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**„Early social environment affects development of ravens’  
social and explorative behavior – using object play and food  
monopolization experiments”**

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## **Abstract**

According to social brain hypothesis, the evolution of cognitive intelligence is driven by social complexity. During family phase, various affiliate, agonistic and neutral interactions shape the development of the offspring. Large-brained birds like corvids tend to have a prolonged period of social maturation. Until now, little is known about the development of social relationships during this time. Here, I observed the effect of parental affiliation and exploration on the development of juveniles' affiliative and explorative interactions in four pairs of captive adult common ravens and their self-raised offspring. I used social observation to assess basic social interactions and two experimental approaches, the playground set-up in order to stimulate exploration behavior and the food monopolization experiment to enhance food manipulation and conflict behavior. I found affiliation among adults to positively influence the level of affiliation among juveniles. The less affiliate adults behaved towards their offspring, the more explorative juveniles were. Although the offspring's development negatively influenced juveniles affiliation with siblings, it had a positive effect on their exploration behavior. Adults' exploration behavior was higher in playground experiment than in social observation. Additionally, they manipulated, monopolized and cached food at similar levels across experimental conditions, indicating that the relationships among breeding pairs are quite stable, and they have good access to food. In the conditions with fixed food pieces, male juveniles tend to show higher food manipulation and caching frequencies and male adults initiated more agonistic interactions than their female peers. These results indicate that juveniles follow behavioral patterns of their parents and that males, independent of age, tend to be more assertive in competition about food.



## **Zusammenfassung**

Die "Social Brain Hypothesis" besagt, dass die Evolution kognitiver Intelligenz von sozialer Komplexität abhängt. Die Entwicklung der Jungtiere während der Familienphase wird von zahlreichen affiliativen, agonistischen und neutralen Interaktionen geformt. Vögel mit großen Gehirnen, wie Corviden, tendieren zu einer verlängerten Periode der sozialen Reifung. Bisher ist nur sehr wenig über die Entwicklung der Sozialbeziehungen während dieser frühen Phase bekannt. Hier wurde der Effekt von elterlicher Affiliation sowie Exploration auf die Entwicklung der Jungtiere in Bezug auf ihre affiliativen und explorativen Verhaltensweisen anhand von vier Rabenpaaren mit ihrem selbst gezogenen Nachwuchs untersucht. Dazu wurden soziale Beobachtungen, um die grundlegenden sozialen Interaktionen herauszufinden, sowie zwei experimentelle Ansätze verwendet. Während durch den sogenannten Spielplatz das Explorationsverhalten stimuliert wurde, verstärkte das Futtermonopolisierungsexperiment die Interaktionen mit Futter sowie Konkurrenz und daraus resultierende Konflikte. Elterliche Affiliation steigerte die Anzahl affiliativer Interaktionen unter Jungtieren. Je weniger affiliativ Eltern gegenüber ihrem Nachwuchs waren, desto explorativer zeigten sich die Jungtiere. Die fortschreitende Entwicklung der Jungtiere führte zur Reduzierung affiliativer Interaktionen, jedoch zu einer Steigerung explorativer Verhaltensweisen. Elterliche Exploration war am Spielplatz deutlich höher als in sozialen Beobachtungen. Levels von Futtermanipulation, -monopolisierung und -verstecken waren ähnlich unter Adulten, welche einerseits darauf hinweisen, dass die Sozialbeziehung zwischen Brutpaaren sehr stabil ist, andererseits, dass Adulte durchgehend Zugang zu Futterressourcen innerhalb der Familie haben. Bei fixierten Futterressourcen zeigten juvenile Männchen eine höhere Anzahl an Futtermanipulation und -verstecken und adulte Männchen initiierten agonistische Interaktionen öfter als gleichaltrige Weibchen. Diese Resultate lassen darauf schließen, dass Jungtiere gewisse Verhaltensmuster ihrer Eltern folgen und Männchen, unabhängig vom Alter, durchsetzungsfähiger sind als weibliche Gleichaltrige.

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# List of content

<b>1. Introduction</b>	<b>- 1 -</b>
1.1. Group living	- 1 -
1.2. Importance of quality of social relationships	- 2 -
1.3. Exploration behavior	- 4 -
1.4. Food sharing & caching	- 5 -
1.5. Ravens	- 6 -
1.6. Hypotheses & Predictions	- 7 -
<b>2. Methods</b>	<b>- 9 -</b>
2.1. Subjects & housing	- 9 -
2.2. Procedure	- 10 -
2.3. Observational approaches	- 12 -
2.4. Behavioral categories	- 14 -
2.5. Statistical Analysis	- 16 -
2.6. Inter-observer reliability	- 17 -
<b>3. Results</b>	<b>- 18 -</b>
3.1. Parental behavior	- 18 -
3.2. Effect of parental behavior on juveniles' behavior	- 19 -
3.3. Effect of development on juveniles' behavior	- 21 -
3.4. Food monopolization experiment	- 23 -
<b>4. Discussion</b>	<b>- 26 -</b>
4.1. Effect of adult behavior on offspring	- 26 -
4.2. Effect of development of offspring	- 29 -
4.3. Effect of observational approach & period	- 30 -
4.4. Sex differences in food monopolization experiment	- 31 -
4.5. Conclusion	- 33 -
<b>5. Appendix</b>	<b>- 34 -</b>
5.1. References	- 34 -
5.2. Tables from Figures	- 42 -
5.3. List of Tables and Figures	- 57 -
5.4. Corvid Ethogram	- 58 -





# **1. Introduction**

## **1.1. Group living**

A wide variety of social systems can be seen in the animal world, from animals that live alone to those that live in large, organized groups. A group can be characterized as ‘any set of organisms, belonging to the same species, that remain together for a period of time interacting with one another to a distinctly greater degree than with other conspecifics’ (Wilson, 1975). Although grouping can bring several different survival advantages (Curley et al., 2015), it can also cause some disadvantages. Advantages of group-living can be individual alertness in a group (Pulliam, 1973), information transfer (Ward & Zahavi, 1973), collective defense against predators or other groups (Alexander, 1974), confusion effects (Miller, 1922), cooperative foraging (Packer & Ruttan, 1988) and cooperative breeding (Emlen, 1982) as well as grooming to reduce parasites (Richard, 1995). However, living in groups can have costs like increased competition among members (Heinrich & Marzluff, 1991), the increased risk of spreading diseases and increased vulnerability to predators (Watson, 2018) as a group can be detected easier by predators than an individual on its own.

When animals live together we may see the evolution of complex social behaviors including increased levels of communication, cooperation and cheating (Curley et al., 2015). The social intelligence hypothesis (Humphrey, 1976) and the social brain hypothesis (Dunbar, 1998) predict that the evolution of cognitive intelligence and brain size, respectively, is driven by social complexity. Complexity can be reflected in the degree of fission-fusion dynamics (Amici et al., 2008), group size and types of relations (Dunbar, 1998). Therefore, individuals living in large groups that are structured by social relationships and engage in high levels of fission-fusion dynamics are expected to have large relative brain sizes and perform well in cognitive tasks. Such a correlation could be found in primates (Dunbar, 1992), while generally in mammals and birds, brain size correlates with long-term relationships. Fission-fusion societies have been defined as ‘stable social units in which individual group members are often found alone or in small subgroups’ (Smith et al., 2008). Size and composition of such subgroups can change frequently over time. High levels of fission-fusion dynamics are associated with higher behavioral flexibility (Amici et al., 2008).

## **1.2. Importance of quality of social relationships**

Social relationships are defined as ‘the frequency, quality, and patterning of diverse interactions among the same individuals over time’ (Hinde, 1979). Social interactions between individuals depend not only on individuals’ specific characteristics (e.g. age and sex) but also on the past interactions between those individuals (Cords & Aureli, 2000). Group members frequently interact with each other in multiple social contexts that range from affiliative interactions to aggressive interactions (Atton et al., 2012; Croft et al., 2008; Boogert et al., 2008; Lusseau, 2003). Affiliative relationships can consist of kinship (between relatives), partnership (between individuals that engage in reproduction) and “friendships” (affiliates that are non-kin and non-mates). Affiliative interactions (e.g. grooming each other and sharing food) are considered reliable indicators of strong social bonds in various taxa (von Bayern et al., 2007; Emery et al., 2007; Mitani & Watts, 2001, Silk et al., 2006).

Evolutionary thinking about social behavior was revolutionized by Hamilton’s kin selection theory (1964), which says that individuals contribute genetically to future generations in two ways. Individuals can enhance one’s own inclusive fitness by either begetting their own offspring (direct effect) or by helping to ensure the survival of relatives’ offspring (indirect effect). Kinship is thus predicted to influence the types of behaviors exhibited within families (Emlen, 1995).

The majority of mammals and birds provide a cost-intensive parental care to ensure the survival of their offspring. Parental care has been defined as ‘any parental trait that enhances the fitness of the offspring, and that is likely to have originated and/or to be currently maintained for this function’ (Smiseth et al., 2012). Parents do not only supply their offspring with essential nutrition, they also protect them from predators and other environmental threats (Royle et al., 2012). However, parenting even goes beyond the point of ensuring the vast survival of the offspring. Parental effects can involve social facilitation of learning and imprinting processes (Carere & Maestripieri, 2013). While the family lives together, various affiliative, agonistic and neutral interactions shape the development of the offspring. These interactions, which are known to have a substantial impact on the development of offspring

and on its future behavior, can differ between families and are defined as different parenting styles (Darling, 1999).

The option of choosing which individual they want to observe and learn from is crucial for naïve individuals for drawing conclusions about group transmission (Thornton & Malapert, 2009; Bugnyar & Heinrich, 2005). This is also influenced by the social connections between conspecifics. Attending to others' behavior can play a significant role in transmission if observation influences future behavior (Coussi-Korbel & Frigaszy, 1995). For instance, ravens use information from their kin when they are in groups of same-aged conspecifics (Schwab et al., 2008), chimpanzees acquire information by observing older and/or dominant group members (Horner et al., 2010; Kendal et al., 2015) and domestic fowl use information from dominant conspecifics (Nicol & Pope, 1994).

The quality of social relationships is known to be essential in the social organization of several species (Silk, 2007; Connor, 2007; Emery et al., 2007; Holekamp et al., 2007). However, until now, most research on social relationships has focused on primates. The existence of three dimensions of relationship quality has been proposed by Cords and Aureli (2000) and only been demonstrated in chimpanzees (*Pan troglodytes*) (Fraser et al., 2008) so far. The first dimension, the value of a relationship, describes the direct benefits received as a result of the relationship, like food sharing or support in agonistic encounters. The second one, the relationship compatibility, is a measure of the tolerance level between individuals. The third factor, the relationship security, refers to the predictability (or consistency) of interactions between partners. It is widely unknown, if relationships in other than primate species also involve the same or similar dimensions.

So far, Fraser and Bugnyar (2010) were the only one showing that these components of relationship quality may also be applicable to corvids, and in particular to ravens. Apart from sophisticated social skills during foraging, there is a growing body of evidence that ravens' social relationships are comparable to those reported from primates (Fraser & Bugnyar, 2010). Individual (Range et al., 2006) and social learning (Schwab et al., 2008), novel object exploration (Stöwe et al., 2006), attention (Scheid et al., 2007) as well as forms of cooperation (Fraser & Bugnyar, 2012; Asakawa-Haas et al., 2016) have been found to be influenced by kinship, sex combination and level of affiliation.

### **1.3. Exploration behavior**

Exploratory behavior can be defined as 'the gathering of information about objects or other aspects of the environment that does not satisfy immediate needs' (Mettke-Hofmann et al., 2002). While exploring, individuals search informations about profitable feeding sites, territory qualities, hiding places, escape routes, or potential mates (Barnett, 1958; Heinrich, 1995; Schwagmeyer, 1995). Exploration is likely to be affected by species ecology and social context (Miller et al., 2015). In parrots, explorative behavior varied depending on the different ecological conditions of each species (Mettke-Hofmann et al., 2002).

Explorative behavior is thought to be crucial at particular developmental stages, like in juveniles or young adults. Similar to several other species, callitrichid monkeys demonstrated age differences regarding exploration behavior. According to Kendal and colleagues (2005), callitrichid monkeys predominantly show high levels of object exploration (like play) in the subadult and early adult stage after sexual maturation. In young birds, object exploration seems to occur mainly when becoming independent and need to find all food by themselves (Pellis, 1981). At the juvenile stage, it is crucial to familiarize with the local food spectrum in order to figure out what kind of items are edible and which are inedible (Heinrich, 1995).

Novel stimuli can either be responded with curiosity, or with hesistance, which is also called neophobia (Miller et al., 2015). These two behavioral responses have been found to exist in several species and are likely to enable animals a safe way to explore their environment (Greenberg and Mettke-Hofmann, 2001). The ratio of explorative and hestistant behavior is influenced by the cost-benefits of the specific context. Animals living in an environment with high numbers of predators may be more neophobic and less explorative than individuals living in more varying surroundings where they need to gain information about potential new resources (Greenberg & Mettke-Hofmann, 2001).

#### **1.4. Food sharing & caching**

Food sharing, defined here as 'joint use of a monopolizable food source' (Stevens & Stephens, 2002) can be active, when the owner of the food piece is offering the food to another individual, or passive, when the owner is simply tolerating another individual that approaches and feeds on the same food piece. In both ways, food sharing seems to be an example for altruistic behavior, as at the moment of sharing, the donating individual has a fitness cost, while the other individual receives a fitness benefit. However, reciprocal altruism (Trivers, 1971) or kin selection (Hamilton, 1964) may work as mechanisms to provide indirect or delayed benefits to the sharer (de Waal, 1989; Mitani & Watts, 2001). Reciprocal altruism means that the benefit is compensated for in the future, which is why such a sharing event may be seen as altruistic only in the short term but selfish in the long term. In social life, food sharing can both lead to and result from friendship (Krebs, 1970; Sahlins, 1972) and high relationship quality (Fraser, Schino & Aureli, 2008).

Social life may increase individuals' foraging efficiency by enabling them access to others' knowledge (e.g. social learning) or resources (kleptoparasitism, scrounging; review in Giraldeau & Caraco, 2000; Laland, 2004). Caching of food may counterbalance its ephemeral occurrence or variable availability (Vander Wall, 1990). Animals that are known to cache food may use a variety of protective measures to minimize the probability of food raiders (for a review see Vander Wall & Smith, 1987). Food-caching birds like corvids or parids carry their resources to areas where potential scavengers are rare and cache it there (Vander Wall, 1990). Previous studies have shown that these birds have the potential to remember the exact locations of multiple caches (e.g. Vander Wall, 1982; Balda et al., 1987; Healy & Krebs, 1992; Clayton & Krebs, 1994). The chance for stealing food could increase if they could learn through observation and remember conspecifics' cache locations (Hampton & Sherry, 1994). Whether or not individuals can remember conspecifics' caches may define which scavenging tactic they will use. Animals with observational spatial memory (Bednekoff & Balda, 1996a, b; Clayton et al., 2001) can wait until the cacher has left the cache site to engage in delayed raiding. In species without observational spatial memory (Bednekoff & Balda, 1996a), the possible time span for efficient raiding is determined by the presence of cachers (e.g. Waite, 1992).

