, agonistic behaviours were hardly seen in ravens, only in Rumo&Gerti and Matte&Lellan, but it was much more common in crows. It is to mention that the agonistic behaviour in the crows occurred mainly in two pairs. The correlation between the categories of agonistic behaviour could not have been tested because the dataset was too small. It was predictable that there will be only little aggression within the pairs. A pair bond should be advantageous for both partners and the costs of conflicts would be too high (Rice 2000). This lack of aggression in pairs was found in rooks too (Emery et. al. 2007).

Agonistic support was higher in ravens than in crows. It is noticeable that pairs, who hardly showed affiliative behaviour, also did hardly show agonistic behaviour and agonistic support. This leads to the assumption that some pairs just do not interact much at all. De Waal and Harcourt (1992) already pointed out the importance of conflict support in primates. But agonistic support also occurs in birds. In groups of rooks for example, this is more likely to occur in partners than non-partners (Emery et. al. 2007).

The results of the analyzed factor proximity were exactly like predicted. Thus, I could not find a significant difference between the species, but between the pairs within the species. Also the pairs which were “forced pair housed” were likely to spend time near their partners. Sitting close together often has a strong sociopositive aspect. In a string pulling experiment from Asakawa-Haas et. al. (2016), where ravens had to choose a partner for solving a task, they preferred to

cooperate with friends. In this experiment, they also considered proximity and suggested that the tolerance of proximity to another individual is an important factor of choosing with whom to cooperate.

Ravens and crows seemed to be equally tolerant when it comes to high quality food. Pairs from both species often fed from the same feeding stone or at least simultaneously from both feeding stones. But tolerance at a food source was very pair-specific. It is interesting, that the pairs in Grünau seemed to be less tolerant than the Haidlhof pairs. It is possible that the surrounding also plays a role in how partners interact. As feeding alone is negatively correlating with cofeeding, I considered that it could also be a tolerance factor, because it showed that pairs, where one partner often feeds alone, are less likely to show cofeeding than pairs, in which feeding alone does not occur often. But when I tested feeding alone with foodsharing and found a positive correlation, I rejected the assumption of feeding alone as a tolerance factor. When an Individual, mostly the male, was observed feeding alone often, the female tended to stay close and get fed from time to time. I also saw the females begging sometimes, before it came to foodsharing. The “begging” behaviour of females in the breeding season was also described by Heinrich (1989). They act as they were young ravens and get fed by the male. As foodsharing is more seen as a sociopositive behaviour in pairs, feeding alone was not taken as a negative tolerance factor.

According to the fact, that none of the crow-pairs, neither at Grünau, nor at Haidlhof had offspring in 2016, the data for parental investment was very low. Interestingly, every successful breeding pair of that year laid between 4-6 eggs and hatched 4 chicks. Maybe this can be seen as the optimal brood and clutch size according to the environmental conditions in captivity. According to Lack (1947), who analyzed the clutch size in partridges (*Perdix perdix*), the optimal clutch size is equal to the most common clutch size. There are upper limiting factors like the maximum of eggs which can be incubated and chicks which can be raised. In hooded crows, an influence of the habitat, predation risk and breeding time on the clutch size was found (Loman 1977). No difference could be found between the pairs in breeding duration and feeding young. Males and females fed equally frequent. Only the females were incubating. In ravens, it is typal that both parents take part in nest building, cleaning and feeding the chicks. While the female is incubating, the male provides his partner with food.

All in all, I found much affiliative behaviour, especially in ravens, low agonistic behaviour, a high trend to spend time in proximity and within the pairs with breeding success, equally good parental investment. The rate of agonistic support though, was relatively low. For the latter, only partner_SAD was considered. Loud calls at the same time or alternate can also be a support.

But this was very difficult to verify and thus, excluded. In general, with some exceptions, I can assume that the pairs in this study have high quality relationships referring to the hypothesis of Van Schaik and Aureli (2000).

Correlations with PCA

The categories in PCA resulted as expected. Contact sit correlated negatively with distance. Much contact sit and low distance are both related to proximity. Autopreening, shake and scratch are self directed behaviours or also called “comfort behaviours”. They occur, mostly in brief bouts when the birds are tense or nervous. Autopreening has a similar function as autogrooming in mammals, but is expected to be even more important as it is very elaborate (Delius 1988).
Chase and displacement are clearly agonistic. Loud_call and SAD were titled as vocal behaviour and beak_wipe as arousal. Beakholding and touch_foot are sociopositive behaviours with a high affiliation factor. I expected allopreening to correlate with these affiliative behaviours too, as this is known to be a sociopositive interaction between pair partners that strengthens a pair bond by increasing cooperation (Kenny et. al. 2017). It is also presumed to increase the partner’s fitness by removing the ectoparasites (Black 1996). But allopreening can have an aggressive context. In some species, it is usually the dominant individual who preens the subordinate. In *Corvus corax*, where the male tends to be the dominant part in a pair, it is also common, that the female preens the male (Harrison 1965).

The categories had very low correlation among each other. So, it can be assumed, that a high rate of affiliative behaviour for example doesn’t mean that the rate of self directed behaviour or agonistic behaviour is low.
I expected, that especially those pairs, who show much affiliative behaviour, would show a very low rate of agonistic and high rate of proximity etc. But it seems as if some pairs just show more interactions as others. Maybe a high rate of agonistic behaviour leads to reconciliation and thus to more affiliative behaviour instead, as found in a raven group before (Fraser & Bugnyar 2011).