## 1.5. Ravens

Ravens, *Corvus corax*, are members of the corvid family that live in long-term monogamy with mates remaining together the whole year round (Fraser & Bugnyar, 2010). Specifically, large-brained birds like corvids tend to have a prolonged period of social maturation, spending extensive time with their parents and/or in non-breeder groups (Haffer, 1993; Ratcliff, 1997). Unfortunately, little is known about the development of social relationships during this time (Loretto et al., 2012). Ravens are known to have one of the longest periods of socio-cognitive development of any avian species. In captivity, they often reproduce successfully for their first time at the age of five, though, in the wild, it sometimes takes until the age of ten (T. Bugnyar, unpublished data).

Ravens are curious and highly explorative, although after about one-month post-fledging they react neophobic towards almost anything new (Heinrich, 1988a, 1995; Heinrich et al., 1995; Kijne & Kotrschal, 2002). Neophobia has been found to reduce explorative behavior and may limit learning, innovation as well as exploitation of novel food sources (Seferta et al., 2001; Greenberg, 2003; Kotrschal et al., 2001; Reader & Laland, 2003). At about 6 months of age, juveniles become independent from their parents and join non-breeder groups (Glutz von Blotzheim & Bauer, 1993; Ratcliffe, 1997). In that developmental period, young ravens could benefit from being neophilic in order to explore new surroundings and food sources and therefore figure out potential options (Sih & Giudice, 2012). After reaching the sub-adult stage, ravens are known to be established within a non-breeder flock, and thereby have access to food and roost within familiar surroundings (Ratcliff, 1997). At that stage, they do not need to explore new environments that frequently (Sih & Giudice, 2012). Living in groups may enhance non-breeders' competitive advantage over rivals like territorial pairs (Marzluff & Heinrich, 1991).

As response to strong competition at feeding sites ravens may react with carrying off consecutive loads of food for caching. Also, they have been found to vary their caching behavior depending on the presence and knowledge of others (Lorenz, 1935; Heinrich & Pepper, 1998). Moreover, previous studies found that ravens hide food behind objects that might disable others' observation (Bugnyar & Kotrschal, 2002). They even take into account conspecifics' knowledge of cache sites when scrounging caches (Bugnyar & Heinrich, 2005).

To protect their food resources, they intensively chase off conspecifics that come near their caches or retrieve food pieces for later re-caching (Heinrich, 1999).

## **1.6. Hypotheses & Predictions**

The aim of my study was to investigate the influence of the early social environment (consisting of parents and siblings) on the development of young ravens' affiliative and exploration-like object handling behavior. This is one aspect that has barely been investigated in ravens, especially with parent-raised birds. Therefore, I used a combination of observational and experimental approaches: the social observation, the object play experiment and the food monopolization experiment. The social observation was used to examine the daily life social interactions within a raven family. The two experiments were designed to stimulate the ravens' exploration and food manipulation behavior and thereby tests their social skills in a playful and competitive setting, respectively.

My first main hypothesis was that the higher the frequency of affiliative interactions is among parents, the higher is also the frequency of affiliative interactions among juveniles. As ravens are renowned for paying attention to others (Bugnyar & Heinrich, 2005) and learning from each other (Schwab et al., 2008; Fritz & Kotrschal, 1999), I predicted that they would develop similar levels of affiliation by experiencing their parents' behavior. As high levels of affiliation have been found to influence social learning (Schwab et al., 2008), I assumed that if parents show high levels of affiliative behavior in that period, the juveniles should try to follow the behavioral pattern of their parents. Additionally, I predicted that affiliative interactions among juveniles would decrease over time, because the older they get the more competitive they should become. This is supported by previous studies which found that the number of both caching events and pilfering attempts increased during the first six months post-fledging with food whereas it remained unchanged with objects. Starting with the second month post-fledging, storers consistently protected their caches against pilfering either by aggressive defence or by interrupting their caching and recovering their item (Bugnyar et al., 2007).

My second main hypothesis was that the higher the amount of affiliative interactions of adults with their offspring is, the more explorative the juveniles will become. Following attachment theory (Rees, 2007) in human children, I assumed that, also in ravens, juveniles tend to be more explorative when they feel like their parents are a kind of a safe haven in times of distress as well as a secure base from which they explore. Levels of affiliation have been shown to influence not only individual learning (Range et al., 2006), but also novel object exploration (Stöwe et al., 2006) in hand-raised ravens. Moreover, I hypothesized that the more explorative the adults were, the more exploration also juveniles should show because especially in the first weeks after fledging, juveniles need to learn a lot, likely through social observation from their parents. As object exploration was found to be most prominent during the period of becoming independent (Pellis, 1981), I assumed that the exploration behavior of juveniles would increase with time.

Additionally, I predicted that there were differences in adults' affiliative, agonistic and explorative behavior depending on whether juveniles were present or not. Therefore, I observed the parental behavior already before the juveniles left the nest, or whenever they were together with their offspring as family and also after the offspring has departed their parents.

### **Experimental settings**

The object play experiment was conducted to enhance the frequency and intensity of social interactions and exploration behavior. My prediction was that ravens would show more exploration behavior when having access to objects that are not available for the rest of the day.

Regarding the food monopolization experiment, I assessed differences in manipulation and monopolization of food as well as aggressive interactions depending on sex, age class (adult or juvenile) and condition. I predicted that the food manipulation behavior would be highest when the food is available freely and if it is in many pieces (scramble condition). Adult ravens should show high amount of affiliative behavior and low amount of aggressive behavior towards their partners, as those two aspects are thought to be a cue for a high valued



relationship. Also, I assumed that in the condition with two food pieces on two different places (2p condition) the subjects will show more aggressive interactions than in the scramble, but less than in the one-piece condition.

## 2. Methods

### 2.1. Subjects & housing

Study subjects were eight hand-raised adult common ravens (*Corvus Corax*) and their offspring situated at Haidlhof research facility near Bad Vöslau, Lower Austria. Each family (e.g., one breeding pair and the yearly offspring) was housed in a separate breeding aviary (10x8x5m) with visual barriers to the neighbor aviaries, making only acoustic interactions possible. All of the aviaries were enriched with several feeding places, one water bowl, one tree and several branches to climb and sit on, as well as some portable objects (e.g. plastic bottles, gloves, toilet brushes and toys). The ground of all aviaries was covered by small gravels and partially by soil and grass, allowing object and food caching.

All animals were fed twice on a daily basis and had ad libitum access to water. Adults were of different age and breeding experience, ranging from first to third brood as well as unrelated (see Table 1). The offspring was raised by their parents.

Table 1: Information about families and juveniles' developmental stages. Table shows age and sex (females\*) of parents as well as brood number, brood size and dates characterizing the developmental stages of offspring.

<i>Family</i>	<i>Astrid* &amp; Horst (AH)</i>	<i>Joey* &amp; Rocky (JR)</i>	<i>Martha* &amp; Arthus (MA)</i>	<i>Bobby* &amp; Laggie (BL)</i>
<i>Year of birth</i>	2010 & 2012	2010 & 2012	2014 & 2014	2014 & 2012
<i>Brood number</i>	3.	2.	1.	1.
<i>Brood size</i>	5	1	4	2
<i>Hatching dates</i>	20.-23.3.17	3.4.17	8.-11.4.17	10.-11.4.17
<i>Fledging date</i>	5.5.17	16.5.17	24.5.17	24.5.17
<i>Date of offspring departure</i>	15.7.17	15.7.17	29.7.17	29.7.17

## **2.2. Procedure**

Data collection started in the end of April/middle of May, approximately two weeks before the assumed fledging date of each families' offspring, and ended at the end of July/beginning of August, about two weeks after the offspring departed their parents. Once the first juvenile left the nest and went on the ground, I stopped observing that family until 10 days after fledging (=day when all juveniles of one specific family were on the ground for the first time), as I wanted to give the offspring enough time to accustom to their surrounding during their first days outside the nest.

The data collection timespan was divided into three periods:

### **Post-hatching period**

observation of adults between hatching and fledging of offspring; characterized by juveniles becoming mobile, but still staying in and around the nest

### **Post-fledging period**

observation of the whole family (adults with juveniles) between fledging and departure of juveniles (period length: <10 weeks)

### **Post-family period**

observation of adults after the juveniles' departed their parents

Data were collected using behavioral observation lasting for 15 minutes per session independent of condition and period. All observations were conducted between the morning and afternoon feeding time, from 9 am to 4pm. Observations were recorded via oral protocol on a videotape, using the cameras provided at Haidlhof research facility, and later coded for different behavioral categories (see 2.4. Behavioral categories). Data collection was conducted by three Master students (S.H., T.F., V.B.).

Table 2: observation timeline of the different approaches (social, playground (PG) and food monopolization experiment (FM)) in the three periods: 1. Post hatching; 2. post-fledging; 3. post-family. Number of observations included in data analysis presented per family (Astrid & Horst (AH), Joey & Rocky (JR), Martha & Arthus (MA), Bobby & Laggie (BL)) and condition for each period.

<i>Period</i>	<i>Post-hatching</i>	<i>Post-fledging</i>	<i>Post-family</i>
<i>Condition</i>	Social	Total (Social/ PG/ FM)	Total (Social/ PG/ FM)
<i>AH</i>	10	62 (27/27/8)	6 (2/ 2/ 2)
<i>JR</i>	9	57 (24/24/9)	8 (3/ 3/ 2)
<i>MA</i>	11	56 (24/24/8)	6 (2/ 2/ 2)
<i>BL</i>	10	60 (25/25/10)	6 (2/ 2/ 2)
<i>Observation period</i>	2 weeks before first fledging until first juvenile fledged	1 week after all juveniles of one family fledged until juveniles departed (10 weeks)	Next 2 weeks after juveniles' departure

In the post-hatching period (1.), I conducted between 9 and 11 social observations of adults per family (see Table 2) using a combination of behavioral sampling and one-zero sampling, resulting in a total observation time of 600 minutes (10 hours) in the post-hatching period.

In the post-fledging period (2.), I observed the families (adults with their offspring) in social observation, and, directly afterwards, I introduced an experiment (playground experiment; see 2.3. Approaches). From that moment on the procedure was always the following: at first social observation, then playground experiment. For both types of observational approaches I used a combination of behavioral sampling and one-zero sampling. In July, when the juveniles were approximately 6-8 weeks old (post-fledging), I added a second experiment (food monopolization experiment; see 2.3. Observational approaches). In this experiment, I coded the food manipulation behavior with instantaneous scan sampling and the social interactions of individuals with continuous behavioral sampling. This procedure led to a final number of 56 to 62 sessions per family (see Table 2) in post-fledging period, resulting in a total observation time of 3525 minutes (58,75 hours) for all families.

In the post-family period (3.), I continued to observe the parental behavior in all three conditions for another 2 to 3 sessions per family (Table 2). This led to a final observation time of 390 minutes (6,5 hours) in the post-family period for all families together.

## **2.3. Observational approaches**

### Social observations

The social observation was conducted without adding any objects or food into the aviaries, so that I could observe their basic (not actively influenced) social (inter-)actions per day and family. For that condition, I used one camera outside the aviary to have an overview of the whole aviary (see Picture 2).

### Experiment 1: Object play (Playground =PG)

Directly after the social observation, I observed the ravens' behavior in an experimental condition, the playground. The so-called playground setup (see Picture 1) was introduced in order to stimulate ravens' manipulation behavior. It consisted of four flexible tubes of different diameter, fixed on a wooden plate. Two of the tubes were positioned horizontally and two vertically. In addition, I provided eight transportable objects next to the playground. Object types were sticks, rings, balls and cubes and all of them were provided at a big/thick size and a small/thin one. The objects were either red, blue or yellow and were provided in a fixed color sequence for each family. The playground and the objects were always placed at the same position inside the aviary as well as one camera outside (see Picture 2). All of the adults had previous experience with the playground. In case objects were hidden by an individual in previous experiments and irretrievable, I replaced the object with corresponding object type from another color. I started recording (using the video camera) before introducing the playground in the aviary. Subjects were observed for 15 minutes, from the moment when the playground was in the aviary, and the experimenter out.



Picture 1: Playground setup with two vertical and two horizontal tubes and yellow transportable objects.

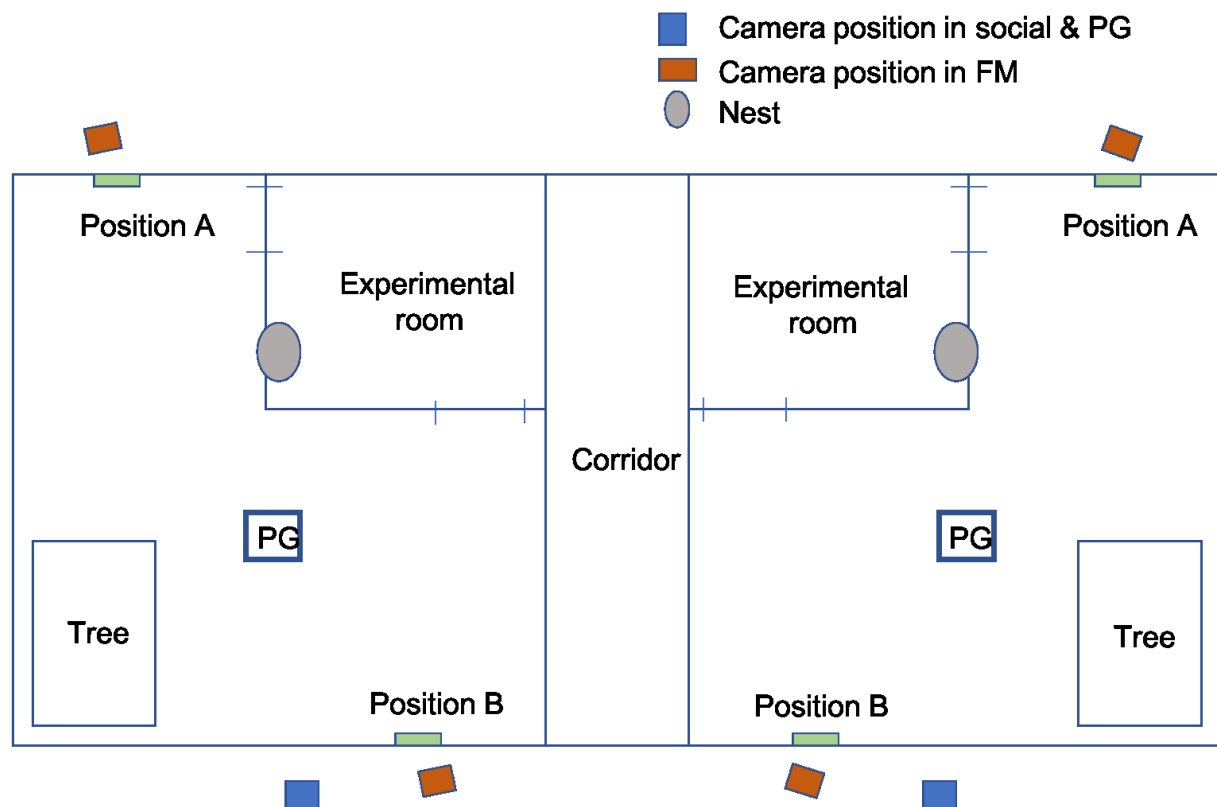
### Experiment 2: Food monopolization (FM)

Experiment 2 started in July, when the juveniles were about 1,5-2months old (post-fledging). This experiment was always conducted after midday before the evening feeding time (between 1 and 4 pm). During this experiment, food was delivered in the aviary in three different conditions: 1) 1 piece fixed at 1 place; 2) 2 pieces fixed at 2 places; 3) scramble condition, where the food was provided in multiple portable (unfixed) pieces at 1 place. Those conditions were conducted in a fixed sequence per family and were thought to stimulate the subjects' food manipulation behavior.

The stimulus I used was a piece of high quality food (chicken neck). The amount of food provided was calculated to be equal for each individual. In 1p condition the stimulus was delivered in 1 piece, in 2 pieces condition the same amount of food was cut in 2 pieces and in the scramble condition it was cut in twice as many pieces as individuals per family.

For the 1 piece and scramble condition I used one camera placed at either position A or position B (see Picture 2), directly in front of the food outside the aviary. For the 2 pieces condition, I used two cameras that were placed at both positions A and B, as the food was fixed on both positions.

The video camera was started before entering the aviary with the food. The observation time was 15 minutes per session, starting as soon as the food was fixed (for 1p and 2p condition) or placed on the ground (for scramble condition) on the corresponding position.



Picture 2: Sketch of two aviaries showing the position of the cameras, the playground (PG; experiment 1) and the food (experiment 2) that were used in the different approaches.

## 2.4. Behavioral categories

In all observations, I considered the following broad behavioral categories: affiliative interactions, agonistic interactions and explorative (inter-)actions. The composition of those behavioral categories is described below; a complete list of all observed behaviors and interactions is given in the appendix (see ethogram). For all behaviors mentioned, I considered the daily frequency of occurrence as means ( $\pm$  SD) per condition and age class (juvenile and adult) as well as the direction of the interactions (towards siblings or parents) and sex of initiator and receiver.

**Affiliative behavior**

Affiliative interactions were composed of the variables allo-preening (to pet/clean another individual for more than 5 seconds), touch (one bird has neutral physical contact with another individual (mostly with beak or wings) for maximum 2 seconds), touch-hold (one bird has neutral physical contact with another individual (mostly with beak or wings) for more than 2 seconds, without preening the receiver) and contact sitting (to sit/stand in another individual's range (individuals range determined by being able to reach the other with beak when looking into the other's direction)).

**Agonistic behavior**

The category of agonistic interactions included approach-retreat (to go out of another individual's way if it comes near oneself), forced-retreat (one individual comes near another and forces it to leave current position), threat (one individual threatens another without the receiver retreating), steal (one individual takes an object (or food) from another individual who is trying to defend it), steal try (one individual tries to steal food from another, but the receiver defends the object), and physical conflict (aggressive physical contact between at least two individuals). In addition to the agonistic variables mentioned above, I also included monopolization (an individual who is in the possession of a food piece is defending it towards others) and monopolization try (an individual tries to prevent others from getting access to a resource) for the food monopolization experiment.

**Explorative behavior**

The category of explorative (inter-)actions was composed of exploration-like object handling behaviors including object manipulation (physical interaction of one individual with an object), caching (an individual is hiding an object), unidirectional (one individual takes an object from another individual) and bidirectional (at least two individuals transfer an object between each other) transfer, co-action (two individuals manipulate non-transportable objects/the enclosure floor side by side) as well as co-manipulation (two individuals manipulate one (transportable) object together). Additionally, I considered the frequency of food manipulation behavior (one individual eats or manipulates food).

## 2.5. Statistical Analysis

Statistical analysis was carried out with the software R (version 1.0.153; R Development Core Team, 2008).

### **Adult behavior across periods and conditions**

First, I calculated a negative binomial generalized linear model (MASS package version 7.3-50; Venables & Ripley, 2002) to investigate whether adult affiliative, agonistic and explorative behavior differs across condition, period and observation day. As I calculated the behavioral categories as means ( $\pm$  SD) of the daily frequencies per condition, I was able to control for the effect of the condition within the trials of a day. The negative binomial model is used for over-dispersed count data, that are not normally distributed. For all three models (affiliative, agonistic and explorative) regarding parental behavior I added period, condition and day as fixed factors and family as random factor.

### **Effect of adult behavior on juveniles' affiliative behavior**

Second, I run a negative binomial model to analyze the effect of adult behavior and development (included as observation day) on juveniles' affiliative behavior using data from post-fledging period. As there was only one juvenile in JR family, I only used data from the families AH, BL and MA. Therefore, I included affiliative interactions among parents (AFF.AD), affiliative interactions from parents towards juveniles (AFF.AD.JUV), condition and observation day as fixed factors as well as family as random factor. The number of offspring was included by using the *offset* option in order to take into account the possible number of interactions partners per family.

### **Effect of adult behavior on juveniles' explorative behavior**

Third, I used the same procedure for analyzing the effect of adults' behavior and development on the exploration behavior of juveniles. For that, I included affiliative interactions among parents (AFF.AD), affiliative interactions from adults to juveniles (AFF.AD.JUV), exploration behavior (EXP.AD) and interactions (EXP.IA.AD) of adults as well as exploration interactions of adults with juveniles (EXP.IA.AD.JUV) besides condition and day as fixed factors. Again, family



was considered as random factor and the number of offspring was included using *offset* option.

### **Food experiment**

As I did use different coding methods and only had about 8-10 sessions per family for the food monopolization experiment, I did not include data from this experiment in the statistical analysis of the models. I checked for differences between age and sex depending on the conditions in the parameters food manipulation, food monopolization, initiated agonistic interactions and caching behavior. Behavioral differences according to sex were tested within age classes (adults and juveniles) and conditions using Mann-Whitney U tests. Differences across conditions were tested by using Friedman tests for each sex/age class. For visualizing results of the FM experiment, I summed up the frequency of different behaviors per individual and session to be able to compare the mean and standard deviation across sex and age classes.

## **2.6. Inter-observer reliability**

As three people were involved in analyzing the video protocols of the social observations and playground experiment, we assessed interrater reliability using two-way mixed, consistency, average-measures intraclass-correlation coefficients (ICC, Landers, 2015) for three observations in the AH (1 pre-fledging,) and MA (2 post-fledging) families. For count data, ICC can be highly biased by low counts or excessive zeros as in our data, which underestimates rater consistency. Nevertheless, ICC for high count variables showed high average consistency (contact sit: ICC = 0.73,  $p = 0.002$ ; manipulation: ICC = 0.96,  $p < 0.001$ ) and can be seen as a proxy for overall rater reliability.

### 3. Results

#### 3.1. Parental behavior

At first, I investigated if the parents differed in their behavior according to the period (post-hatching, post-fledging, post-family), the type of data collection (observational or experimental approach) and the observation day using a negative binomial generalized linear model (glm.nb). As expected, adults showed significantly higher exploration frequencies in the playground experiment than during social observation ( $z = 5.193$ ;  $p < 0.001$ ; Figure 1). However, their exploration did not differ according to period ( $z = 0.521$ ;  $p = 0.603$ ) or day ( $z = -1.343$ ;  $p = 0.179$ ). Adults' agonistic interactions decreased over time ( $z = -2.052$ ;  $p = 0.040$ ), but did not change between periods ( $z = -1.662$ ;  $p = 0.097$ ) or approaches ( $z = 0.986$ ;  $p = 0.324$ ). Adults' affiliative interactions did not differ, neither regarding the period ( $z = -0.337$ ;  $p = 0.736$ ), the approach ( $z = 0.434$ ;  $p = 0.666$ ) nor the observation day ( $z = 0.534$ ;  $p = 0.593$ ).

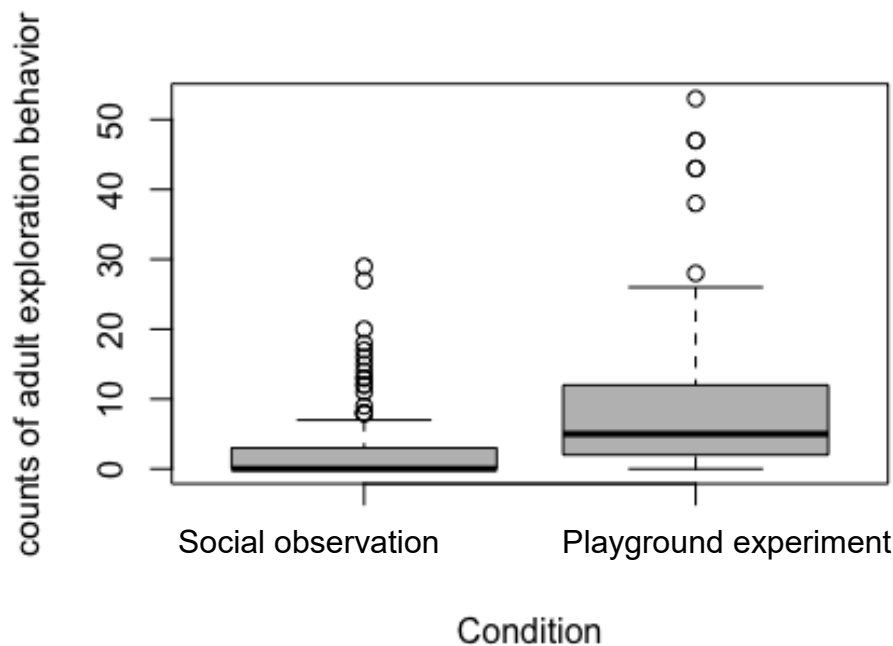


Figure 1: The effect of offering a playground (experimental approach as compared to daily observations) on the frequency of adult exploration behavior.

### **3.2. Effect of parental behavior on juveniles' behavior**

In a next step, I examined if adult affiliative behavior influenced juveniles' affiliative and explorative behavior. I again used negative binomial generalized linear models and included approach and observation day in the models.

Adults' affiliative interactions did positively influence affiliative interactions among juveniles when considering the entire observation period and all families together ( $z = 2.045$ ;  $p = 0.041$ ; Figure 2). However, when considering the influence for each family separately (Figure 3), the same effect did only occur in two of three families (AH & BL).

Interestingly, affiliative interactions of adults towards their juveniles did not have an effect on the affiliative interactions among juveniles ( $z = 0.644$ ;  $p = 0.520$ ), but influenced the explorative behavior of juveniles ( $z = -4.273$ ;  $p < 0.001$ ). The less affiliative interactions parents had with their offspring, the more explorative their juveniles were (Figure 4).

The explorative behavior of adults did not affect juveniles' explorative behavior ( $z = -0.196$ ;  $p = 0.845$ ). Neither the explorative interactions among adults ( $z = -0.196$ ;  $p = 0.845$ ) nor explorative interactions of adults with their offspring ( $z = 1.317$ ;  $p = 0.188$ ) had an influence on the offspring's explorative behavior. Also, the type of approach (observational or experimental) did not affect juveniles' affiliative interactions ( $z = -1.425$ ;  $p = 0.154$ ) nor their explorative behavior ( $z = 1.862$ ;  $p = 0.063$ ).

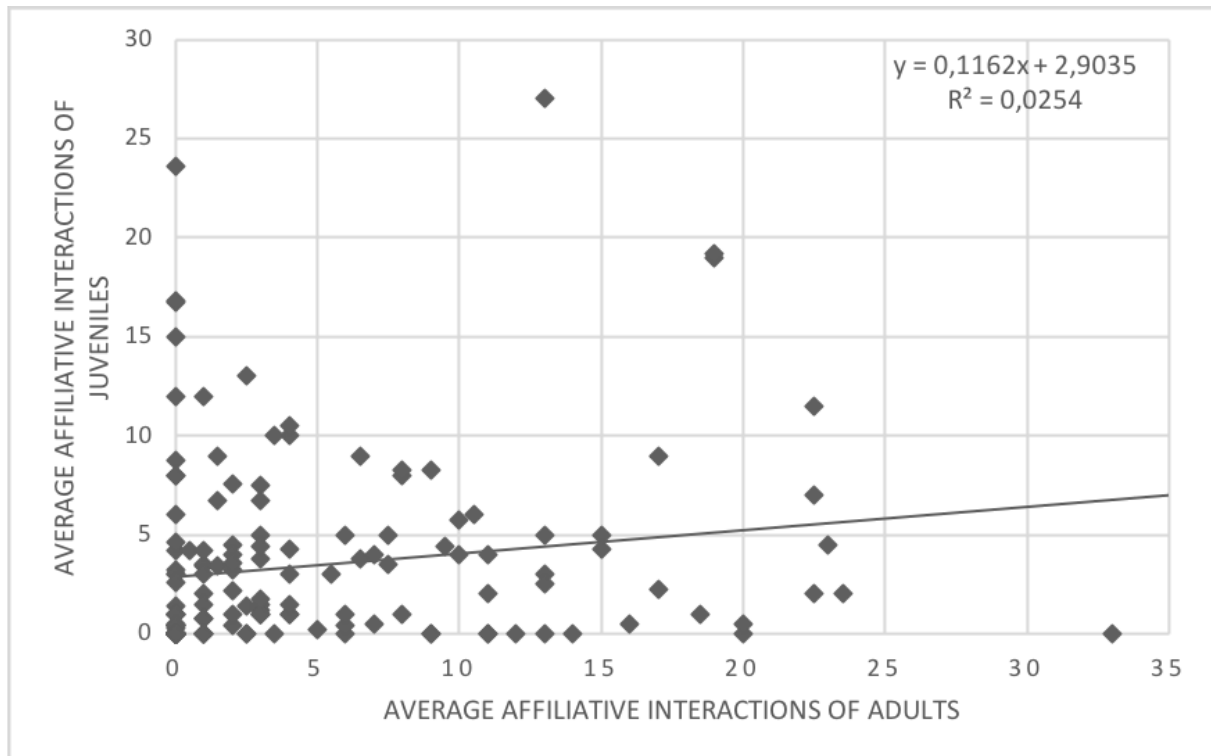


Figure 2: The effect of adult affiliative interactions on affiliative interactions among juveniles, both per individual. One dot represents the correlation of the level of affiliation among adults and among juveniles in one observation. Regression line representing the general correlation across all three families (AH, MA, BL). Formula showing the factor of the regression.  $R^2$  representing the coefficient of determination.