6.2. Factors influencing pair bond quality

Under scramble competition, I found an effect of experience, proximity and breeding success on cofeeding. Thus it can be assumed, that those, who had former breeding experience, showed less cofeeding than others. A possible explanation could be that those, who had offspring before are better coordinated. It would also be interesting to statistically analyze the possible affect of

pair duration, but as there are just one or two pairs in each category, this could not have been done.
Individuals, who sit close often, show that they trust each other and that indicates a close relationship. In rooks for example, cofeeding is linked to pair bonding (Scheid et. al. 2008). A high proximity rate is an important factor of a high quality relationship. Individuals, who share a good relationship, seem to be more likely to tolerate each other at a food source.

Breeding success was also affecting the cofeeding time. This could be because those, who had offspring, had a priority to feed their chicks and thus had to be more tolerant.

Interestingly, I found no effect of any analyzed variable on foodsharing. As foodsharing is described as highly affiliative in literature and is signaling the quality of the male breeding partner in many bird species (Lack 1940; black-lagged kittiwakes: Helfenstein et.al 2003), I expected an affect of breeding success and affiliative behaviour. Galván and Sanz (2011) found a correlation between food sharing and breeding success but only in the incubation phase (here: phase1). Sharing food with the partner should compensate the large energetic investment in passerine species, where only the female incubates. This phase was not analyzed in this study because there were too little pairs with offspring.

6.3. Additional Comments

It is interesting, that none of the crow pairs had offspring and just two of them even tried to build a nest. This could be an effect of the environment. Maybe the aviaries did not provide an optimal place to build a nest. It also could have been because 3 oft those pairs were “forced pair housed” and Corbi has only one leg, so we cannot be sure if he is physically capable of showing reproductive behaviour. Anyway, it wasn’t possible to verify the fertility of the studying subjects.

It is to mention that, because of the small sample size, the results should be seen as a trend. Many more tests have to be made to really be able to take a strong statement about pair bond quality. To learn more about the effects of pair bond quality on for example breeding success, studies over more than one year and with a bigger sample size would be necessary.

It has to be considered, that all individuals lived in captivity and most of them were hand raised. Hence, these results cannot be directly transferred to free-living individuals.

7. Conclusion

Previous studies on common ravens and carrion/hooded crows typically concentrated on nonbreeder groups and there are only a few studies about relationship qualities, especially pair bond quality in these species. Thus, this study shows an overview of corvid pair bond quality and what influences it. The pair bond quality, as defined in this study should be reflected in the occurrence of different behaviours. The analyzed behavioral categories were predicted to correlate to be able to assess the quality of those relationships. This may results from the fact, that the sample size of 7 pairs of common ravens and 6 pairs of carrion/hooded crows, what had to be decimated again in some factors like breeding or feeding young, were only the successful breeding pairs could be analyzed, is too low. Further studies over more than one breeding season and with more breeding pairs would be necessary to get meaningful results.

On the basis of the current data, it can be assumed, that breeding pairs of common ravens and carrion crows do share good quality relationships with a high rate of sociopositive interactions including affiliative behaviours and proximity and a very low rate of socionegative behaviours. There seem to be a difference between those species, what would be very interesting to analyze in more detail in the future. When it comes to scramble competition, the individuals seem to tolerate their partner, sometimes by letting him or her feed on the same food source and sometimes by feeding the female from a source that is already monopolized. I think behaviours shown under a competitive situation, especially when it comes to high quality food plays an important role in measuring pair bond quality. Letting another bird feed on a limited food source is disadvantageous in the first place, but sharing food on the other hand compensates the female’s energy costs of incubating and may increases the breeding success and thus the fitness.

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10. Appendix

10.1. Additional Study – Loose String

Additionally, a loose string experiment was performed to see, if the pairs are willing to work together to get to high quality food (cheese). This experiment was also performed by me in Bad Vöslau and by Friederike Böhm in Grünau. We both used the same material. A board of 100cmx50cm was placed in front of every aviary. On the board, a smaller, movable board of 80cmx10cm was fixed. On the small board, there was one flap on either site, were we could thread a 160cm long rope. The birds could only move the board, when they both pulled the rope simultaneously. To avoid nephobia, we placed the boards a few weeks bevor we started the experiments and moved the small board forwards and backwards many times. The experiments were splitted in two different trials, motivation trial and experimental trial. During the motivation trial, two pieces of cheese were placed on the small board, one on each side. Then the plate was moved by the experimenter to the grid and the birds could take it. In the experimental trial, the food was placed as before. Then, the rope was thread through the flaps and one end was offered the birds on two sides. The trials alternated, first one motivation trial, followed by 3 test trials and then again one motivation trial – this sequence was repeated 3 times per experiment. Every pair was tested 5 times, except those, who showed no motivation at all.

Picture4: Astrid (right) and Horst (left) pulling the string

Table14 shows the number of experiments performed per pair, according to their motivation. Success shows, in how many experiments the pairs showed at least one successful test trial. The only pairs, who could solve the task, were Astrid&Horst, Paul&Luise and Tom&Heidi. It is to mention, that all of the raven pairs had former experience with the loose string experiment, but with another partner. None of the crows and Grünau raven pairs had former experience. Further experiments are necessary to make a statement.

Table14: results loose string

Pair	Experiments	Success
RumoGerti	5	0
MatteLellan	1	0
SophieOrm	0	0
BärchenPetra	5	0
WalterBärbel	5	0
WilliMomo	2	0
AstridHorst	5	5
TomHeidi	5	2
PaulLuise	5	5
RockyJoey	0	0
CorbiReiner	4	0
JunoCaruso	5	0

11. Statement of Authorship

I hereby confirm, that this Mater's Thesis, entitled: "The quality of breeding-pair relationships in ravens and crows" was written only by myself and that I did use only those references and resources that are stated.

Daniela Schwarz, BSc

Sooß, 23.05.2018