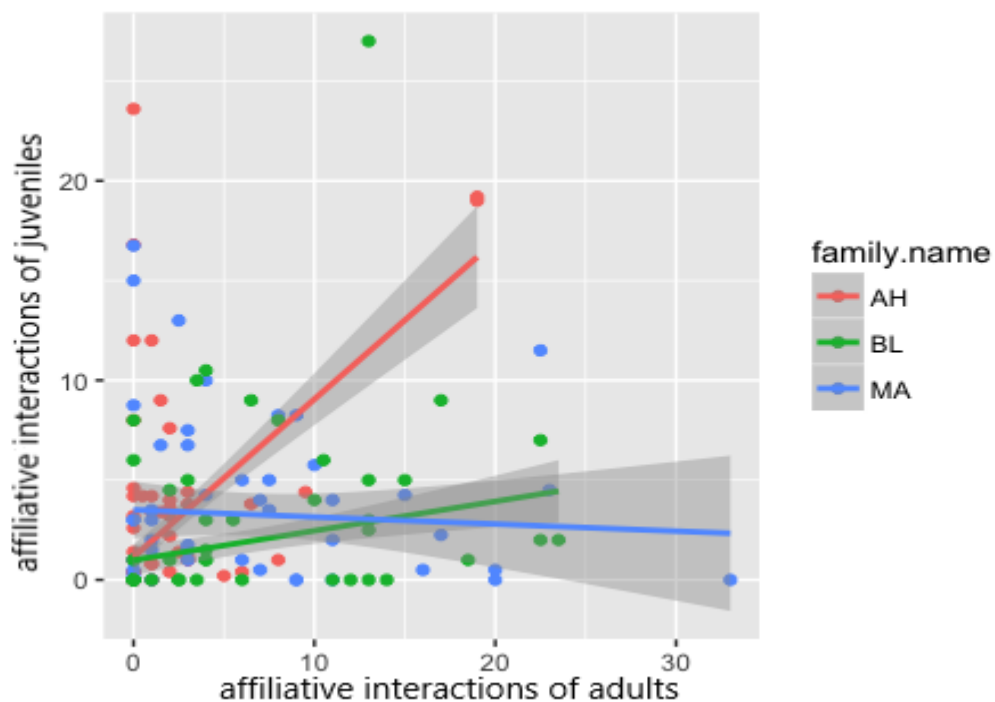


Figure 3: The effect of adults' affiliative interactions on affiliative interactions among juveniles (the same as in Figure 2), showing regression lines for each family separately. Family AH (Astrid & Horst) in red, BL (Bobby & Laggie) in green and MA (Martha & Arthus) in blue.

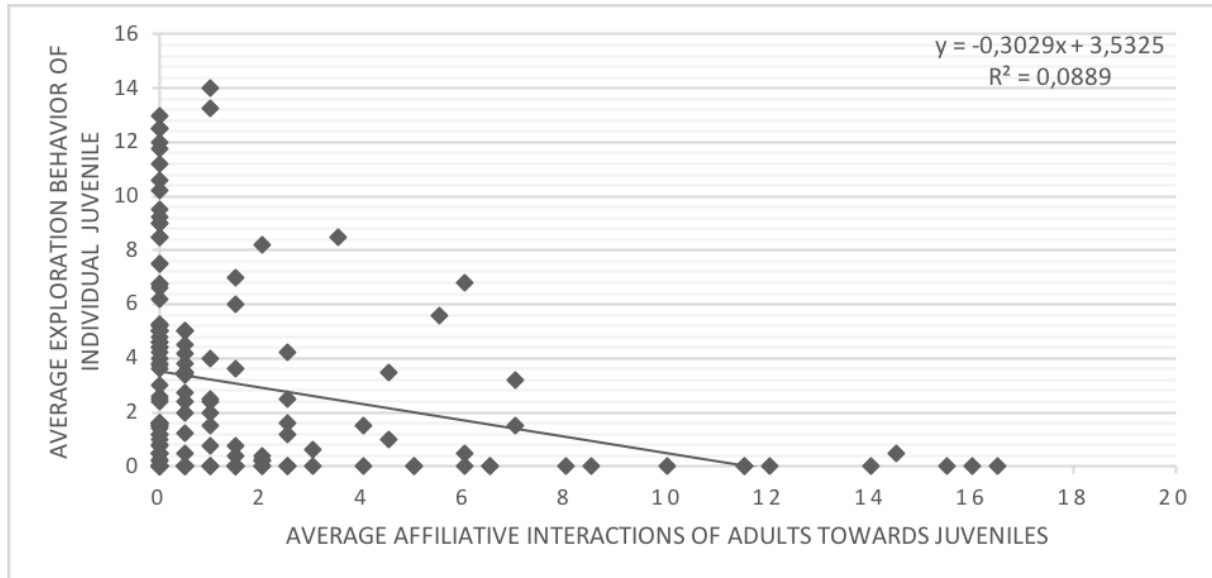


Figure 4: The effect of the average affiliative interactions of adults towards juveniles on the average exploration behavior of juveniles. Formula showing the factor of the regression.  $R^2$  representing the coefficient of determination.

### 3.3. Effect of development on juveniles' behavior

The effect of development on juveniles' behavior was measured by including the parameter 'observation day' in the statistical analysis. While the observation day did not affect parental affiliative interactions ( $z = 0.534$ ;  $p = 0.593$ ), juveniles' affiliative interactions decreased significantly over time (Figure 5). The older the young became, the less affiliative interactions they showed with their siblings ( $z = -4.637$ ;  $p < 0.001$ ). In contrast, the age of the young positively correlated with their exploration behavior, meaning the older they became the more explorative behavior they showed (Figure 6;  $z = 15.465$ ;  $p < 0.001$ ).

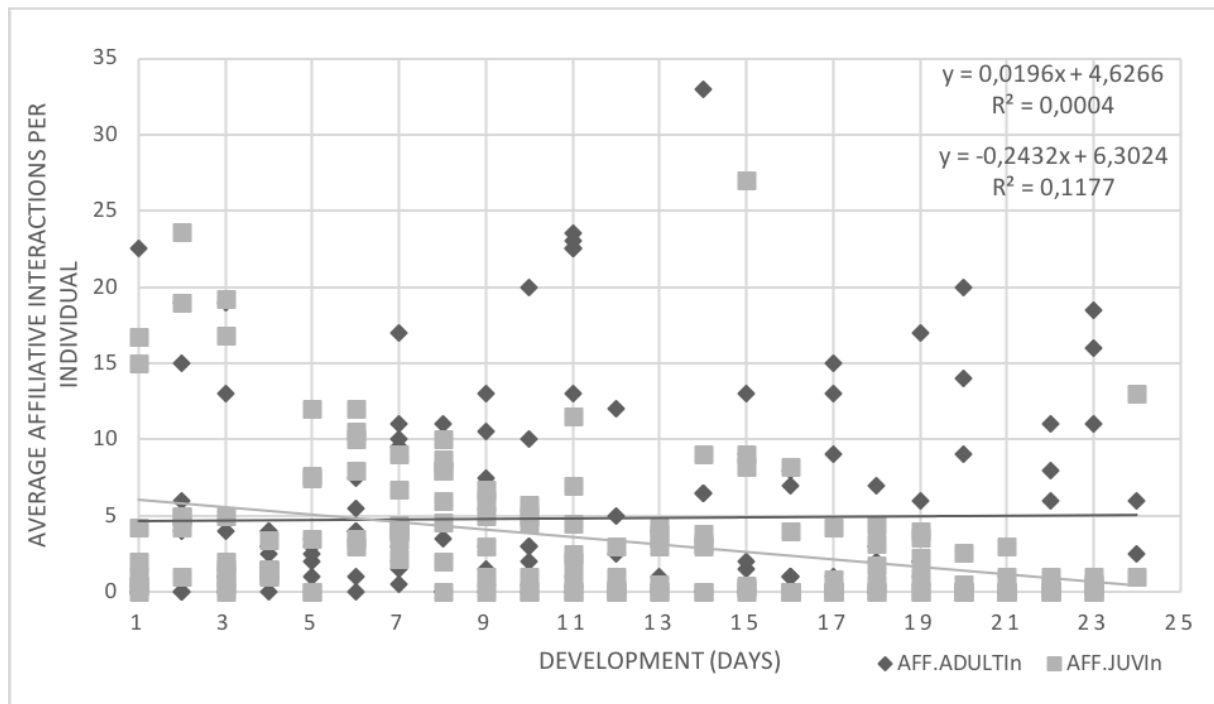


Figure 5: The effect of observation day (representing development of juveniles) on the average affiliative interactions among adults (dark grey diamonds) and among juveniles (bright grey squares). Formulas showing the factors of the regressions (adults regression in first line, juveniles beneath).  $R^2$  representing the coefficients of determination.

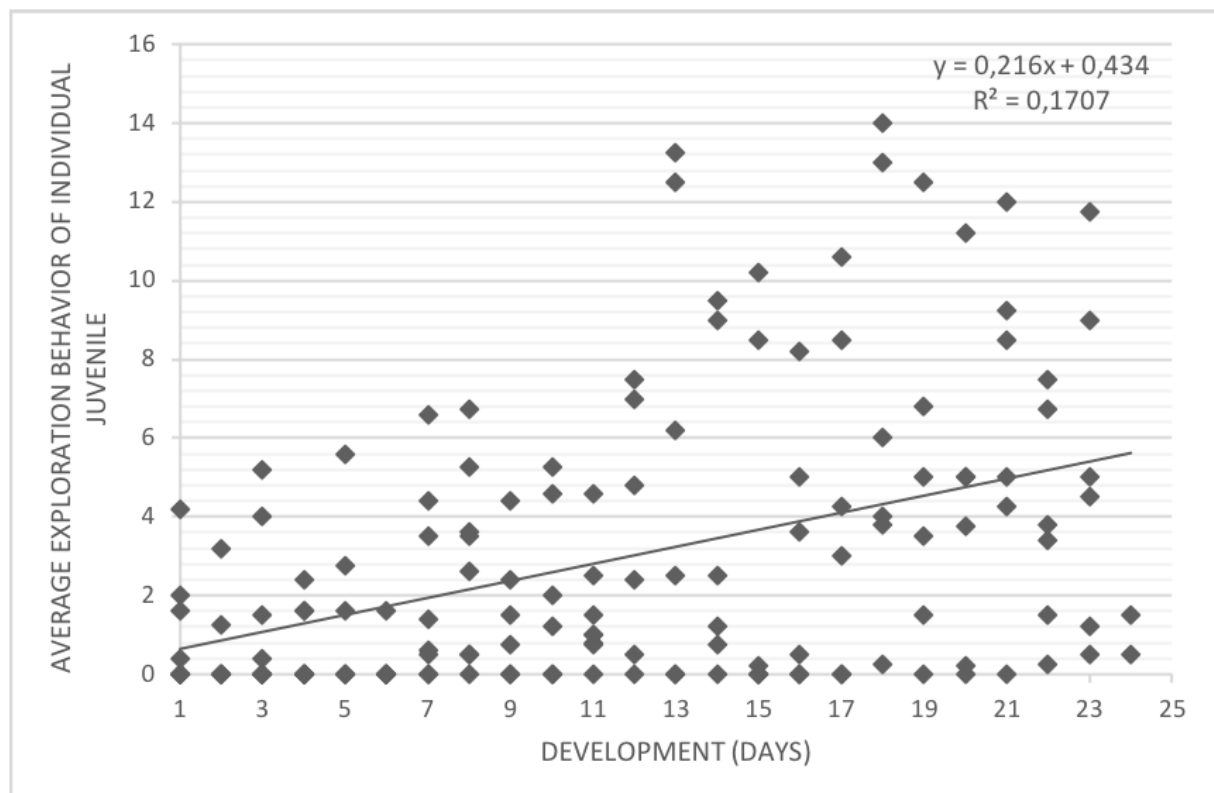


Figure 6: The effect of the development of juveniles (represented by the observation day) on the average exploration behavior of juveniles per individual. Formula showing the factor of the regression.  $R^2$  representing the coefficient of determination.

### 3.4. Food monopolization experiment

#### Food manipulation behavior

When considering the whole food monopolization experiment, the food manipulation frequencies did not differ between males and females, neither among adults ( $p= 0.886$ ;  $U=9$ ), nor among juveniles ( $p= 0.268$ ;  $U= 10$ ).

When considering the different food monopolization (FM) conditions separately, female juveniles manipulated food in the one-piece ( $p= 0.009$ ;  $U= 1$ ) and two-piece ( $p= 0.030$ ;  $U= 4$ ) condition less than male juveniles, whereas both sexes showed similar frequencies in the scramble condition ( $p= 1.000$ ;  $U= 18$ ; Figure 7). Among adults, sex differences in food manipulation could not be found within FM conditions, neither in the one-piece ( $p= 0.381$ ;  $U= 4.5$ ), two-pieces ( $p= 0.686$ ;  $U= 6$ ) nor the scramble condition ( $p= 0.562$ ;  $U= 10.5$ ; Figure 7). Moreover, sex differences across conditions could not be detected, neither in adults (females:  $p= 0.539$ ;  $F= 2.2$ ; males:  $p= 0.281$ ;  $F= 3.8$ ) nor in juveniles (females:  $p= 0.611$ ;  $F= 4.5$ ; males:  $p= 0.663$ ;  $F= 2.4$ ).

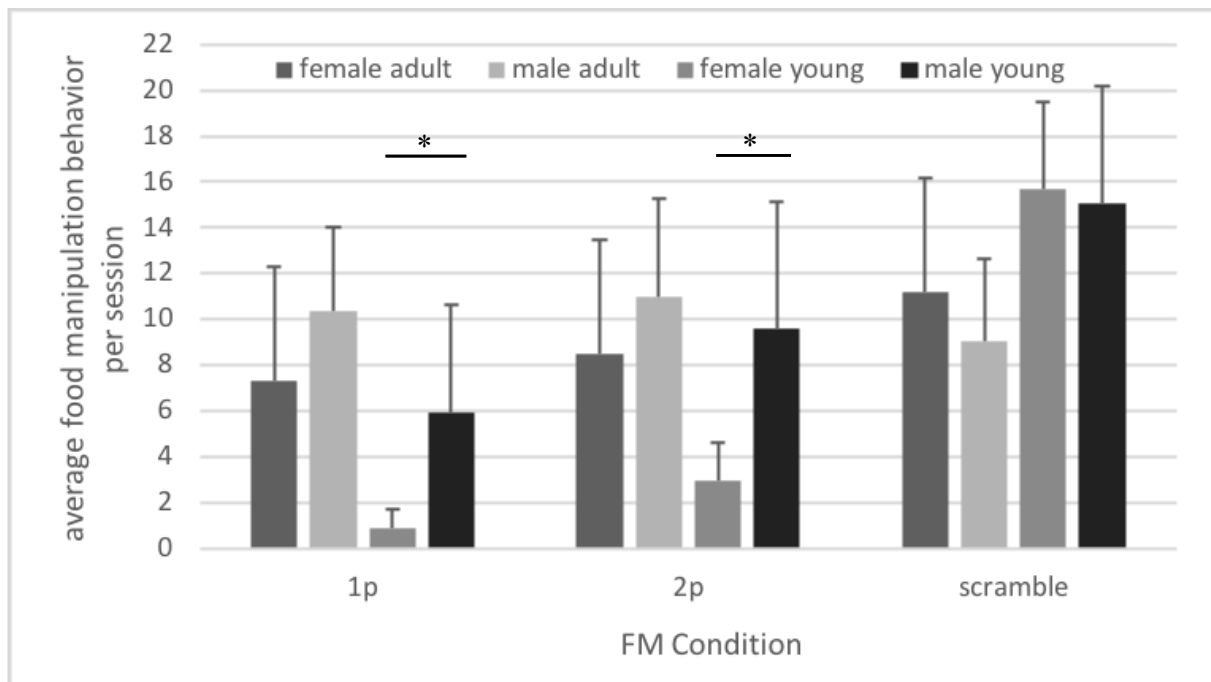


Figure 7: Sex and age differences of the food manipulation behavior (means + SD) per individual and session according to the different FM (food monopolization) conditions (1p = food available in one fixed piece; 2p = food available in two fixed pieces; scramble = food freely available in twice as many

pieces as birds). Female adults in dark grey, male adults in bright grey, female young in middle grey and male young in black bars.

### **Monopolization behavior**

Considering adults' monopolization behavior depending on the different food monopolization (FM) conditions, a clear pattern could be seen. Adults never monopolized in scramble condition, where the food pieces were freely available. Adults did not show sex differences in food monopolization within conditions (one-piece:  $p=0.661$ ;  $U=6$ ; two-pieces:  $p=0.882$ ;  $U=7$ ; scramble:  $p=NA$ ;  $U=8$ ), nor across conditions (females:  $p=0.514$ ;  $F=2.3$ ; males:  $p=0.148$ ;  $F=5.4$ ).

### **Agonistic interactions**

Adult males showed higher frequencies of initiated agonistic interactions than their female partners in the condition with one fixed food piece ( $p=0.029$ ;  $U=16$ ; Figure 8). This effect could neither be found in the condition with two fixed food pieces ( $p=0.309$ ;  $U=12$ ) nor in the scramble condition ( $p=0.874$ ;  $U=9$ ), where food was available freely (Figure 8). Differences in initiated agonistic interactions across conditions could neither be found in adult females ( $p=0.217$ ;  $F=4.5$ ), nor males ( $p=0.096$ ;  $F=6.3$ ). Females showed equally rare agonistic interactions over all three conditions (personal comment, S.H.). In juveniles, sex differences in their initiated agonistic interactions could not be found, neither within conditions (one-piece:  $p=0.370$ ;  $U=23.5$ ; two-pieces:  $p=0.806$ ;  $U=15.5$ ; scramble:  $p=0.367$ ;  $U=23.5$ ), nor across conditions (females:  $p=0.137$ ;  $F=9.7$ ; males:  $p=0.444$ ;  $F=3.7$ ).



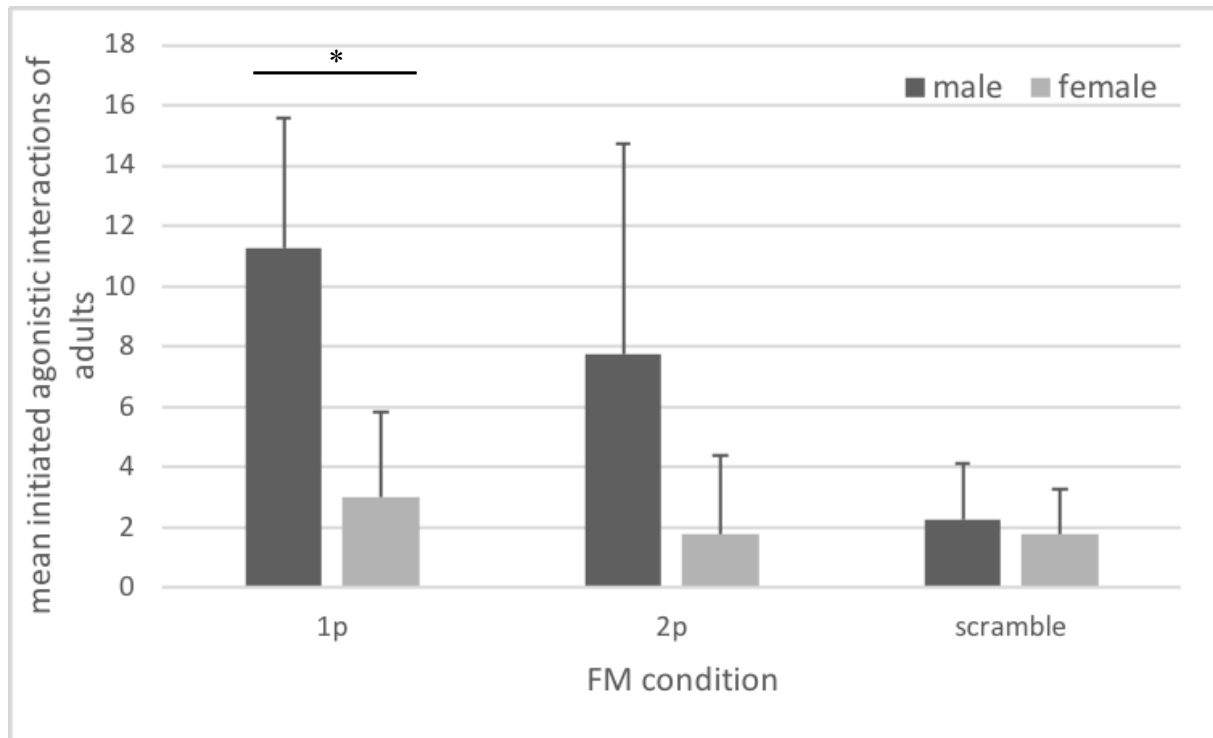


Figure 8: Sex and condition differences of initiated agonistic interactions of adults (means + SD). Males are presented in dark grey bars, females in bright grey bars. FM (food monopolization) conditions: 1p = food available in one fixed piece; 2p= food available in two fixed pieces; scramble = food freely available in twice as many pieces as birds.

### Caching behavior

In general, caching behavior was rather low in the FM (food monopolization) experiment. Among adults, sex differences within the three FM conditions could not be detected (one-piece:  $p=1.000$ ;  $U=8.5$ ; two-pieces:  $p=0.882$ ;  $U=7.0$ ; scramble:  $p=0.110$ ;  $U=2.0$ ). In juveniles, sex differences in caching behavior could be found in the one-piece condition, with males showing higher caching frequencies than their female siblings ( $p=0.036$ ;  $U=30.0$ ; Figure 9), but not in the conditions with two-pieces ( $p=0.507$ ;  $U=22.0$ ) and scrambled food ( $p=0.682$ ;  $U=14.5$ ). Considering caching behavior across FM conditions, neither adults (females:  $p=0.097$ ;  $F=6.3$ ; males:  $p=0.332$ ;  $F=6.9$ ) nor juveniles (females:  $p=0.332$ ;  $F=6.9$ ; males:  $p=0.611$ ;  $F=2.7$ ) showed significant sex differences.

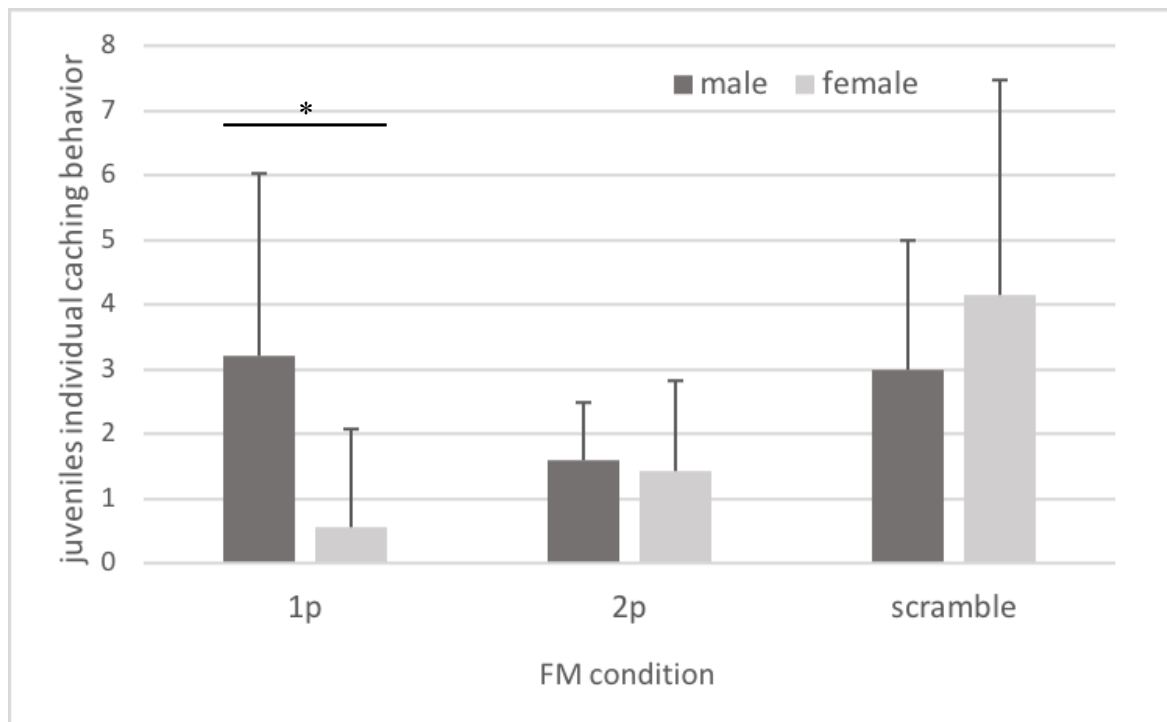


Figure 9: Juveniles caching behavior (as means + SD) in the three different conditions of FM experiment (1p, 2p, scramble). Males are visualized in dark grey, females in bright grey color.

## 4. Discussion

This study aimed to demonstrate the influence of the early social environment on the development of affiliative and explorative behavior in post-fledging ravens.

### 4.1. Effect of adult behavior on offspring

High affiliation among adults had a significant effect on the frequency of affiliation between juveniles in the post-fledging period. The more affiliative interactions adults had, the more affiliative interactions also juveniles showed, confirming my first main hypothesis. These results suggest behavioral or emotional contagion to be a possible underlying mechanism for similar levels of affiliation in juveniles and their parents. Behavioral contagion occurs when an unlearned species-typical behavior arises in an individual which has observed another individual demonstrating the same behavior before (e.g., Zentall, 2001; Osvath & Sima, 2014).

Emotional contagion – the alignment of emotions between individuals through behavioral

synchronization – is proposed as a key, basic component of human social cognition and empathy` (Osvath & Sima, 2014). The requirement for emotional contagion is that the copied behavior leads to a similar emotional state in the observer and demonstrator (e.g., Hatfield et al., 2009). Moreover, ravens are known to be very attentive towards conspecifics (Bugnyar & Heinrich, 2005), which could be especially important to be acquired during early social development, where juveniles need to get to know their surroundings and learn how to interact with their conspecifics to be able to adapt to daily life challenges. Different levels of affiliation could lead to different intensities of paying attention, which could influence the likelihood of using information given by the demonstrator (Schwab et al., 2008). Previous experimental studies have revealed that the early social environment has the potential to influence the animals' behavior in socially challenging situations such as resource competition (Bastian et al., 2003; Arnold & Taborsky, 2010), mating success (White et al., 2010) or the efficiency of forming dominance hierarchies (Branchi et al., 2006, 2009).

Considering the effect of adults' affiliation on juveniles' affiliative interactions per each family separately, it seems as if there were specific characteristics that influence the status of parents as demonstrators. In the family of Martha and Arthus, juveniles showed higher affiliative interactions when the parents did not affiliate much. Considering that this family was the only one with both parents being born in 2014, while in all other families at least one of the parents was older, these findings open the question whether age (leading to life-time experience) and/or the personality of the parents are even more important for being a high-quality demonstrator than the fact of being a parent. For ravens, starting to breed with the age of three is quite early and probably would not have happened so successfully (with four healthy juveniles) in the wild. Wild ravens are often not reproducing successfully until their fifth year, and sometimes even delaying reproduction until the age of ten (Bugnyar, unpublished data).

To my surprise, the frequency of adults' affiliation towards their juveniles did not affect the affiliation between juveniles. It seemed as if the interactions of adults with their offspring were – in contrast to the affiliation among adults – not an important factor for the development of affiliation among juveniles. However, maybe there would have been a closer relation of those two factors if I had focused the analysis on individual basis instead of family basis. It could be the case that for some individuals of the family the affiliative interactions

with their parents are more crucial than for others, depending on the personality. Social rank, sex and age are thought to be characteristics of demonstrator and observer that can frequently influence the likelihood of social learning (Coussi-Korbel & Frigaszy, 1995). In order to find out which other characteristics could be important - or even crucial - for social learning, future studies should focus on individual personality differences during the early development. A previous study on the effect of social networks and information transmission in ravens (Kulahci et al., 2016) revealed that in juveniles, the strong social bonds between siblings may be crucial for information transmission. In support of that, Schwab and colleagues (2008) found that juveniles [when living in a group of kin and non-kin] maintained affiliate relations mainly with their siblings, indicating that kinship and levels of affiliation covary during the first half year of life.

However, adult's affiliative interactions towards their offspring had a significant effect on the explorative behavior of their juveniles. Against my hypothesis, the lower the frequency of adults' affiliation towards their offspring was, the more explorative the offspring behaved. That link could occur due to time constraint, as when parents groom their offspring less, the offspring has more time to explore the surrounding. However, the underlying mechanism could also be behavioral or emotional contagion among siblings. When a juvenile observes a sibling exploring the surrounding, it is likely that the juvenile starts to be explorative too due to contagion effect. In non-human animals, contagion usually applies to species-typical unlearned behaviors like feeding or fleeing (Zentall, 2001).

In contrast to my prediction, the explorative behavior of adults did not have any effect on the explorative behavior and interactions of juveniles. One could suggest that for ravens in the post-fledging period the level of affiliation with their parents plays a more crucial role than their exploration. This seems to be similar as in humans. The attachment theory suggests that the attachment figure, who cares for and shares most affiliative interactions with the infant, acts as a secure base for exploring the world (Bowlby, 1969). This theory also suggests that there is a critical period for developing an attachment relationship, which is thought to act as a prototype for all future social relationships. Apart from that, the level of exploration of

juveniles could be broadly influenced by contagion among siblings. That would indicate that the relationship with and behavior of their siblings is more important for the development of exploration behavior in juvenile ravens than the behavior of their parents. At that point, it would be very interesting to do further research on the same individuals in the future to find out if these patterns remain consistent over time. Future studies should also consider the effect of family size and differences in levels of affiliation among siblings, because these differences could influence the effect of contagion. In a previous study, siblings maintaining high levels of affiliation showed better and also more specific information transfer between each other than did non-siblings who hardly showed any socio-positive interactions. This might be due to more directed attention towards them and a higher motivation to copy their behaviors (Schwab et al., 2008).

#### **4.2. Effect of development of offspring**

The development of juveniles (measured in observation days) had a significant effect on the affiliation and exploration of the offspring. In accordance with my hypotheses, juveniles showed less affiliative interactions and more explorative behavior the older they became. One reason for the higher exploration rate could be that the older they get, the less they are fed by their parents. This is also supported by Pellis (1981) who found out that object exploration can occur predominantly during the period of becoming independent and seems to be related to the development of self-feedings. Typically, competition over restricted items such as food arise at the same time. Such a developmental step could be on the one hand the reason for the increase in exploration and on the other hand the decrease in affiliation among juveniles. As the exploration of juveniles seemed to increase over the whole observation period (2-4 months of age), it seems very likely that juveniles at first need some time to get practice in being agile before being able to explore their environment intensively. Previous studies found that at six months of age, ravens spent significantly more time near novel objects than at three months of age (Stöwe et al., 2006). Similar results in other species revealed that object exploration was predominant in subadults that had achieved puberty and young-adults that were sexually mature, as well as in younger individuals (e.g. in callitrichid monkeys; Kendal et al. 2005).

The development of the offspring did neither influence the affiliation nor the exploration of adults, but had an effect on the agonistic interactions among adults. Agonistic interactions among adults decreased over time, although they have been very rare over the whole observation period. On the one hand, the low levels of agonistic interactions among adults indicate good relationships between breeding partners. On the other hand, the decrease in agonistic interactions could be a cue for the stress reduction in adults when juveniles get older and become more independent. Affiliative interactions among adults were relatively consistent over time and context, indicating a high-quality relationship between breeding partners. Kummer (1978) proposed that social relationships are investments that maximize the long-term gain for both partners. Therefore, it is likely that individuals, who have interacted for a longer time, would display a more valuable and compatible relationship than those who have spent less time together. These results are underlined by many observations of agonistic support, food sharing and high tolerance of the breeding partners (Cords & Aureli, 2000; personal observation, S.H.).

#### **4.3. Effect of observational approach & period**

Despite not finding an effect of the observational approaches (social observation and object play) on the affiliative and explorative behavior of juveniles, adults showed significantly more exploration behavior when exposed to the playground than in the social observation. The fact that this difference could not be found among juveniles may indicate that they were still too young for responding selectively to specific object arrays at the time of data collection. Possibly, such a selectivity may arise later, after their departure from parents, when the juveniles need to care for themselves all alone. At the age of three and six months, juveniles were demonstrating an increase in the latency to approach novel objects, but also increased the manipulation frequency when a sibling was present (Stöwe et al., 2006). However, it could be the case that juveniles were, independent of the observational approach, always exploring their environment at quite a high level and therefore no such effect could be detected. This would indicate that for adult ravens, their surrounding is not that much worth of being

explored in the social approach because they are – in contrast to their offspring – already accustomed to all the different stimuli of their environment.

To my surprise, the period did neither influence the affiliative, agonistic nor the explorative interactions of adults. These results suggest that the relationships of breeding pairs were so stable across both, time and context, that they were not influenced by the presence or absence of offspring.

#### **4.4. Sex differences in food monopolization experiment**

Whereas in the one-piece and two-pieces condition, female juveniles manipulated less than males, their food manipulation behavior in the scramble condition was comparable to those of their male siblings. Additionally, male juveniles cached food more often in the one-piece condition than female peers. These results lead to the assumption that already in early developmental phases, males tend to be more dominant in competitive situations than females and therefore managed to manipulate and cache food more often. Male juveniles try to reach a high rank within non-breeder flocks in order to gain better access to restricted resources and to build social bonds without interventions from others (Fraser & Bugnyar, 2012; Massen et al., 2014). Female juveniles tend to experience more affiliative interactions and maybe therefore less competition with other group members (personal observation: Ersoy, 2017). Former studies found rates of food caching to increase during the first half-year period postfledging, whereas rates of object caching to remain constant (Bugnyar et al., 2007). Furthermore, in the same study, an increase in distance and decrease in visibility to others with food caches, but not with object caches was found. These findings support the idea that young ravens become experienced in caching. While protective behavior was only demonstrated with high quality food items, object caching by young ravens could be interpreted as play, as it differs in performance from serious (food) caching (Burghardt, 2005). In addition, playing at caching with objects may allow birds to practice motor skills (Clayton, 1992). Also, it could be that females are simply too shy to manipulate and cache besides others. However, the assumption that female juveniles are generally too shy seems not to be the true for all females as some of them seemed to manipulate more than same-aged males (personal comment, S.H.). In a previous study, fathers were more likely to feed heavy male

than light female offspring (Ersoy, 2017), which could also be an explanation for the sex differences here. Considering the one-piece condition, the highest levels of agonistic interactions were initiated from male adults, while juveniles' initiated agonistic interactions did not differ according to sex. This indicates that also within the family, male adults could be highest in hierarchy. A typical dominance hierarchy in birds demonstrates mated birds to be dominant over singles, males over females and older birds to be dominant over young ones (Gauthreaux, 1978; Lamprecht, 1986; Piper & Haven Wiley, 1989; Moore et al. 2003). In wild ravens, stable dominance relationships with unidirectional dyads were found within non-breeding groups (Braun & Bugnyar, 2012). However, one must be aware that a so-called hierarchy within families cannot be the same kind of hierarchy like within non-breeder flocks. Due to genetic relatedness, family dynamics can be supposed to differ from the dynamics of other types of social groupings (Emlen, 1995). These results supported my expectation that clumped food (one-piece and two-piece) would increase the level of conflict, as the animals would have to compete for the food resource. The same results could also be found in a previous study (Masterthesis: Sima, 2012) with young ravens in their first winter.

Food manipulation and monopolization frequencies were similar in male and female adults during the whole experiment. In the condition with food freely available, monopolization was not observed at all in adults. In addition, the same low levels of initiated agonistic interactions and caching behavior were found among male and female adults. It happened more than once that male adults supported females in agonistic interactions when juveniles tried to steal from their mothers (personal observation, S.H.). If female adults tried to, they almost always received access to the food if their partners were monopolizing, even in the one-piece condition. This supports my hypothesis and former studies that found food sharing and affiliation to be good cues for high valued relationships (Cords & Aureli, 2000). However, even if the sharing event is supposed to be of altruistic motivation, one has to be aware that the sharer may have delayed benefits through kin selection as well as reciprocal altruism (de Waal, 1989; Mitani & Watts, 2001; Perry and Rose, 1994). Within families, the factor of kinship, following Hamilton's theory of kin selection, and partnership should always be more important than the private access to any limited resource as the fitness and survival of one's own genes (and therefore also of their offspring) should always have priority.



During my observational period, juveniles seemed to be too young to show clear sex differences for all measured behaviors. In the future, somebody should analyze data on individual level to be able to include individual personality differences. This could have an outstanding effect on the understanding of underlying characteristics that form a link between adult and offspring behavior.

#### **4.5. Conclusion**

Taken together, this study revealed the first cues of early social environments' influence on the development of fledging ravens. To my knowledge, this is the first time that fledging ravens, raised by their own parents in captivity, have been subjects in experimental studies concerning their exploration and food manipulation behavior while still living within their family. Regarding their affiliative interactions, I could find cues that juveniles follow the behavioral pattern of their parents. The more affiliative interactions adults had, the more affiliative interactions could also be observed among juveniles. In addition, we found that the development of offspring had effects on their level of affiliation as well as exploration. The older they were, the less affiliative interactions could be observed among siblings, but the more explorative they were. Interestingly, the offspring's exploration behavior was negatively influenced by adults' affiliative interactions with their offspring, but not by adults' exploration behavior. This leads to the assumption that affiliation and probably contagion effect play a special role within the family-period. According to our findings of the food monopolization experiment, it can be suggested that male ravens are more assertive in competitive situations than their female peers, independent of age. Similar levels of food manipulation, monopolization and caching in adults seem to be a cue for high-valued relationships in breeding pairs. Further research must be done to clarify the underlying characteristics that seem to be crucial for parents' role as demonstrator.

## 5. Appendix

### 5.1. References

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## 5.2. Tables from Figures

Table 3: Table presenting the daily counts of each family per period and approach of affiliative interactions among adults (AFF.ADULT), exploration behavior of adults (EXP.ADULT) and agonistic interactions among adults (AGO.ADULT).

FAMILY	PERIOD	DAY	OBSERVATIONAL APPROACH	AFF.AD ULT	EXP.ADULT	AGO.ADULT
AH	1	1	natural	19	0	0
AH	1	1	natural	4	0	0
AH	1	2	natural	8	0	0
AH	1	3	natural	22	0	0
AH	1	4	natural	4	0	0
AH	1	4	natural	0	0	0
AH	1	5	natural	0	0	0
AH	1	5	natural	0	12	2
AH	1	6	natural	14	0	0
AH	1	6	natural	6	0	0
AH	2	7	natural	0	0	0
AH	2	7	natural	0	0	0
AH	2	8	natural	0	0	0
AH	2	9	natural	0	7	0
AH	2	9	natural	0	0	0
AH	2	10	natural	0	0	0
AH	2	10	natural	5	0	0
AH	2	11	natural	0	3	0
AH	2	12	natural	2	2	0
AH	2	13	natural	19	0	0
AH	2	13	natural	3	0	0
AH	2	14	natural	0	5	0
AH	2	15	natural	6	13	0
AH	2	16	natural	6	0	0
AH	2	17	natural	2	6	2
AH	2	18	natural	10	8	0
AH	2	19	natural	6	0	0
AH	2	20	natural	13	0	0
AH	2	21	natural	3	2	0
AH	2	22	natural	2	1	0
AH	2	23	natural	2	8	0
AH	2	24	natural	4	1	0
AH	2	25	natural	4	0	0
AH	2	26	natural	0	0	0
AH	2	27	natural	0	1	0
AH	2	28	natural	12	3	0

AH	2	29	natural	0	0	0
AH	3	30	natural	0	2	0
AH	3	31	natural	0	6	0
BL	1	1	natural	0	0	0
BL	1	1	natural	16	0	0
BL	1	2	natural	14	0	0
BL	1	3	natural	6	0	0
BL	1	4	natural	0	0	0
BL	1	4	natural	0	1	1
BL	1	5	natural	2	4	0
BL	1	5	natural	13	0	0
BL	1	6	natural	0	27	1
BL	1	6	natural	12	6	1
BL	2	7	natural	45	1	0
BL	2	8	natural	30	8	0
BL	2	9	natural	26	1	0
BL	2	10	natural	8	13	0
BL	2	11	natural	7	29	0
BL	2	12	natural	8	0	1
BL	2	13	natural	34	2	0
BL	2	14	natural	16	1	1
BL	2	14	natural	0	0	0
BL	2	15	natural	26	0	0
BL	2	16	natural	4	0	0
BL	2	17	natural	0	0	0
BL	2	17	natural	47	0	0
BL	2	18	natural	5	20	0
BL	2	19	natural	8	2	0
BL	2	20	natural	0	0	0
BL	2	21	natural	26	1	0
BL	2	22	natural	0	0	1
BL	2	23	natural	26	0	0
BL	2	24	natural	0	0	0
BL	2	25	natural	12	0	0
BL	2	26	natural	28	0	0
BL	2	27	natural	0	0	0
BL	2	28	natural	0	1	0
BL	2	29	natural	37	0	0
BL	3	30	natural	0	0	0
BL	3	31	natural	0	8	0
JR	1	1	natural	0	0	0
JR	1	2	natural	0	0	0

JR	1	2	natural	8	0	0
JR	1	3	natural	0	0	0
JR	1	3	natural	0	0	0
JR	1	4	natural	7	2	1
JR	1	5	natural	0	0	0
JR	1	5	natural	0	0	0
JR	1	6	natural	0	1	1
JR	2	7	natural	8	2	0
JR	2	7	natural	0	12	0
JR	2	8	natural	0	4	0
JR	2	9	natural	1	3	0
JR	2	10	natural	19	0	0
JR	2	10	natural	0	3	0
JR	2	11	natural	0	0	0
JR	2	12	natural	0	18	0
JR	2	13	natural	0	0	0
JR	2	14	natural	0	16	0
JR	2	15	natural	0	0	0
JR	2	16	natural	3	3	0
JR	2	17	natural	4	5	0
JR	2	18	natural	0	0	0
JR	2	19	natural	34	0	0
JR	2	20	natural	0	8	0
JR	2	21	natural	0	0	0
JR	2	22	natural	0	15	0
JR	2	23	natural	0	5	0
JR	2	24	natural	0	0	0
JR	2	25	natural	0	4	0
JR	2	26	natural	0	0	0
JR	2	27	natural	0	9	0
JR	3	28	natural	3	2	0
JR	3	29	natural	0	0	0
JR	3	30	natural	5	6	0
MA	1	1	natural	10	0	0
MA	1	1	natural	27	0	0
MA	1	2	natural	0	0	0
MA	1	3	natural	2	0	3
MA	1	3	natural	0	2	0
MA	1	4	natural	0	3	3
MA	1	5	natural	0	0	0
MA	1	5	natural	0	0	0
MA	1	6	natural	0	0	0

MA	1	6	natural	0	0	0
MA	1	7	natural	1	17	1
MA	2	8	natural	0	0	0
MA	2	9	natural	12	11	0
MA	2	10	natural	2	0	0
MA	2	11	natural	6	1	0
MA	2	12	natural	2	14	1
MA	2	13	natural	8	0	0
MA	2	14	natural	22	0	0
MA	2	15	natural	0	4	0
MA	2	16	natural	15	0	1
MA	2	17	natural	40	0	0
MA	2	18	natural	46	0	0
MA	2	19	natural	0	1	0
MA	2	20	natural	0	0	0
MA	2	21	natural	66	0	0
MA	2	22	natural	0	0	0
MA	2	23	natural	14	0	0
MA	2	24	natural	18	0	0
MA	2	25	natural	6	0	0
MA	2	26	natural	34	0	0
MA	2	27	natural	18	6	0
MA	2	28	natural	2	6	0
MA	2	29	natural	0	1	0
MA	2	30	natural	22	0	0
MA	2	31	natural	5	0	0
MA	3	32	natural	0	0	0
MA	3	33	natural	0	1	0
AH	2	7	PG	0	7	0
AH	2	7	PG	0	4	0
AH	2	8	PG	38	0	0
AH	2	9	PG	0	5	0
AH	2	9	PG	38	4	0
AH	2	10	PG	6	3	0
AH	2	10	PG	2	13	0
AH	2	11	PG	4	5	0
AH	2	12	PG	0	4	0
AH	2	13	PG	4	14	0
AH	2	13	PG	1	12	0
AH	2	14	PG	0	3	1
AH	2	15	PG	0	10	0
AH	2	16	PG	0	8	0

AH	2	17	PG	0	24	0
AH	2	18	PG	0	22	0
AH	2	19	PG	2	16	0
AH	2	20	PG	0	2	0
AH	2	21	PG	4	5	0
AH	2	22	PG	2	4	0
AH	2	23	PG	0	6	0
AH	2	24	PG	6	2	0
AH	2	25	PG	4	1	0
AH	2	26	PG	0	2	0
AH	2	27	PG	0	1	0
AH	2	28	PG	16	0	0
AH	2	29	PG	0	2	0
AH	3	30	PG	6	10	3
AH	3	31	PG	8	2	1
AH	3	32	PG	0	8	0
BL	2	7	PG	0	53	1
BL	2	8	PG	0	43	0
BL	2	9	PG	8	6	0
BL	2	10	PG	8	5	0
BL	2	11	PG	5	13	0
BL	2	12	PG	11	15	0
BL	2	13	PG	20	11	0
BL	2	14	PG	7	25	0
BL	2	14	PG	0	25	0
BL	2	15	PG	21	12	0
BL	2	16	PG	6	6	5
BL	2	17	PG	45	20	0
BL	2	17	PG	26	5	0
BL	2	18	PG	24	0	0
BL	2	19	PG	0	2	0
BL	2	20	PG	13	9	0
BL	2	21	PG	0	24	0
BL	2	22	PG	2	8	0
BL	2	23	PG	0	13	0
BL	2	24	PG	0	9	0
BL	2	25	PG	4	6	0
BL	2	26	PG	0	0	0
BL	2	27	PG	0	20	0
BL	2	28	PG	22	5	0
BL	2	29	PG	0	5	1
BL	3	30	PG	0	1	0

BL	3	31	PG	0	5	0
BL	3	31	PG	24	0	0
JR	2	7	PG	3	3	0
JR	2	7	PG	0	22	0
JR	2	8	PG	10	12	0
JR	2	9	PG	0	38	1
JR	2	10	PG	10	0	0
JR	2	10	PG	0	4	0
JR	2	11	PG	6	11	0
JR	2	12	PG	0	47	0
JR	2	13	PG	0	14	1
JR	2	14	PG	17	0	0
JR	2	15	PG	33	2	0
JR	2	16	PG	44	0	0
JR	2	17	PG	8	0	0
JR	2	18	PG	0	47	0
JR	2	19	PG	11	0	0
JR	2	20	PG	0	3	0
JR	2	21	PG	0	43	0
JR	2	22	PG	0	24	0
JR	2	23	PG	0	4	0
JR	2	24	PG	0	2	0
JR	2	25	PG	0	0	0
JR	2	26	PG	0	26	0
JR	2	27	PG	0	10	0
JR	3	28	PG	0	28	0
JR	3	29	PG	0	1	0
JR	3	30	PG	4	3	0
MA	2	8	PG	0	3	0
MA	2	9	PG	8	1	0
MA	2	10	PG	2	3	0
MA	2	11	PG	6	4	1
MA	2	12	PG	6	2	0
MA	2	13	PG	15	0	0
MA	2	14	PG	6	0	0
MA	2	15	PG	22	11	0
MA	2	16	PG	3	2	0
MA	2	17	PG	20	0	0
MA	2	18	PG	45	0	0
MA	2	19	PG	0	8	0
MA	2	20	PG	0	8	0
MA	2	21	PG	0	6	0

MA	2	22	PG	18	0	0
MA	2	23	PG	16	0	0
MA	2	24	PG	30	0	0
MA	2	25	PG	14	12	0
MA	2	26	PG	2	1	0
MA	2	27	PG	40	0	0
MA	2	28	PG	0	4	0
MA	2	29	PG	0	2	0
MA	2	30	PG	32	0	0
MA	2	31	PG	12	0	0
MA	3	32	PG	0	3	0
MA	3	33	PG	0	5	0

Table 4: Table presenting the daily counts per family and approach of affiliative interactions among adults per individual (AFF.ADIN), affiliative interactions among juveniles per individual (AFF.JUVIN), affiliative interactions of adults towards juveniles per individual (AFF.AD.JUVIN) and the exploration behavior of juveniles per individual (EXP.JUVIN).

FAMILY	DAY	AFF.ADIN	AFF.JUVIN	APPROACH	AFF.AD.JUVIN	EXP.JUVIN
AH	1	0	4,2	natural	2	0,4
AH	1	0	0,4	natural	0,5	2
MA	1	0	15	natural	6	0
BL	1	22,5	2	natural	1,5	0
AH	1	0	1	PG	0	1,6
AH	1	0	0,4	PG	0,5	4,2
MA	1	0	16,75	PG	0	0
BL	1	0	0	PG	0	0
AH	2	0	23,6	natural	1,5	0
MA	2	6	5	natural	0,5	0
BL	2	15	5	natural	3	0
AH	2	19	19	PG	7	3,2
MA	2	4	4,25	PG	0,5	1,25
BL	2	0	1	PG	0	0
AH	3	0	0,4	natural	0	4
AH	3	0	16,8	natural	1,5	0
MA	3	1	2	natural	0	0
BL	3	13	5	natural	2	0
AH	3	0	0	PG	0	5,2
AH	3	19	19,2	PG	1,5	0,4
MA	3	1	1,5	PG	1	1,5
BL	3	4	1	PG	2,5	0
AH	4	0	1,4	natural	2,5	1,6
AH	4	2,5	1,4	natural	0	1,6



MA	4	3	1,5	natural	2,5	0
BL	4	4	1	natural	0	0
AH	4	3	1,2	PG	0	0
AH	4	1	3,4	PG	1	2,4
MA	4	3	1	PG	0,5	0
BL	4	4	1,5	PG	2,5	0
AH	5	0	12	natural	5,5	5,6
MA	5	1	3,5	natural	0,5	2,75
BL	5	3,5	0	natural	0	0
AH	5	2	7,6	PG	0	1,6
MA	5	3	7,5	PG	1,5	0
BL	5	2,5	0	PG	0	0
AH	6	1	12	natural	0	0
MA	6	4	10	natural	0,5	0
BL	6	4	10,5	natural	2	0
AH	6	0	8	PG	0	1,6
MA	6	7,5	3,5	PG	4	0
BL	6	5,5	3	PG	0,5	0
AH	7	9,5	4,4	natural	3	0,6
AH	7	1,5	3,4	natural	0	1,4
MA	7	11	4	natural	0,5	3,5
BL	7	17	9	natural	6,5	0
AH	7	2	2,2	PG	0	6,6
AH	7	0,5	4,2	PG	0	4,4
MA	7	3	6,75	PG	0	0,5
BL	7	10	4	PG	5	0
AH	8	0	0	natural	0	2,6
MA	8	0	8,75	natural	0	5,25
BL	8	8	8	natural	1,5	0
BL	8	0	6	natural	14,5	0,5
AH	8	0	4,6	PG	1,5	3,6
MA	8	11	2	PG	0	6,75
BL	8	3,5	10	PG	6	0,5
BL	8	0	8	PG	0,5	3,5
AH	9	3	1	natural	0	2,4
MA	9	7,5	5	natural	1	0
BL	9	13	3	natural	6,5	0
AH	9	0	0	PG	0	4,4
MA	9	1,5	6,75	PG	1,5	0,75
BL	9	10,5	6	PG	0	1,5
AH	10	3	1	natural	0	1,2
MA	10	20	0	natural	0	5,25

BL	10	2	4,5	natural	11,5	0
AH	10	0	0	PG	0	4,6
MA	10	10	5,75	PG	1	2
BL	10	3	5	PG	0,5	0
AH	11	1	0,8	natural	0	0,8
MA	11	23	4,5	natural	16,5	0
BL	11	0	0	natural	7	1,5
BL	11	23,5	2	natural	4,5	1
AH	11	0	0	PG	0	4,6
MA	11	22,5	11,5	PG	0	0,75
BL	11	22,5	7	PG	0	1
BL	11	13	2,5	PG	2,5	2,5
AH	12	5	0,2	natural	0	4,8
MA	12	0	3	natural	16	0
BL	12	2,5	0	natural	0	7,5
AH	12	0	0	PG	0,5	2,4
MA	12	0	1	PG	1,5	7
BL	12	12	0	PG	0	0,5
AH	13	3	3,8	natural	1,5	0
MA	13	0	0,5	natural	1	13,25
BL	13	4	3	natural	1	2,5
AH	13	1	4,2	PG	0	6,2
MA	13	0	0	PG	0	12,5
BL	13	0	0	PG	12	0
AH	14	6,5	3,8	natural	2,5	1,2
MA	14	33	0	natural	0	9,5
BL	14	0	0	natural	15,5	0
AH	14	0	3,2	PG	0	9
MA	14	0	3	PG	1	0,75
BL	14	6,5	9	PG	0	2,5
AH	15	1,5	9	natural	2	0,2
MA	15	0	0,25	natural	10	0
BL	15	13	27	natural	0	0
AH	15	2	0,4	PG	0	10,2
MA	15	9	8,25	PG	14	0
BL	15	0	0	PG	0	8,5
AH	16	1	0	natural	0	3,6
MA	16	7	4	natural	1	0
BL	16	0	0	natural	0	0,5
AH	16	1	0	PG	2	8,2
MA	16	8	8,25	PG	5	0
BL	16	1	0	PG	0,5	5

AH	17	1	0,8	natural	0	3
MA	17	9	0	natural	8,5	0
BL	17	13	0	natural	11,5	0
AH	17	0	0	PG	0	10,6
MA	17	15	4,25	PG	0	4,25
BL	17	0	0	PG	0	8,5
AH	18	2	3,2	natural	1	4
MA	18	3	1,75	natural	2	0,25
BL	18	0	0	natural	1	14
AH	18	3	4,4	PG	0,5	3,8
MA	18	7	0,5	PG	1,5	6
BL	18	0	0	PG	0	13
AH	19	2	4	natural	0,5	0
MA	19	17	2,25	natural	0	1,5
BL	19	6	0	natural	4,5	3,5
AH	19	2	3,6	PG	6	6,8
MA	19	1	0	PG	0	5
BL	19	2	1	PG	0	12,5
AH	20	0	2,6	natural	0	0,2
MA	20	9	0	natural	0,5	5
BL	20	14	0	natural	1	0
AH	20	0	0	PG	0	11,2
MA	20	20	0,5	PG	0	3,75
BL	20	0	0	PG	0	5
AH	21	0	1	natural	8	0
MA	21	1	3	natural	2,5	4,25
BL	21	0	0	natural	3,5	8,5
AH	21	0	0	PG	0	5
MA	21	0	0	PG	0	9,25
BL	21	0	0	PG	0	12
AH	22	6	0,4	natural	0,5	3,4
MA	22	0	0	natural	0	0,25
BL	22	0	0	natural	0	1,5
AH	22	8	1	PG	0	3,8
MA	22	0	0	PG	0	6,75
BL	22	11	0	PG	0	7,5
AH	23	0	0,4	natural	0	1,2
MA	23	11	0	natural	0	0,5
BL	23	18,5	1	natural	0,5	4,5
AH	23	0	0	PG	0	9
MA	23	16	0,5	PG	0	11,75
BL	23	0	0	PG	0	5

<b>MA</b>	24	2,5	13	natural	0,5	0,5
<b>MA</b>	24	6	1	PG	4	1,5

Table 5: Mean and standard deviations of behaviors analyzed in food experiment depending on age class and sex.

<b>Food manipulation</b>				
mean	female adult	8,835		
STD	female adult	4,755		
mean	male adult	10,499		
STD	male adult	3,315		
mean	female juvenile	5,929		
STD	female juvenile	1,374		
mean	male juvenile	9,231		
STD	male juvenile	3,488		
<b>conditions</b>		<b>1p</b>	<b>2p</b>	<b>scramble</b>
mean	female adult	7,313	8,458	11,167
STD	female adult	2,897	6,373	5,821
mean	male adult	10,333	11,000	9,042
STD	male adult	3,719	4,277	3,591
mean	female juvenile	0,857	2,964	15,714
STD	female juvenile	0,841	1,683	3,789
mean	male juvenile	5,933	9,600	15,067
STD	male juvenile	4,709	5,515	5,124
<b>Food monopolization</b>				
<b>conditions</b>		<b>1p</b>	<b>2p</b>	<b>scramble</b>
mean	female adult	10,833	6,917	0,000
STD	female adult	2,537	3,073	0,000
mean	male adult	4,500	3,833	0,000
STD	male adult	1,299	0,862	0,000
<b>Initiated agonistic interactions</b>				
<b>conditions</b>		<b>1p</b>	<b>2p</b>	<b>scramble</b>
mean	female adult	3,000	1,750	1,750
STD	female adult	2,828	2,630	1,500
mean	male adult	11,250	7,750	2,250
STD	male adult	4,349	6,994	1,893
mean	female juvenile	10,857	7,143	1,429
STD	female juvenile	9,788	2,734	1,512
mean	male juvenile	10,400	7,400	2,400
STD	male juvenile	5,225	5,595	2,608

Table 6: Output of Negative Binomial Linear Mixed Models in R.

MODEL	Convergence	AIC	Parameter	Estimate	Std. Error	Z value	P value
EXP.ADULT	0.0000066	1271.5	Period	0.13800	0.26506	0.521	0.603
			ConditionPG	<b>1.13019</b>	<b>0.21764</b>	<b>5.193</b>	<b>2.07e-07 ***</b>
			Day	-0.02251	0.01676	-1.343	0.179
AGO.ADULT	0.0000103	209	Period	-0.78529	0.47258	-1.662	0.0966
			ConditionPG	0.54901	0.55712	0.986	0.3244
			Day	<b>-0.08598</b>	<b>0.04190</b>	<b>-2.052</b>	<b>0.0402 *</b>
AFF.ADULT	0.0000012	1393.5	Period	-0.11938	0.35388	-0.337	0.73585
			ConditionPG	0.11722	0.27034	0.434	0.66458
			Day	0.01119	0.02095	0.534	0.59337
AFF.JUV	0.0000062	1007.3	AFF.ADULT	<b>0.02090</b>	<b>0.01022</b>	<b>2.045</b>	<b>0.0408 *</b>
			AFF.AD.JUV	0.01199	0.01862	0.644	0.5195
			ConditionPG	-0.34408	0.24142	-1.425	0.1541
			Day	<b>-0.08270</b>	<b>0.01783</b>	<b>-4.637</b>	<b>3.53e-06 ***</b>
EXP.JUV	0.0000058	953.4	AFF.ADULT	-0.004415	0.007717	-0.572	0.567268
			AFF.AD.JUV	<b>-0.092528</b>	<b>0.021656</b>	<b>-4.273</b>	<b>1.93e-05 ***</b>
			EXP.ADULT	-0.004313	0.022012	-0.196	0.844651
			EXP.IA.ADULT	0.010705	0.066757	0.160	0.872595
			EXP.IA.AD.JUV	0.114989	0.087333	1.317	0.187948
			Day	<b>0.072711</b>	<b>0.021052</b>	<b>3.454</b>	<b>0.000553 ***</b>
			ConditionPG	0.463033	0.248657	1.862	0.062584

Table 7: Sex differences in food manipulation frequencies according to age groups within the FM experiment.

Variable	Groups	P-value	U
Food manipulation	♂-♀ adults	0,8857	9
	♂-♀ juveniles	0,2677	10

Table 8: Frequency differences in food manipulation, food monopolization, initiated agonistic interactions and caching behavior within FM conditions according to age groups tested with Mann-Whitney U-test.

Variable	Groups	Condition	P - value	U
Food manipulation	♂-♀ adults	1p	0,381	4,5
	♂-♀ adults	2p	0,686	6,0
	♂-♀ adults	scramble	0,562	10,5
	♂-♀ juveniles	1p	0,009 *	1,0
	♂-♀ juveniles	2p	0,030 *	4,0
	♂-♀ juveniles	scramble	1,000	18,0
Food monopolization	♂-♀ adults	1p	0,661	6,0
	♂-♀ adults	2p	0,882	7,0
	♂-♀ adults	Scramble	NA	8,0
Initiated agonistic interactions	♂-♀ adults	1p	0,029 *	16,0
	♂-♀ adults	2p	0,309	12,0
	♂-♀ adults	scramble	0,874	9,0
	♂-♀ juveniles	1p	0,370	23,5
	♂-♀ juveniles	2p	0,806	15,5
	♂-♀ juveniles	scramble	0,367	23,5
Caching behavior	♂-♀ adults	1p	1,000	8,5
	♂-♀ adults	2p	0,882	7,0
	♂-♀ adults	scramble	0,110	2,0
	♂-♀ juveniles	1p	0,036*	30,0
	♂-♀ juveniles	2p	0,507	22,0
	♂-♀ juveniles	scramble	0,682	14,5

Table 9: Frequency differences in food manipulation, food monopolization, initiated agonistic interactions and caching behavior across FM conditions according to age groups tested by Friedman test.

<b>Variable</b>	<b>Conditions</b>	<b>Group</b>	<b>P – value</b>	<b>F</b>	<b>Df</b>
<b>Food manipulation</b>	1p – 2p - scramble	♀ adult	<i>0,539</i>	2,2	3
	1p – 2p - scramble	♂ adult	<i>0,281</i>	3,8	3
	1p – 2p - scramble	♀ juvenile	<i>0,611</i>	4,5	6
	1p – 2p - scramble	♂ juvenile	<i>0,663</i>	2,4	4
<b>Food monopolization</b>	1p – 2p - scramble	♀ adult	<i>0,514</i>	2,3	3
	1p – 2p - scramble	♂ adult	<i>0,148</i>	5,4	3
<b>Initiated agonistic interactions</b>	1p – 2p - scramble	♀ adult	<i>0,217</i>	4,5	3
	1p – 2p - scramble	♂ adult	<i>0,096</i>	6,3	3
	1p – 2p - scramble	♀ juvenile	<i>0,137</i>	9,7	6
	1p – 2p - scramble	♂ juvenile	<i>0,444</i>	3,7	4
<b>Caching behavior</b>	1p – 2p - scramble	♀ adult	<i>0,097</i>	6,3	3
	1p – 2p - scramble	♂ adult	<i>0,332</i>	6,9	6
	1p – 2p - scramble	♀ juvenile	<i>0,332</i>	6,9	6
	1p – 2p - scramble	♂ juvenile	<i>0,611</i>	2,7	4



### 5.3. List of Tables and Figures

Figure 1: The effect of observational approach (natural or playground) on the frequency of adult exploration behavior.....	18
Figure 2: The effect of adult affiliative interactions on affiliative interactions among juveniles, both per individual. Regression line representing the general correlation across all three families (AH, MA, BL). .....	20
Figure 3: The effect of adults' affiliative interactions on affiliative interactions among juveniles (the same as in Figure 4), showing regression lines for each family separately. ....	20
Figure 4: The effect of the average affiliative interactions of adults towards juveniles on the average exploration behavior of juveniles. ....	21
Figure 5: The effect of observation day (representing development of juveniles) on the average affiliative interactions among adults (dark grey diamonds) and among juveniles (bright grey squares). .....	22
Figure 6: The effect of the development of juveniles (represented by the observation day) on the average exploration behavior of juveniles per individual.....	22
Figure 7: Sex and age differences of the food manipulation behavior (means + SD) per individual and session according to the different FM (food monopolization) conditions. ....	23
Figure 8: Sex and condition differences of initiated agonistic interactions of adults (means + SD).....	25
Figure 9: Juveniles caching behavior (as means + SD) in the three different conditions of FM experiment (1p, 2p, scramble).....	26
Picture 1: Playground setup with two vertical and two horizontal tubes and yellow transportable objects.....	13
Picture 2: Sketch of two aviaries showing the position of the cameras, the playground (PG; experiment 1) and the food (experiment 2) that were used in the different approaches.....	14
Table 1: Information about families and juveniles' developmental stages.....	9
Table 2: observation timeline of the different approaches (social, playground (PG) and food monopolization experiment (FM)) in the three periods.....	11
Table 3: Table presenting the daily counts of each family per period and approach of affiliative interactions among adults (AFF.ADULT), exploration behavior of adults (EXP.ADULT) and agonistic interactions among adults (AGO.ADULT).....	42-48
Table 4: Table presenting the daily counts per family and approach of affiliative interactions among adults per individual (AFF.ADIN), affiliative interactions among juveniles per individual (AFF.JUVIN), affiliative interactions of adults towards juveniles per individual (AFF.AD.JUVIN) and the exploration behavior of juveniles per individual (EXP.JUVIN).....	48-52
Table 5: Mean and standard deviations of behaviors analyzed in food experiment depending on age class and sex.....	53
Table 6: Output of Negative Binomial Linear Mixed Models in R.....	54
Table 7: Sex differences in food manipulation frequencies according to age groups within the FM experiment.....	54
Table 8: Frequency differences in food manipulation, food monopolization, initiated agonistic interactions and caching behavior within FM conditions according to age groups tested with Mann-Whitney U-test.....	55
Table 9: Frequency differences in food manipulation, food monopolization, initiated agonistic interactions and caching behavior across FM conditions according to age groups tested by Friedman test.....	56

## 5.4. Corvid Ethogram

### Social observation:

#### Neutral

- **Auto-preening (aup):** to pet/clean oneself for more than 5 seconds
- **Distance:** the number of compartments between two individuals (measured every 30 seconds) → only used in *pre-fledging phase*
- **Nearest neighbour:** the distance (in m) to the next individual (measured at the beginning (00:00min), in the middle (07:30min) and at the end (15:00min) of one observation) → used in *post-fledging phase*
- **Approach (appr):** one animal reduces intentionally distance to another (followed by watch, interaction or retreat)
- **Watch (w):** showing interest(=observing) of another's animal action, subsequently to approach (e.g.: A is manipulating, B is approaching to A to watch A's action)
- **Follow:** an individual is following (and watching) another, subsequently to approach when the approached individual is changing position (e.g.: A approaches to B, B is leaving, A follows B to be able to keep on watching)
- **Manipulation (man):** one individual manipulates an object/the ground
- **Food manipulation (manf):** an individual eats or manipulates food

#### Affiliative

- **Touch (t):** one bird has neutral physical contact with another individual (mostly with beak or wings) for maximum 2 seconds
- **Touch-hold (t-h):** one bird has neutral physical contact with another individual (mostly with beak or wings) for more than 2 seconds, without preening the touched individual
- **Allo-preening (alp):** to pet/clean another individual for more than 5 seconds (usually parallel to contact-sitting)
- **Contact-sitting (cs):** to sit/stand in another individual's range (individuals range determined by being able to reach the other with beak when looking into the other's direction)
- **Feeding (f):** transport food from own beak into other individual's opened beak
- **Unidirectional object transfer (uni-tr):** one individual takes an object from another individual; active giving (uni-tra): owner of the object gives it to another individual; passive (uni-trp): the individual with the object allows it to be taken from another individual
- **Bidirectional object transfer (bi-tr):** two individuals transfer an object between each other
- **Co-manipulation (co-m):** two individuals manipulate one (transportable) object together (e.g. stick, ball)
- **Co-action (co-a):** two individuals manipulate untransportable objects (e.g. underground, big objects, playground) side by side (maximum distance between individuals is about 50cm)

- **Play:** affiliative interaction between at least two individuals that seem to have no sense -> just fun! (e.g. jumping up and down, jumping over the other, flying together up and down)

### Agonistic

- **Approach-retreat (a-r):** to go out of another individual's way if it comes near oneself (without vocalization -> low intensity retreat)
- **Forced-retreat (f-r):** one individual(A) comes near another(B) and makes it to leave current position (B leaves with defensive vocalization -> higher intensity retreat; either with or without physical contact between A and B)
- **Defensive threat:** submissive signals (e.g. fluffing up head feathers, turning beak up/away from the other individual) given by a young raven in response to another individual approaching
- **No retreat (=refused retreat):** one individual refuses to leave its position
- **Threat/peck:** one individual threatens another without the receiver retreating (can be visual: pecking in the direction of another individual, pulling up head feathers, showing typical hosen rock; or with physical contact: pecking another individual, (agonistic) pulling of another individual's feathers)
- **Physical conflict:** aggressive physical contact between at least two individuals (jumping in the air, hitting with feet, beaks, jumping on another individual, pulling on other individual's feathers)
- **Chasing:** an individual pursues another in its flight (e.g. after physical conflict, stealing) -> can also be with food/object
- **Unidirectional transfer try:** one individual tries to steal an object from another, but the manipulating individual does not let the other one take it

### Food Experiment:

#### Neutral

- **Food manipulation (manf):** an individual eats or manipulates food
- **Caching food (cachf):** an individual is hiding food (e.g.: at the ground, in other objects) -> if you are not sure if the individual is really caching the food, call it food manipulation
- **Recovering (rec):** uncovering and manipulating an object/food an individual has hidden before
- 

### Affiliative

- **Approach (appr):** one animal reduces intentionally distance to another (followed by watch, interaction or retreat)
- **Feeding (f):** transport food from own beak into other individual's opened beak
- **Sharing:** an individual in possession of food resource is giving another individual access to the resource -> they both manipulate on the same food piece or on splitted food pieces at the same place
- **Co-manipulation (co-m):** two individuals manipulate one (transportable) object/food piece together (e.g. stick, ball)

- **Co-action (co-a):** two individuals manipulate untransportable objects (e.g. underground, big objects, playground, fixed food piece) side by side (maximum distance between individuals is about 50cm)

#### Agonistic

- **Steal try:** one individual tries to steal food from another, but the manipulating individual does not let the other one take it
- **Stealing (steal):** an individual takes an object (or food) from another individual who is trying to defend it;
- **Monopolizing food:** an individual who is in the possession of a food piece is defending it towards others (the other individual can only try to steal)
- **Monopolizing try:** an individual tries to prevent others from getting access to a resource (food or object) by holding position between the other individual and the resource, flapping the wings, defensive vocalizations, pecking
- **Approach-retreat (a-r):** to go out of another individuals' way if it comes near oneself
- **Forced-retreat (f-r):** one individual(A) comes near another(B) and makes it to leave current position (B leaves with defensive vocalization -> higher intensity retreat; either with or without physical contact between A and B)
- **Defensive threat:** submissive signals (e.g. fluffing up head feathers, turning beak up/away from the other individual) given by a young raven in response to another individual approaching
- **No retreat(=refused retreat):** one individual refuses to leave its position
- **Threat/peck:** one individual threatens another without the receiver retreating (can be visual: pecking in the direction of another individual, pulling up head feathers, showing typical hosen rock; or with physical contact: pecking another individual, (agonistic) pulling of another individuals' feathers)
- **Physical conflict:** aggressive physical contact between at least two individuals (jumping in the air, hitting with feet, beaks, jumping on another individual, pulling on other individuals feathers)
- **Chasing:** an individual pursues another in its flight (e.g. after physical conflict, stealing) -> can also be with food/object

#### Playground Experiment:

##### Neutral

- **Approach (appr):** one animal reduces intentionally distance to another (followed by watch, interaction or retreat)
- **Approach PG:** an individual comes closer to the playground to have a look or to manipulate it (maximum distance to PG about one bird's body length or 0,5m)
- **Manipulation (man):** one individual manipulates an object/the ground
- **Watch (w):** showing interest(=observing) of another's animal action, subsequently to approach (e.g.: A is manipulating, B is approaching to A to watch A's action)
- **Recovering (rec):** uncovering and manipulating an object/food another individual has hidden before

##### Affiliative

- **Bidirectional object transfer (bi-tr):** two (or more) individuals transfer an object between each other

- **Unidirectional object transfer (uni-tr):** one individual takes an object from another individual
- **Co-manipulation (co-m):** two individuals manipulate one (transportable) object together (e.g. stick, ball)
- **Co-action (co-a):** two individuals manipulate untransportable objects (e.g. underground, big objects, playground) side by side (maximum distance between individuals is about 50cm)

#### Agonistic

- **Steal try:** one individual tries to steal an object from another, but the manipulating individual does not let the other one take it
- **Stealing (steal):** an individual takes an object (or food) from another individual who is trying to defend it
- **Approach-retreat (a-r):** to go out of another individual's way if it comes near oneself (without vocalization -> low intensity retreat)
- **Forced-retreat (f-r):** one individual(A) comes near another(B) and makes it to leave current position (B leaves with defensive vocalization -> higher intensity retreat; either with or without physical contact between A and B)
- **Defensive threat:** submissive signals (e.g. fluffing up head feathers, turning beak up/away from the other individual) given by a young raven in response to another individual approaching
- **No retreat(=refused retreat):** one individual refuses to leave its position
- **Threat/peck:** one individual threatens another without the receiver retreating (can be visual: pecking in the direction of another individual, pulling up head feathers, showing typical hosen rock; or with physical contact: pecking another individual, (agonistic) pulling of another individual's feathers)
- **Physical conflict:** aggressive physical contact between at least two individuals (jumping in the air, hitting with feet, beaks, jumping on another individual, pulling on other individual's feathers)
- **Chasing:** an individual pursues another in its flight (e.g. after physical conflict, stealing) -> can also be with food/object